

Ectoparasites and endoparasites of fish form networks with different structures

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(Received 28 November 2014; revised 8 January 2015; accepted 12 January 2015; first published online 16 March 2015)

SUMMARY

Hosts and parasites interact with each other in a variety of ways, and this diversity of interactions is reflected in the networks they form. To test for differences in interaction patterns of ecto- and endoparasites we analysed subnetworks formed by each kind of parasites and their host fish species in fish–parasite networks for 22 localities. We assessed the proportion of parasite species per host species, the relationship between parasite fauna composition and host taxonomy, connectance, nestedness and modularity of each subnetwork ($n = 44$). Furthermore, we evaluated the similarity in host species composition among modules in ecto- and endoparasite subnetworks. We found several differences between subnetworks of fish ecto- and endoparasites. The association with a higher number of host species observed among endoparasites resulted in higher connectance and nestedness, and lower values of modularity in their subnetworks than in those of ectoparasites. Taxonomically related host species tended to share ecto- or endoparasites with the same interaction intensity, but the species composition of hosts tended to differ between modules formed by ecto- and endoparasites. Our results suggest that different evolutionary and ecological processes are responsible for organizing the networks formed by ecto- and endoparasites and fish.

Key words: host–parasite metazoan networks, antagonistic networks, connectance, nestedness, modularity.

INTRODUCTION

Interaction networks are usually characterized by non-random topological patterns and some degree of phylogenetic signal in the interactions (Rezende *et al.* 2007; Bellay *et al.* 2011; Krasnov *et al.* 2012). Different structures have been recorded and the specific configuration of an ecological network depends mainly on the type of interaction (e.g. mutualistic *vs* antagonistic) and the level of intimacy among species (e.g. symbiotic *vs* non-symbiotic interactions) (Guimarães *et al.* 2007; Fontaine *et al.* 2011). Interactions involving parasites and hosts are a classical example of antagonistic network with high intimacy, and they are often characterized by a phylogenetic signal in the interactions (Fontaine

et al. 2011; Krasnov *et al.* 2012; Lima *et al.* 2012). The network approach in studies about host–parasite interactions stand out among the traditional approaches involving only a few species, to contribute to the elucidation of the mechanisms governing these systems (Bellay *et al.* 2013).

The diversity of host–parasite interactions is reflected in the network structure and the similarity between parasite faunas tends to increase with host relatedness (Bellay *et al.* 2011; Krasnov *et al.* 2012; Lima *et al.* 2012). In addition, a convergence of ecological traits among phylogenetically distant host species may also increase the similarity among their parasite faunas (Krasnov *et al.* 2012). Parasite faunas may comprise species with different life strategies, which are grouped mainly as ectoparasites (with direct contact with the external environment) or endoparasites (without direct contact with the external environment) (Bush *et al.* 2001). Studies on the variations in the structure of ecto- and endoparasite interactions with hosts are still scarce.

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Parasite life strategy and host phylogeny seem to affect specialization in host–parasite interactions, which in turn explains why fish–parasite networks are characterized by low levels of connectance and nestedness, and high levels of modularity (Bellay *et al.* 2011, 2013; Krasnov *et al.* 2012; Lima *et al.* 2012; Poulin *et al.* 2013). Connectance is calculated as the proportion of interactions that are actually realised in relation to the total number of interactions that could be realised in the network (Pimm, 1982). Nestedness occurs if the interactions of species with fewer connections in a bipartite network represent a subset of the interactions made by species with more connections (Almeida-Neto and Ulrich, 2011). On the other hand, if there are subgroups of species interacting with each other more than with other species of the same network (modules), the network has a modular structure (Mello *et al.* 2011). Although those archetypical topologies have often been considered in studies on interaction patterns in different mutualistic and antagonistic networks (see Lewinsohn and Prado, 2006), this approach is not commonly applied to studies on host–parasite networks (Poisot *et al.* 2013).

Interactions between hosts and parasites may differ among parasite groups, if their biological traits and infestation processes result in distinct interaction constraints (Poisot *et al.* 2013). Therefore, by looking at similarities and differences in the structure of interactions among ecto- and endoparasites, we can gain some insight on the underlying mechanisms of host–parasite networks. Lima *et al.* (2012) observed that variations in the specificity of interactions may be responsible for differences in the structure of ecto- and endoparasite–fish networks. It is known that a single individual host can harbour both ecto- and endoparasites. Some processes that may lead fish species to share ectoparasites may also lead them to share endoparasites, thereby putting those host species in the same module within a network.

Our goal in the present study was to understand the structure of networks formed by ecto- and endoparasites of fish. To fulfil this goal, we asked the following questions (i) Do fish–ectoparasite and fish–endoparasite subnetworks from the same locality differ in terms of host taxonomy and topology (proportion of parasite species per host species, connectance, nestedness and modularity)? (ii) Do host species that share the same ectoparasites also share the same endoparasites? First, we expected differences in the biology of interactions between fish and their endo- and ectoparasites to result in networks with different structures. Second, the composition of modules in fish–parasite networks was expected to reflect the taxonomic distance between host species, as host niches tend to be phylogenetically conserved (e.g. distribution in the water column, foraging strategy). Furthermore, ecto- and endoparasites infestations are different

phenomena, but they are not independent from each other, because they may occur in the same individual host. Therefore, we expected high similarity in host composition between the modules found in ecto- and endoparasite networks.

MATERIALS AND METHODS

Data

Twenty-two fish–parasite networks were obtained from the literature. The number of host and parasite species in the networks range from 6 to 91 and from 20 to 420, respectively (Table 1). We built the networks as adjacency matrices with host species in the rows, parasite species in the columns and binary values in the cells (presence of absence of interaction between a *i* row and a *j* column). To control for an effect of spatial variations, we analysed pairs of subnetworks formed by either endo- or ectoparasites that belonged to the same complete network from a given locality.

We restricted our analysis to metazoan parasites. The studied ectoparasites belong to the following taxonomic groups: Acari, Branchiura, Copepoda, Hirudinea, Isopoda, Mollusca, Monogenea and Myxosporea. The studied endoparasites were represented by Acanthocephala, Aspidobothrea, Cestoda, Digenea, Nematoda, Pentastomida, and some species of Monogenea and Myxosporea (see Supplementary Material). In the studied networks, the larval and adult stages of a parasite species can have different niches (host species) in the same network. Therefore, different stages were regarded as different ‘functional species’ in the network, as in Vázquez *et al.* (2005) and Bellay *et al.* (2013).

Network characteristics

To test for an influence of host taxonomy on host–parasite interactions, we calculated a correlation between the matrix of taxonomic distances (a proxy for phylogenetic distance; Koehler *et al.* 2012) between fish species and the dissimilarity matrix of parasite fauna composition with a Mantel test, using 1000 randomizations and the Pearson method in the package *vegan* (Oksanen *et al.* 2014) for R 3.1.1 (R Development Core Team, 2014). To build the dissimilarity matrix used in this analysis, we used the Jaccard index available in the function *vegdist* in the package *vegan*. We calculated the matrix of taxonomic distance (MTD) for each network using the following equation:

$$\text{MTD} = Md - (Cw + Ow + Fw + Gw + Sw)$$

where *Md* is the maximum distance found in the fish community (maximum distance = 5, referring to the taxonomic category class) and *Cw*, *Ow*, *Fw*, *Gw* and

Table 1. Fish–parasite networks analysed in the present study. H is the number of host species and P is the number of parasite species of each network

Network ^a	Country	H	P	References
1. Middle Paraná River	Argentina	54	93	Chemes and Takemoto (2011)
2. Floodplain of Upper Paraná River	Brazil	65	311	Takemoto <i>et al.</i> (2009), Lima <i>et al.</i> (2012)
3. Smallwood Reservoir	Canada	6	25	Chinniah and Threlfall (1978)
4. Parsnip River	Canada	17	53	Arai and Mudry (1983)
5. McGregor River	Canada	14	51	Arai and Mudry (1983)
6. Lake of the Woods	Canada	30	144	Dechtiar (1972)
7. Cold Lake	Canada	10	40	Leong and Holmes (1981)
8. Aishihik Lake	Canada	7	29	Arthur <i>et al.</i> (1976)
9. Coastal Waters of Rio de Janeiro	Brazil	59	420	Bellay <i>et al.</i> (2011, 2013)
10. Little Colorado River	USA	11	20	Choudhury <i>et al.</i> (2004)
11. Lake Michigan	Canada–USA	43	117	Muzzall and Whelan (2011)
12. Lake Superior	Canada–USA	36	174	Muzzall and Whelan (2011)
13. Guandu River	Brazil	22	85	de Azevedo <i>et al.</i> (2010)
14. Lake Huron	Canada–USA	79	300	Muzzall and Whelan (2011)
15. Lake Erie	Canada–USA	91	308	Muzzall and Whelan (2011)
16. Lake Ontario	Canada–USA	61	257	Muzzall and Whelan (2011)
17. Gulf of Riga	Latvia	52	94	Kirjušina and Vismanis (2007)
18. Lake Raznas	Latvia	48	80	Kirjušina and Vismanis (2007)
19. Tres Palos Lagoon	Mexico	13	40	Violante-González <i>et al.</i> (2007)
20. Mekong River Delta	Vietnam	52	123	Arthur and Te (2006)
21. Gulf of Tonkin	Vietnam	80	215	Arthur and Te (2006)
22. Coyuca Lagoon	Mexico	10	34	Violante-González and Aguirre-Macedo (2007)

^a See Supplementary Material (online version only).

Sz are matrices for each taxonomic category (class, order, family, genus and species, respectively) generated by the function `weight.taxo` available in package `ape` (Paradis *et al.* 2004) for R. Nomenclature followed the taxonomic descriptions provided by FishBase (Froese and Pauly, 2013). Therefore, species of the same genus exhibit a value of taxonomic distance (*td*) equal to 1, different genera have *td* = 2, different families have *td* = 3, different orders have *td* = 4 and different classes have *td* = 5 (see Rezende *et al.* 2007).

We evaluated three general descriptors of network structure: connectance (C), nestedness (NODF), and modularity (M). To control the intrinsic negative relationship between connectance and species richness (Thébault and Fontaine, 2008), we used the residual connectance instead of absolute connectance values. The residual connectance is calculated by the residuals of the simple linear regression between the \log_{10} -transformed values of observed and possible interactions in each network (e.g. Fonseca and John, 1996). This analysis was carried out in Statistica 7.0 (Statsoft, 2005).

The degree of nestedness was calculated using the NODF index (nestedness metric based on overlap and decreasing fill; Almeida-Neto *et al.* 2008). The significance of the observed NODF-values was estimated with a Monte Carlo procedure (1000 randomizations) based on the row–column probability null model, *Ce*, in the program `Aninhado` (Guimarães and Guimarães, 2006).

To test for a modular structure in the host–parasite networks, we used a simulated annealing algorithm

to calculate the degree of modularity (M) of each network (Guimerà and Amaral, 2005). Values of *M* = 0 indicate the absence of subgroups in the network, whereas values near the maximum (*M* = 1) indicate networks strongly divided into subgroups. Modularity was calculated in the program `NETCARTO` (Guimerà and Amaral, 2005). As `NETCARTO` does not include the *Ce* model for the estimation of significance, we used a function for R (developed by Professor Nadson RS da Silva) to estimate the significance of M. With this function, we generated 1000 randomizations of each network based on the null model *Ce*. For each matrix, M was calculated in `NETCARTO` using a Fortran code (developed by Flávia M. D. Marquitti and first used by Mello *et al.* 2011) to automate the calculation and compilation of M-values. For each network, the significance (P) was obtained from the number of random matrices with M-values equal or higher than the observed M-value, divided by the number of randomized matrices. The R scripts are available from the authors upon request.

Data analysis

Differences in the proportion of parasites per host, host taxonomy (Mantel r coefficient), residual connectance, nestedness and modularity between ecto- and endoparasite networks were tested with a Wilcoxon test for paired samples. We applied a chi-squared test to compare the frequency of significant nested and modular structure between ecto- and endoparasite networks.

If the subnetworks of ecto- and endoparasites from the same locality were significantly modular, we evaluated the similarity in the formation of modules with a Mantel test (with the same procedure mentioned above), considering only the host species that were present in both networks. For this purpose, we identified the host species in each module of the network using the program NETCARTO, and built matrices whose rows and columns corresponded to the host species present in both networks. The value '1' was given to pairs of host species that occurred in the same module, and the value '0' was given to pairs of host species that did not occur in the same module.

RESULTS

The species richness of ecto- and endoparasites varied in subnetworks from 6 to 181 and from 11 to 239, respectively. The values of all network descriptors obtained for each subnetwork are presented in Table 2. The endoparasite subnetworks showed a higher proportion of parasite species per host species (PPH_{ecto} : mean = 1.49; PPH_{endo} : mean = 2.48; Wilcoxon $T = 9$; $Z = 3.81$; $P < 0.001$; Fig. 1a).

Thirty-three (75%) out of 44 subnetworks presented a positive and significant relation of parasite fauna composition with host taxonomy. There were no differences in the Mr -values between ecto- and endoparasite subnetworks (Mr_{ecto} : mean = 0.41; Mr_{endo} : mean = 0.46; Wilcoxon $T = 46$; $Z = 0.40$; $P = 0.683$; Fig. 1b). We found significant differences in connectance, nestedness and modularity between ecto- and endoparasite subnetworks. Residual connectance was higher in endoparasite subnetworks (Cr_{ecto} : mean = 12.53; Cr_{endo} : mean = 14.58; Wilcoxon $T = 0$; $Z = 4.10$; $P < 0.001$; Fig. 1c).

Endoparasite subnetworks were more nested than ectoparasite subnetworks ($NODF_{ecto}$: mean = 16.23; $NODF_{endo}$: mean = 23.11; Wilcoxon $T = 39$; $Z = 2.84$; $P = 0.004$; Fig. 1d). In addition, nestedness was significant in 17 (39%) out of 44 networks, and the number of significantly nested subnetworks was higher among endoparasites ($\chi^2 = 4.69$; $gl = 1$; $P = 0.03$).

The ectoparasite subnetworks were more modular than the endoparasite networks (M_{ecto} : mean = 0.62; M_{endo} : mean = 0.47; Wilcoxon $T = 11$; $Z = 3.74$; $P < 0.001$; Fig. 1E). Twenty-eight (64%) out of 44 networks showed significant modularity, and the frequency of the significantly modular structures did not differ between subnetwork types ($\chi^2 = 0$; $gl = 1$; $P = 1$).

In 12 (55%) of the studied localities, both subnetworks (ecto- and endoparasites) were significantly modular. In eight of the localities with both modular subnetworks (67%) host module composition was correlated between ecto- and endoparasite subnetworks. However, we observed low Mr -values,

which suggests a weak relationship ($r = 0.23 \pm 0.08$) (Table 3).

DISCUSSION

In the present study, we found that ecto- and endoparasite subnetworks from the same local assemblage differed in their topologies, thus implying that differences in the biology of parasitic interactions may lead to different interaction patterns at the community level. Those differences were observed in all topological metrics analysed.

One key point to consider is that the interior of host can offer a higher diversity of sites (organs and tissues) for parasite attachment than the external surface of host. This might explain, for instance, the greater number of endoparasite than ectoparasite species found. Another factor that potentially influenced the richness patterns is the various routes of infection that are available to fish endoparasites (i.e. active penetration through the skin or trophic transmission). Those routes of infection contribute to species diversity, because they increase the probability of host-parasite encounters and may reduce competition among parasite species (Poulin, 1998; Dobson *et al.* 2008; Lima *et al.* 2012).

Host characteristics, such as density, body size, diet and biogeographic distribution, may directly influence parasite diversity (Takemoto *et al.* 2005; Poulin and Leung, 2011; Timi *et al.* 2011). Host species that are phylogenetically close tend to present more similar parasite faunas than unrelated host species (Bellay *et al.* 2011, 2013; Krasnov *et al.* 2012; Lima *et al.* 2012). This tendency would result from parasite species persistence after speciation events of the ancestral host and of the ecological similarity of these hosts (Poulin, 1998), and how we observed, independent of the habitat type used by parasites (ecto- or endoparasites).

The residual connectance values were higher for endoparasite than ectoparasite networks. In networks, connectance provides important information that may allow the understanding of other structural parameters, for example, an increase in connectance can reduce the possibility of nested and modular structures simultaneously in a network (Fortuna *et al.* 2010). Due to the high specificity of host-parasite networks, the connectance values are generally low (Bellay *et al.* 2013). In addition, several studies have shown that the range of host species of the endoparasites of fish may be wider than the range of host species of the ectoparasites (particularly monogeneans; Strona *et al.* 2013). The presence of endoparasites in larval stages, that tend to be more generalist than adults (Bellay *et al.* 2013), also contributed to increase the connectance.

In the present study, the nested structure of some networks was more closely related to the life strategy of endoparasites, which suggests differences in the

Table 2. Parameters calculated for host–parasite networks in 22 localities considering ecto- and endoparasites in separate subnetworks

Subnetwork ^a	S	H	Pa	I	PHP	Mr	<i>P</i>	<i>C</i>	<i>rC</i>	NODF	$p^{(CE)}$	<i>M</i>	$p^{(CE)}$	<i>mo</i>
1	ecto	52	20	32	44	1.60	0.10	6.88	-0.23	4.72	0.980	0.81	0.001	13
	endo	103	42	61	102	1.45	<0.001	3.98	-0.21	5.02	0.690	0.79	<0.001	20
2	ecto	169	40	129	155	3.23	0.04	3.00	-0.21	2.57	1.000	0.84	<0.001	32
	endo	237	55	182	317	3.31	0.18	3.17	-0.07	5.38	0.010	0.68	<0.001	24
3	ecto	13	6	7	11	1.17	0.29	26.19	-0.14	20.83	0.730	0.56	0.076	–
	endo	24	6	18	42	3.00	0.93	38.89	0.19	33.18	0.960	0.29	0.449	–
4	ecto	22	12	10	23	0.83	0.25	19.17	-0.09	24.02	0.480	0.58	0.050	5
	endo	60	17	43	135	2.53	<0.001	18.47	0.22	29.82	0.010	0.42	0.013	5
5	ecto	20	9	11	16	1.22	0.38	16.16	-0.20	13.74	0.740	0.74	0.005	5
	endo	54	14	40	98	2.86	0.49	17.50	0.14	26.96	0.110	0.41	0.327	–
6	ecto	72	30	42	76	1.40	0.23	6.03	-0.16	6.94	0.720	0.73	0.011	13
	endo	132	30	102	308	3.40	0.39	10.07	0.21	17.25	<0.001	0.45	0.004	7
7	ecto	16	8	8	19	1.00	0.94	29.69	-0.01	33.04	0.630	0.37	0.444	–
	endo	42	10	32	72	3.20	0.72	22.50	0.15	26.23	0.660	0.44	0.050	5
8	ecto	17	7	10	16	1.43	0.76	22.86	-0.11	15.91	0.890	0.46	0.356	–
	endo	26	7	19	62	2.71	0.95	46.62	0.31	50.09	0.760	0.22	0.660	–
9	ecto	236	55	181	276	3.29	0.22	2.77	-0.13	2.71	1.000	0.79	<0.001	20
	endo	298	59	239	433	4.05	0.36	3.07	-0.02	3.75	0.930	0.70	<0.001	15
10	ecto	17	8	9	14	1.13	-0.12	19.44	-0.17	15.63	0.810	0.60	0.075	–
	endo	22	11	11	36	1.00	0.17	29.75	0.10	56.82	0.010	0.30	0.783	–
11	ecto	42	20	22	40	1.10	0.07	9.09	-0.17	10.11	0.660	0.69	0.050	9
	endo	138	43	95	197	2.21	0.32	4.82	-0.05	11.32	<0.001	0.63	0.002	16
12	ecto	72	24	48	71	2.00	0.40	6.16	-0.17	6.63	0.770	0.77	0.003	10
	endo	161	35	126	307	3.60	0.39	6.96	0.12	12.91	<0.001	0.54	<0.001	9
13	ecto	60	22	38	59	1.73	0.50	7.06	-0.17	6.46	0.930	0.77	0.002	9
	endo	66	19	47	82	2.47	0.11	9.18	-0.05	11.23	0.650	0.61	0.038	11
14	ecto	164	60	104	208	1.73	0.27	3.33	-0.13	5.44	0.070	0.72	<0.001	18
	endo	269	73	196	765	2.68	0.30	5.35	0.21	14.38	<0.001	0.45	<0.001	6

Table 2. (Cont.)

Subnetwork ^a	S	H	Pa	I	PHP	Mr	<i>P</i>	<i>C</i>	<i>rC</i>	NODF	<i>p</i> ^(CE)	<i>M</i>	<i>p</i> ^(CE)	<i>mo</i>	
15	ecto	154	57	97	207	1.70	0.18	<0.001	3.74	-0.10	8.67	<0.001	0.67	0.002	17
	endo	300	89	211	910	2.37	0.39	<0.001	4.85	0.23	15.83	<0.001	0.43	<0.001	10
16	ecto	159	51	108	188	2.12	0.52	<0.001	3.41	-0.15	6.09	0.020	0.73	<0.001	18
	endo	207	58	149	404	2.57	0.23	<0.001	4.67	0.07	12.32	<0.001	0.53	0.001	10
17	ecto	57	31	26	82	0.84	0.23	0.022	10.17	-0.02	34.23	<0.001	0.46	0.770	-
	endo	120	52	68	371	1.31	0.39	<0.001	10.49	0.25	29.67	<0.001	0.41	<0.001	4
18	ecto	66	31	35	125	1.13	<-0.01	0.472	11.52	0.08	41.78	<0.001	0.41	0.735	-
	endo	93	48	45	311	0.94	0.30	<0.001	14.40	0.30	48.76	<0.001	0.33	0.208	-
19	ecto	24	13	11	34	0.85	0.06	0.394	23.78	0.03	51.56	0.010	0.30	0.957	-
	endo	42	13	29	98	2.23	0.63	<0.001	25.99	0.24	36.39	0.170	0.30	0.767	-
20	ecto	112	48	64	125	1.33	0.45	<0.001	4.07	-0.17	6.5	0.170	0.77	<0.001	14
	endo	91	32	59	137	1.84	0.31	<0.001	7.26	-0.01	12.09	0.060	0.61	0.764	-
21	ecto	95	38	57	98	1.50	0.43	<0.001	4.52	-0.19	4.6	0.900	0.81	<0.001	20
	endo	234	76	158	425	2.08	0.40	<0.001	3.54	0.01	11.33	<0.001	0.56	0.001	15
22	ecto	16	10	6	22	0.60	0.36	0.146	36.67	0.06	35	0.870	0.24	0.911	-
	endo	38	10	28	82	2.80	0.52	0.035	29.29	0.24	37.85	0.370	0.30	0.672	-

Abbreviations: S, species richness; H, host species; Pa, parasite species; I, host–parasite interactions; PHP, proportion of parasite species per host species; Mr, Mantel r statistic obtained between the host taxonomic distance matrix and the host–parasite dissimilarity matrix; *C*, connectance; *rC*, residual connectance; NODF, nestedness; *M*, modularity; *mo*, module number; ecto, ectoparasite–host network; endo, endoparasite–host network.

^a The identity of networks by numbers corresponds to that in Table 1.

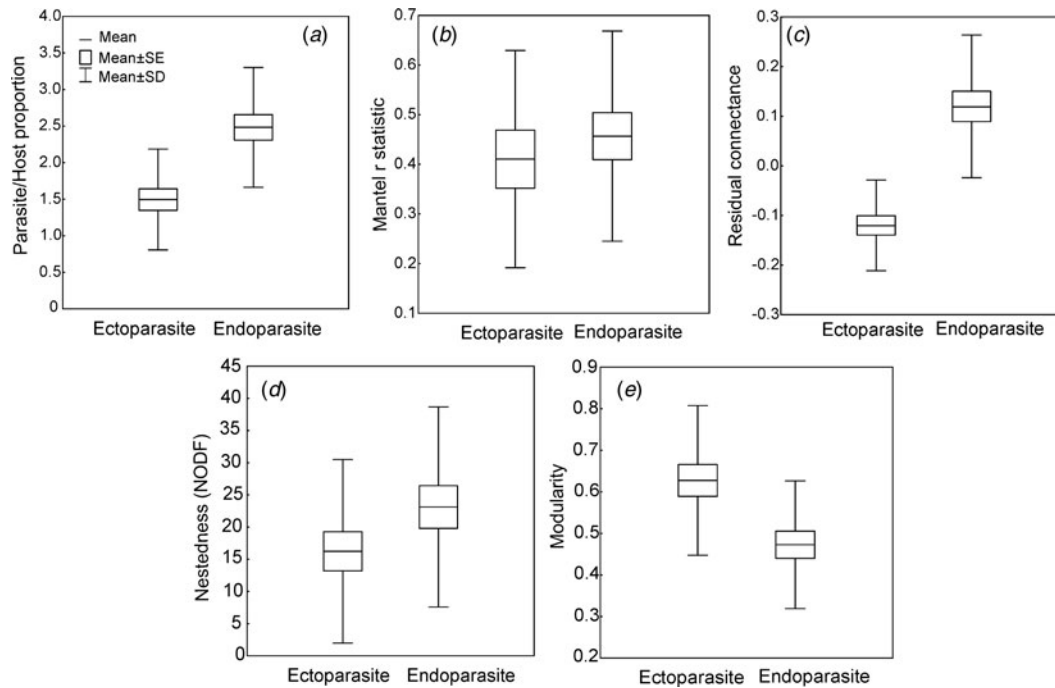


Fig. 1. Parameters calculated for host–parasite networks in 22 localities considering ecto- and endoparasites in separate subnetworks. (a) Proportion of parasite species per host species; (b) Mantel r statistic (the influence of host taxonomy on host–parasite interactions); (c) residual connectance; (d) nestedness and (e) modularity.

Table 3. Mantel r statistic (M_r) calculated for the correlation between the dissimilarity in host species composition of the modules found in ecto- and endoparasites networks

Network ^a	M_r	P
1. Middle Paraná River	−0.04	1.000
2. Floodplain of Upper Paraná River	0.02	0.518
4. Parsnip River	0.35	0.017
6. Lake of the Woods	0.08	0.108
9. Coastal Waters of Rio de Janeiro	0.25	<0.001
11. Lake Michigan	0.24	0.005
12. Lake Superior	0.21	0.007
13. Guandu River	0.14	0.087
14. Lake Huron	0.16	<0.001
15. Lake Erie	0.09	0.006
16. Lake Ontario	0.25	<0.001
21. Gulf of Tonkin	0.31	<0.001

^a See Supplementary Material (online version only)

organization of host–parasite networks as a function of host type (e.g. taxonomic group; aquatic or terrestrial). Studies on terrestrial hosts showed that the endoparasites have a greater degree of host specificity than the ectoparasites in the networks (see Brito *et al.* 2014). A high degree of specificity in the use of host species may result in relatively low levels of nestedness. This has been used as a basis to infer that mutualistic and antagonistic networks have similar organizations, particularly for a model system in which ectoparasites use terrestrial hosts (Graham *et al.* 2009). Several hypotheses have been presented in previous studies to explain the nestedness structure in networks (see Suweis *et al.*

2013). For example, the ecology and factors related to the parasite life cycle may contribute to the nestedness pattern, particularly among endoparasites (Lima *et al.* 2012). The reason for this effect is that the larval stages of these parasites tend to be more generalist than the adult parasites (Bellay *et al.* 2013), as mentioned above. Furthermore, the adult stages may have been obtained by trophic transmission, and the host species may have nested diets, thus allowing the formation of nested parasitic fauna.

We observed no differences between subnetworks in the frequency of a significantly modular structure, but they differed from one another in their degree of

modularity. The presence of specialized interactions is an important factor when interpreting the modular structure of ecological networks (Mello *et al.* 2011). Parasitism in general is expected to be highly specialized (Thompson, 1994), which may explain the lack of difference in the frequency of modular structures. But variations in specificity made endoparasite subnetworks be more nested than modular, while the opposite was observed for ectoparasites. The studied ectoparasite subnetworks presented an average high modularity values, probably because ectoparasites, particularly monogeneans, are more specialized than endoparasites (Strona *et al.* 2013).

Although the co-occurrence of ecto- and endoparasites in the parasitic fauna of hosts is common, we observed a weak relationship (reflected in low M_r coefficients) between the host species composition of modules found in ecto- and endoparasite subnetworks. Thus, for example, hosts that shared the same module, when only ectoparasites were evaluated, normally tended to occur in distinct modules when we evaluated only endoparasites. Consequently, we may infer that different factors influence module organization in ecto- and endoparasite networks. However, the high specificity presented by the ectoparasites suggests that host phylogeny is a key factor in module organization (see Krasnov *et al.* 2012), whereas host diet could have a stronger influence for endoparasites than phylogeny, due to the trophic transmission of endoparasites (see Garrido-Olvera *et al.* 2012). Future studies that include information of the phylogenetic, biological and ecological characteristics of host species may clarify which factors are most important to build up the modular structure of host–parasite networks.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0031182015000128>

ACKNOWLEDGEMENTS

The authors thank Nadson R. S. da Silva for the elaboration of the function that allowed us to run the null model C_e in R, Flávia M. D. Marquitti for kindly providing us with the Fortran code for the automation of the modularity analysis, and Vanessa M. Algarte for her suggestions to an early version of the manuscript.

FINANCIAL SUPPORT

Manuscript funded by PEA/CAPES/PROEX, DIRPPG/UTFPR – Campus Londrina and the Brazilian Research Council (CNPq). MAR Mello was sponsored by Ulm University, Humboldt Foundation (AvH, 1134644), São Paulo Research Foundation (FAPESP, 06/00265-0, 05/00587-5; 07/50633-9), Federal University of Minas Gerais (UFMG, PRPq 01/2013, 14/2013, 02/2014), Minas

Gerai Research Foundation (FAPEMIG, APQ-01043-13), CNPq (472372/2013-0), Research Program on Atlantic Forest Biodiversity (PPBio-MA/CNPq) and Ecotone Inc. ('Do Science and Get Support Program'). MAN received research fellowships (306843/2012-9 and 306870/2012-6, respectively) from CNPq. The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

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