Influence of the ecological opportunity of interaction on the structure of host-parasite networks

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Abstract

31 Despite the great interest to quantify the structure of ecological networks, the influence of morphological,

32 ecological and evolutionary characteristics of the species still remains poorly understood. One of the

33 challenging issues in ecology is how the interaction opportunity influences and provides changes to the

34 associations between species, and which effects these changes have on ecological systems. To explore

35 topological patterns in host-parasite networks, we sampled endoparasites-anurans interactions in South

36 America in order to determine whether the effect of the ecological opportunity affects our understanding

37 of the topological structure of the interaction networks. To identify the effect of the ecological opportunity

38 for interaction, we investigated interactions in environments with and without flood pulse, where

39 presence would promote higher ecological opportunity of interaction. Moreover, we created three

40 theoretical models with filters to test the influence of the ecological opportunity for interaction: random,

41 phylogeny and host body size. We then calculated commonly used binary network metrics (connectance,

42 nestedness and modularity) for the networks generated by the theoretical models. We demonstrated that

43 the interaction ecological opportunity changes the structure of host-parasite networks, and was

44 influenced mainly by phylogeny and body size of the host. Our results indicate that environments that

45 offer greater opportunities for interaction between species present networks with the most

46 connectance/nestedness and less modularity. Networks in environments that do not have such

47 opportunities for interaction depict the opposite pattern. Our results indicate that the ecological

48 opportunity of interaction is reflected in an increase in interaction associations between species and

49 affect/change the organization of these interactive assemblages. From an epidemiological point of view,

50 changes in the composition of parasitic species are associated with risks of invasions and emerging

51 diseases. In part, emerging diseases are the result of processes such as those occurring during the flood

52 pulse, in which climate change, travel, and global trade create opportunities for new species

53 associations. Our results provide insight into the dynamics of incorporating a new resource, considering

54 an evolutionary factor responsible for these changes in species composition.

55 **Keywords**: Body size · Community assembly · Dispersal limitation · Endoparasite-anuran · Phylogeny

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Introduction

59

60 Understanding factors that determine the establishment and persistence of interactions

61 between species is fundamental to comprehend the factors that structure ecological

62 communities [40]. Host-parasite interactions are influenced by characteristics of the

63 hosts and associated parasites. For hosts, characteristics such as body size and

64 structure, diet, age, and immune system are considered significant [43,48,23], but these

65 and others are the resources that dictate the feasibility of the association with specific

66 parasite species [7, 15]. Important characteristics on the parasite species include life

67 cycle complexity [23], virulence, transmissibility, strategies to evade immune responses

68 [65], host species recognition, and trophic requirements [45], among others. Therefore,

69 the effects of these features directly influence the structure of interaction networks.

70 Hence, intrinsic factors/characteristics of each association determine the potential

71 for an interaction to occur, and compose what Combes [21], Araujo et al. [7], and [15]

72 designate as compatibility. However, the effective establishment of a compatible

73 interaction depends on the encounter opportunity [7,15,73]. This effectiveness is often

74 the result of ecological adaptation [38], which postulates that key characteristics shared

75 with previous host species are necessary for a successful infection [33,12,74]. The

76 ecological adaptation is the process that allows the parasite organism to successfully

77 colonize a new host without the need of evolutionary novelties [3,50].

78 The support to this new vision of parasitism lies in the fact that the

79 macroevolutionary process, commonly named host-switching, has proven to be much

80 more common in nature than previously thought [74,15]. Many human pathogens

81 originate through host-switching, including HIV and malaria [76], and host-shifts are also

82 the predominant cause of new host-parasite associations for rabies viruses in bats [70],

83 malaria in birds [28], and among other associated diseases [14, 50, 55,59].

84   The ecological opportunity for interaction is significantly influenced by the

85   environment [15]. Cyclical changes in expansion and isolation, for instance, generate

86   Taxon Pulse processes [27, see also 34].   Taking this into account, Taxon Pulse

87   processes can lead to increase or limitation of opportunities for interaction between

88   hosts and parasites and, consequently, alter the structure of the community. The flood

89   pulse, for example, is considered a key factor in the ecological functioning and the

90   patterns of lowland communities [63,71]. These flood pulses [41] tend to reduce spatial

91   variability and biological as well as environmental factors [9,71]. According to this

92   hypothesis, during low water periods, floodplains are more isolated from each other and

93   disconnected from the main channel of the river, creating isolated habitats, often with

94   distinct environmental characteristics. On the other hand, subsequent increases in water

95   levels represent an expansion event for aquatic and semiaquatic organisms. We

96   postulate that this pattern of isolation/expansion between neighboring aquatic habitats

97   (flood plain/flood pulse system) provides the ecological opportunity for encounter

98   between endoparasites and anurans species, which may result in new interactions

99   through ecological adjustment. By contrast, continuously isolated habitats provide more

100 limited opportunities for encounter between hosts and parasitic species. In fact, some

101 studies have reported greater similarity between species in the composition of different

102 aquatic habitats during floods than during non-flood periods [5,9,63,72]. We also expect

103 that the structure of communities subjected to cycles/pulses of isolation and expansion

104 will present greater sharing and connectivity of endoparasites between hosts. Limited

105 ecological opportunity in continuously isolated habitats should exhibit less parasite

106 sharing and lower endoparasites connectivity among the anuran hosts, changing the

107 structure of the network.

108   In this study, we tested whether this structure is influenced by phylogeny and body

109   size hosts and whether the periodic ecological opportunity of encounters influences the

110   structure of an anuran-endoparasite (endoparasite-anuran) interaction network in

111   environments with and without annual flood pulses. We used a database of anuran-

112   endoparasite interactions to infer how the network structure of each environment can be

113   explained by randomly sampled networks obtained under different theoretical models

114   with filters: neutral, host phylogeny, and host body size. If phylogeny or body size

115   imposes restrictions on species interactions, we expect to find compartments in the

116   random networks. On the other hand, if there are no restrictions, networks would show

117   nested patterns with interaction indirectly reflecting the abundance of species. We

118   conclude that, among the filters analyzed, host body size and phylogeny greatly explain

119   the observed host-endoparasite networks. However, similar networks of environments

120   with cyclic flood pulse were not well explained by these filters, strongly suggesting that

121   the increased opportunities provided by the environment can intensify encounters and

122   promote and increase connectivity in the host-parasite local network.

123

Materials and Methods

125   To test for differences in ecological opportunity, we selected four parasite-host

126   interaction networks compiled from literature data and described them using network

127   metrics (nestedness, connectance, and modularity). Next, we sought to know if it was

128   possible to explain their structure based on the phylogenetic characteristics and body

129   size of the hosts analyzed. For this, we created theoretical models with filters (see

130   below) and then compared the structure of the four networks analyzed with the networks

131   generated by theoretical models to test the effect of the process of interaction of

132   opportunity in different environments. See the methods for details.

133

Host-parasite database

135 We created a database with reports on the association of interactions between anurans

136 and helminth parasites (endoparasite) from South America. All possible combinations

137 (e.g. amphibians, endoparasites, helminth, anura) were used to search for anuran-

138 endoparasite (endoparasites belonging to the phylum Acanthocephala, Nematoda, and

139 Platyhelminthes, associated with amphibians of the order Anura) empirical studies

140 conducted in South America from 01-Jan-1925 to 20-Dez-2017. These data were

141 collected using online database platforms such as BioOne, Isi JSTOR, PubMed,

142 SciELO, Scopus, and Web of Science. We have updated the amphibian's nomenclature

143 according to the American Museum of Natural History [29]. *Leptodactylus latrans*

144 interaction reports were not included in the analyses due to many changes in

145 nomenclature. From here on we will call "host" for anuran and "parasite" for helminth

146 parasites. We then generated a binary matrix with these real interactions in which the

147 rows represented host species and the columns represented parasite species. This

148 matrix was used as an interaction database to generate random networks through the

149 theoretical models (filters). We collected 157 peer-reviewed articles and recorded 686

150 real interactions between 215 species of parasites and 170 species of hosts (Appendix

151 S1).

152

Selection of analyzed environments

154 During the bibliographical review, four (4) community studies of host-parasite

155 interactions (observed networks) were selected: (i) two studies of flood pulse

156 environments (with annual cycles of water expansion and retraction), which could

157 promote environmental homogenization and higher ecological opportunity for host-

158 switching: Pantanal - Campião et al. [18], and Chaco - González and Inés [30] flood

159 pulse. The Pantanal network was composed by 11 hosts and 16 parasites (Appendix

160 S2) while the Chaco, by 35 and 46, respectively (Appendix S2) [18,30]. (ii) Two studies

161 from environments without flood pulse, which potentially promote less ecological

162 opportunity for host-switching: Atlantic Rainforest Graça et. [31], and Amazonian forest

163 Bursey et al. [16]. The Atlantic Rainforest network was composed by 11 host and 15

164 parasites (Appendix S2), while the Amazonian forest by 43 and 16 respectively

165 (Appendix S2) [31,16].

166

167 **Theoretical models**

168 To answer our questions, we chose to test the effect of random, phylogeny, and host

169 body size to see the changing structure (ecological opportunity) of host-parasite

170 networks in different environments. We chose phylogeny because it was revealed as a

171 potential driver of parasitic diversity. Host species vary in their evolutionary time of

172 exposure for parasites acquisition and sharing, therefore, suffering variable co-

173 evolutionary constraints [32] which would influence the interactions and the structure of

174 their networks' interaction. We also chose the host body size as it was a good predictor

175 of the diversity of parasite species [17,42,53]. Large hosts can provide more space and

176 resources, and possibly a greater breadth of niches for parasites. Moreover, larger hosts

177 live longer and represent fewer ephemeral habitats than small species and are therefore

178 also more exposed to parasites [61].

179   Three theoretical models with filters were created (random, phylogeny and body

180 size of hosts models - Appendix S3), to test the influence of the ecological opportunity

181 on the structure of host-parasite networks. Each model is characterized as a specific

182 filter that randomly selects hosts and their parasites from the interaction database that

183   resulted in random networks. Unlike what is commonly used to analyze the structure of

184   networks, our random networks considered only real interactions extracted from the

185   interaction database (collected from the literature). Our models have generated random

186   networks using real interactions and may give a more accurate answer about the

187   topology of the interaction network than other simpler null models commonly used that

188   consider only random interaction simulations, or that weigh only by the interaction ratio

189   of the species network for example. Given this approach the following theoretical models

190   were proposed: i. Neutral Model: No other filter besides the number of host species,

191   being the same number in each observed network (11 hosts for Pantanal, 35 for Chaco,

192   11 for Atlantic Rainforest and 43 for Amazonian forest respectively - Appendix S3 - Filter

193   i); ii. Phylogeny Model: This model randomly samples from the database the same

194   number of host species belonging to the same families in the same proportion of the

195   original network, as reported in each observed network (Appendix S3 - Filter ii; Appendix

196   S4 - families of the species by observed network); iii. Body Size Model: This model

197   randomly samples from the database the same number of hosts species with the same

198   body size distribution (considering a standard error of ±5%) as reported for hosts species

199   in each observed network (Appendix S3 - Filter iii; Appendix S4 - body size of the

200   species by observed network).

201   For each one of the four environments analyzed, the random networks maintained

202   the number of host species of each observed network (Pantanal, Chaco, Atlantic

203   Rainforest and Amazonian forest). In this way, the number of hosts remained constant

204   (according to each environment), while the number of parasites varied between the

205   random networks, according to the association in the database of recorded interaction.

206   We sampled 1.000 random networks for each model in each environment (random

207   networks per model in Appendix S5). Each random sample was always included in the

208 interactions database after each randomization, so that a species could be included in

209 more than one random network. We then compared how well the filters explain the

210 observed network (the comparison methods are detailed below). Unfortunately, it was

211 not possible to impose on a similar real filter the ecological opportunity to evaluate the

212 effect of interaction opportunity because we have no observation that refers to such a

213 factor. Aquatic and terrestrial systems have different physical and chemical conditions,

214 which seem to influence the biology and diversity of the organisms living in each of these

215 habitats [75], that is why we assumed phylogenetic conservatism of the organisms living

216 in each of these analyzed habitats. Given their aspects, we hypothesized that flood

217 pulse environments are not as well explained by the filters (neutral, phylogeny, and host

218 body size) as the other environments. We postulate that in environments without flood

219 pulse the phylogenetic conservatism could be higher, that is, as it is an environment with

220 few opportunities the species maintain their interactions over evolutionary time. If this is

221 true, we expect that the networks will be better described by the phylogeny and body

222 size models that are supposed to have their most preserved interactions. This is

223 something we would not observe in the cyclic flood pulse because there is a constant

224 change that interferes with this conservatism.

225

226 **Data analysis**

227 **Network Metrics**

228 We used the metrics nestedness, connectance, and modularity to characterize the

229 structure of all networks. The nestedness was calculated using the metric proposed by

230 Almeida-Neto et al. [6], to evaluate the presence of interactions that belong to subsets of

231 other interactions. Therefore, a high nestedness value indicates a hierarchy of

232 interactions, in which species that interact with fewer partners (have a lower degree)

233 interact with a subset of partners from species that have more partners (a higher degree)

234 [8]. Connectance is the proportion of interactions performed for all possible interactions

235 between species in a community [52]. Modularity was calculated using the method

236 proposed by Dormann and Strauβ [24], to describe the presence of network groupings,

237 where species interact more with species within their group than with species belonging

238 to other groups [58]. These groups are commonly called network modules, and to

239 calculate these network metrics, we used the commands implemented in the "bipartite"

240 package [25] in R [22].

241

242 **Standardization for network metrics**

243 To allow comparison between networks of different sizes, we standardized the network

244 metrics using a simple linear regression between metrics and number of parasites. This

245 standardization is necessary because although the host species richness was constant

246 in the different samples, the size of the whole network differed in each sample due to

247 variation in parasite richness. See below:

248 $$\bar{Y} = Y - \alpha * par + \beta,$$

249   where $\bar{Y}$ is the value of the standardized metric (equivalent to the regression

250 residue), Y is the value of the non-standardized metric, par is the number of parasites,

251 and α and β are the slope and the linear coefficient of the regression, respectively.

252

253 **Comparison of the network structure**

254 From here onwards we call "observed network" any of the four observed networks for

255 tested environments, and "random network" any network generated by filters. We

256 identify which model best explains each observed network as well as which network is

257 best described by the models. To compare networks, we first calculated the distance (D)

258   for each metric, from each random network of each theoretical model to the observed

259   network in units of standard deviation:

260                            $D = (\bar{Y}_{obs} - \bar{Y}_{rand})/\sigma_{rand}$

261   where $\bar{Y}_{obs}$ is the standardized value of the observed network, $\bar{Y}_{rand}$ is the

262   normalized value of the random network metric, and σ_{rand} the standard deviation of 1.000

263   values of $\bar{Y}_{rand}$. Subsequently, for a given metric and observed network, a unidirectional

264   analysis of variance (ANOVA) was applied to evaluate whether there was a difference

265   between these groups. Tukey's test [79] was used to determine the occurrence of

266   differences between treatments. After measuring the difference, the distance averages

267   between the real networks and each random network of each model was compared to

268   verify which theoretical model best described the observed networks. When the metric

269   and the observed network were fixed, we compared which model best explained the

270   observed network. When the metrics and model were fixed, we compared which

271   observed network was best explained by the models. All statistical analyses were

272   performed using the "stats" package in the R software [22]. For all tests, we assumed

273   the significance of $p < 0.05$.

274

Results

Structure of host-parasite interaction networks

277   Some of the random networks presented a range from smaller to greater number of

278   parasite species than the observed networks (Fig. 1, 2, 3 - black bars, upper x axis -

279   frequency of the number of parasites), except for the Amazon, whose smallest random

280   network had at least twice more parasites than the observed network. Thus, by

281   correcting the effect of network size, the theoretical models could not reach a network as

282   small as that analyzed in the Amazon due to low parasitic richness analyzed in this

283   environment (Fig. 1, Fig. 2 and Fig. 3 - j to l). Despite our attempt to control the effect of

284   network size by a standardization method, we were unable to ensure that the ratio of the

285   metric and the number of parasites maintained the same linear tendency for such low

286   numbers of parasites for Amazon. Therefore, the Amazonian simulations were removed

287   from subsequent analysis.

288   The nestedness increases with the number of parasites in the network for the

289   remaining three environments (Fig. 1, Appendix S6). Connectance and modularity were

290   negatively correlated with the number of parasites in most simulated models (Fig. 2 and

291   3, Appendix S6), except for the connectance in simulated neutral models for the

292   Pantanal (R^2 = 0.01, p = 0.98) and Atlantic Rainforest, which were not correlated (R^2 =

293   0.002, p = 0.15).

294

295   **Fig. 1** Nestedness values according to the number of parasite species before standardization. The black

296   dots indicate the nestedness value of random networks for three theoretical models. Grey dot - Pantanal

297   (a, b, c), green dot - Chaco (d, e, f), orange dot - Atlantic Forests (g, h, i) and violet dot - Amazonian forest

298   (j, k, l). The blue lines represent linear regression and the gray shadow represents standard deviation in

299   random networks. The black bars indicate the frequency distribution of the random networks: right y axis -

300   nestedness frequency, upper x axis - frequency of the number of parasites (details: Appendix S10 in

301   Supporting Information).

302

303   **Fig. 2** Connectance values according to the number of parasite species before standardization. The black

304   dots indicate the connectance value of random networks for three theoretical models. Grey dot - Pantanal

305   (a, b, c), green dot - Chaco (d, e, f), orange dot - Atlantic Forests (g, h, i) and violet dot - Amazonian forest

306   (j, k, l). The blue lines represent linear regression and the gray shadow represents standard deviation over

307   the random networks. The black bars indicate the frequency distribution of the random networks: right y

308   axis - connectance frequency, upper x axis - frequency of the number of parasites (details: Appendix S10

309   in Supporting Information).

310

311 **Fig. 3** Modularity values according to the number of parasite species before standardization. The black

312 dots indicate the modularity value of random networks for three theoretical models. Grey dot - Pantanal (a,

313 b, c), green dot - Chaco (d, e, f), orange dot - Atlantic Forests (g, h, i) and violet dot - Amazonian forest (j,

314 k, l). The blue lines represent linear regression and the gray shadow represents standard deviation over

315 the random networks. The black bars indicate the frequency distribution of the random networks: right y

316 axis - modularity frequency, upper x axis - frequency of the number of parasites (details: Appendix S10 in

317 Supporting Information).

318

319 **Host body size and phylogeny models usually better describe the observed**

320 **network than neutral models**

321 The distance (D) between random networks and their respective observed network were

322 significantly different among the models (Table 1). The body size model that better

323 resembled the nestedness pattern was observed in the Pantanal and Chaco, while in the

324 Atlantic Rainforest, it was the phylogeny model. The connectance values in the Atlantic

325 Rainforest were better resembled by the neutral model, while in the Pantanal and Chaco

326 were better resembled by the body size and phylogeny models, respectively. The

327 modularity was better resembled by the phylogeny model in the Pantanal and Chaco

328 networks, while modularity in the Atlantic Rainforest was best explained by the body size

329 model (Table 1). Such results, with the exception for connectance in the Atlantic

330 Rainforest, show that the body size and phylogeny of the hosts resemble better the

331 network structure than neutral model.

332

333 **Table 1**. Analysis of variance (statistical significance test F_{2-2997}), Tukey Test between neutral models (N),

334 phylogeny (P) and body size (BS) for each metric and environment (observed network).

Metric	Environment	ANOVA	Tukey HSD		<D>
		F_{2-2997}	Theoretical Model		
Nestedness	Pantanal	9.10*	P - N	BS	5.85
			BS - N*	P	5.94
			BS - P	N	6.04

	Chaco	396.70*	P - N*	BS	3.21
			BS - N*	N	4.07
			BS - P*	P	4.43
	Atlantic Rainforest	31.34*	P - N*	P	1.27
			BS - N*	BS	1.49
			BS - P *	N	1.62
Connectance	Pantanal	2166.00*	P - N*	BS	12.56
			BS - N*	P	13.58
			BS - P *	N	15.46
	Chaco	251.70*	P - N*	P	4.86
			BS – N	BS	5.68
			BS - P *	N	5.77
	Atlantic Rainforest	220.60*	P - N*	N	3.68
			BS - N*	P	4.17
			BS - P *	BS	4.62
Modularity	Pantanal	166.50*	P - N*	P	- 5.15
			BS - N*	BS	- 5.33
			BS - P *	N	- 5.93
	Chaco	140.50*	P - N*	P	- 3.70
			BS - N*	S	- 4.21
			BS - P *	N	- 4.43
	Atlantic Rainforest	59.74*	P - N*	BS	- 1.34
			BS - N*	P	- 1.68
			BS - P *	N	- 1.81

The right column of "Theoretical Model" is ordered according to the model that better describes the observed network for a given metric, followed by the average distance ($<D>$) between the observed network and the random networks. * = significant difference <0.01.

335

336

The theoretical models describe environments without flood pulse better than the flood pulse environments

The resemblance of the network metrics from randomly sampled networks to observed networks environments with and without flooding for each metric presented different distances (Table 2). All metrics pointed network structure of the Pantanal as the furthest from the network structure of the theoretical models (statistics for support Table 2), followed by the Chaco and the Atlantic Rainforest. This shows that the environment without flood pulse is better described by the proposed models than the flood pulse environments. All theoretical models pointed that Pantanal network is the most nested,

346 connected and less modular one followed by Chaco and Atlantic Rainforest (see the

347 statistics for support test for each metric between random networks of the models and

348 observed network - average distance value, <D>, in Table 2).

349

350 **Table 2**. Analysis of variance (statistical significance test F_{2-2997}), Tukey Test between neutral (N),

351 phylogeny (P) and body size (BS) theoretical models, for each metric and environment.

Metric	Model	ANOVA F_{2-2997}	Tukey HSD Environment	Environment	<D>
Nestedness	N	4923*	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	6.04 4.07
			Pantanal - Atlantic Rainforest *	Atlantic Rainforest	1.61
	P	5704*	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	5.94 4.43
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	1.26
	BS	4840*	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	5.85 3.21
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	1.48
Connectedness	N	39508*	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	15.46 5.77
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	3.68
	P	27554**	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	13.58 4.86
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	4.17
	BS	18577*	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	12.56 5.68
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	4.62
Modularity	N	39508*	Atlantic Rainforest- Chaco* Pantanal - Chaco*	Pantanal Chaco	-5.93 -4.53
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	-1.81
	P	27554*	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	-5.15 -3.79
			Pantanal - Atlantic Rainforest *	Atlantic Rainforest	-1.68
	BS	18577*	Atlantic Rainforest - Chaco* Pantanal - Chaco*	Pantanal Chaco	-5.33 -4.30
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	-1.34

The fourth column is ordered according to the environment with the most distance between the observed network and random networks, followed by the average distance (<D>) between the observed network and the random networks. *=significant difference <0.01.

352

353 **Discussion**

354 The method we developed to infer how the structure of anuran-endoparasite interaction

355 networks under different conditions of encounter opportunities could be described by

356 theoretical models based on neutral, host phylogeny and host body filters. We found that

357 the theoretical models described the network without flood pulse - i.e low ecological

358 opportunity for interaction (Atlantic Rainforest) – better than the networks with cyclic

359 flood pulse (Pantanal and Chaco). In addition, the networks of the three environments

360 were best described by the theoretical models with phylogeny or host body size filters

361 rather than the neutral filter. This result suggests that, in fact, the increased ecological

362 opportunity for encounters provided by the environment increases connectivity through

363 the incorporation of new host species in the repertoire of the parasites.

364 The topology patterns observed in the communities reflect the mechanisms that

365 structure their respective networks. Some studies suggest randomness as an underlying

366 mechanism for explaining the structure of parasitic communities [44,62]. However, the

367 metrics we tested in our study did not indicate the neutral model as the main structuring

368 mechanism for network topology, except for the connectance of the network in the

369 Atlantic Rainforest. The interactions of the Atlantic Rainforest can be the result of

370 random neutral encounters between individuals, whose probability is mediated by the

371 relative abundances of the populations involved and by compatibility in the case of

372 parasites.

373 In parasitic communities, the evolutionary history of the host acts as one of the

374 determinants of the community structure [19,67]. Phylogenetic relationships function as

375 a good proxy for describing ecological differences between hosts and host groups. This

376 may indicate that these attributes are phylogenetically conserved, modulating

377 interspecific barriers for parasite colonization among hosts [19,36], and outlining current

378 interactions [26,64].

379   Many life-history traits are positively correlated with body size and therefore may

380   have affected the structure and dynamics of ecological networks at multiple scales of

381   biological organization, from the individual to the ecosystem [20,60,66,77]. Currently, the

382   major challenge is to develop a body of theory that can explore the implications of body

383   size on the structure and functioning of the host-parasite networks.

384   The metrics of the Atlantic Rainforest networks were more similar to the theoretical

385   models than the Pantanal and Chaco networks (Fig. 1, 2, 3 and Table 2). These points

386   to other potential factor(s), besides phylogeny and size, acting on the structure of the

387   Pantanal and Chaco networks. Unlike the Atlantic Rainforest, the Pantanal and Chaco

388   are environments marked by large annual floods. As we suggested, the presence of

389   these floods promotes greater contact between aquatic and semi-aquatic species, thus

390   increasing the ecological opportunity for the establishment of new host-parasite

391   associations [2,4]. The encounters can lead to new associations by ecological fitting, i.e.

392   the ability of organisms to adapt quickly to new resources due to their phenotypic

393   flexibility, without genetic novelties [3,7,38].

394   Moreover, species may expand habitat use in response to the availability of new

395   resources [49,78], which would be associated with the encounter of different hosts in this

396   study. Some examples of habitat expansion (colonization and adaptation to new

397   resources or other new selective ecological adjustment scenarios) arise directly from the

398   events associated with the ecological opportunity [51]. Cyclical expansion of host-

399   parasitic communities in the ecosystems subjected to annual flood pulses favors

400   seasonal contact of infectious forms of parasites with hosts. The colonization of new

401   host species should in fact generate more connected, more nested, and less modular

402   networks (since modules are broken due to the new connections promoted by the

403   environment - Fig. 3, a-f). These events increase the repertoire of the parasite, and may

404 represent the beginning of speciation processes, or, they could maintain its repertoire of

405 host as well as postulated by "Oscillation hypothesis" [10,37,56]. This hypothesis

406 consists largely of micro and macroevolutionary aspects. The microevolutionary part

407 deals with how novel hosts are incorporated during host expansions and, as a

408 consequence, pathogenic lineages can diversify in resource use. The second part is

409 largely macroevolutionary and foresees that these episodes of increased host use

410 should lead to elevated rates of diversification. The particularities of the

411 microevolutionary part affect the specific patterns expected at the macroevolutionary

412 level. In this context, over the course of evolutionary time, true generalist species may

413 become specialists, and vice versa [4,37,56].

414   In environments without flood pulse, such as the Atlantic Rainforest, the host-

415 parasite interaction may be restricted by the low dispersion of species among aquatic

416 environments, since for many semi-aquatic and aquatic species, the forest environments

417 may represent ecological barriers. As contact is the main route of parasite transmission

418 (expected for endoparasites with heteroxenous and monoxenic cycle), the structure of

419 the Atlantic Rainforest network is very similar to the structure of random networks, since

420 hosts share fewer parasites. Our results suggest that the ecological opportunity for

421 interaction may play an important role in determining the structure of interaction

422 networks and the evolutionary dynamics of host-parasite associations. These results

423 create new perspectives for studies on parasitic community assemblages, particularly as

424 few studies relate the connectivity of host communities to the opportunity for parasitic

425 dispersion. This may, in fact, increase our understanding on the influence of the

426 dynamics of the physical environment on the structure of host-parasites interactions.

427   From an epidemiological perspective, changes in the composition of parasitic

428 species or in the frequency of host-parasite interactions are associated with the risks of

429   parasitic invasions and emerging diseases [1,4,11,13,33,39,46,54]. Some examples

430   come from studies with the introductions of species [35,57]. In birds, for instance, the

431   occurrence of nematode parasites increases with the ecological opportunity due to

432   migratory habits and the use of aquatic habitat [47,57]. This results in a change in

433   community structure and the formation of new species associations through a

434   combination of mechanisms, such as ecological adaptation and opportunity for

435   interaction between species [68,69]. In part, the emerging diseases are a result of

436   processes such as those that occur during the flood pulse, in which climate change,

437   travel, and global trade generate opportunities for new species associations [57]. We

438   show that an insight is provided into the dynamics of the incorporation of a new

439   resource, as an evolutionary factor considered to be responsible for changes in species

440   composition.

441   Our results may have been influenced by the fact that the host-parasites interaction

442   database was built from several studies, with different sampling efforts in different

443   regions. This could have increased the interaction records, and, consequently, increased

444   the connectance and reduced the modularity of theoretical models. On the other hand,

445   the interaction database had a larger spatial scale than the local studies in the analyzed

446   environments, so that the random networks could have selected hosts that did not co-

447   occur and, therefore, did not share the same species of parasites, resulting in more

448   modular, but less connected random networks. Even so, the variation in network size

449   between the simulations is high; there is a risk that methodological artifacts (low sample

450   effort) may have been affected, especially in the Amazon network. The fact that the

451   Amazon has a low parasitic richness could be due to the lower sampling effort.

452   Therefore, we opted for excluding this environment from our analyses. However, even

453 with these factors, all the observed networks had the same tendency; they were all more

454 connected and less modular than predicted by the models, thus validating our results.

455

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462

Author Contributions

464 KMC, WAB, SBLA and EDB originally formulated the idea. SBLA and EDB developed the

465 mathematical models, conducted work and generated data analyses. EDB, SBLA, KMC

466 and WAB wrote the manuscript.

467

Conflict of interest

469 The authors declare that they have no conflict of interests.

470

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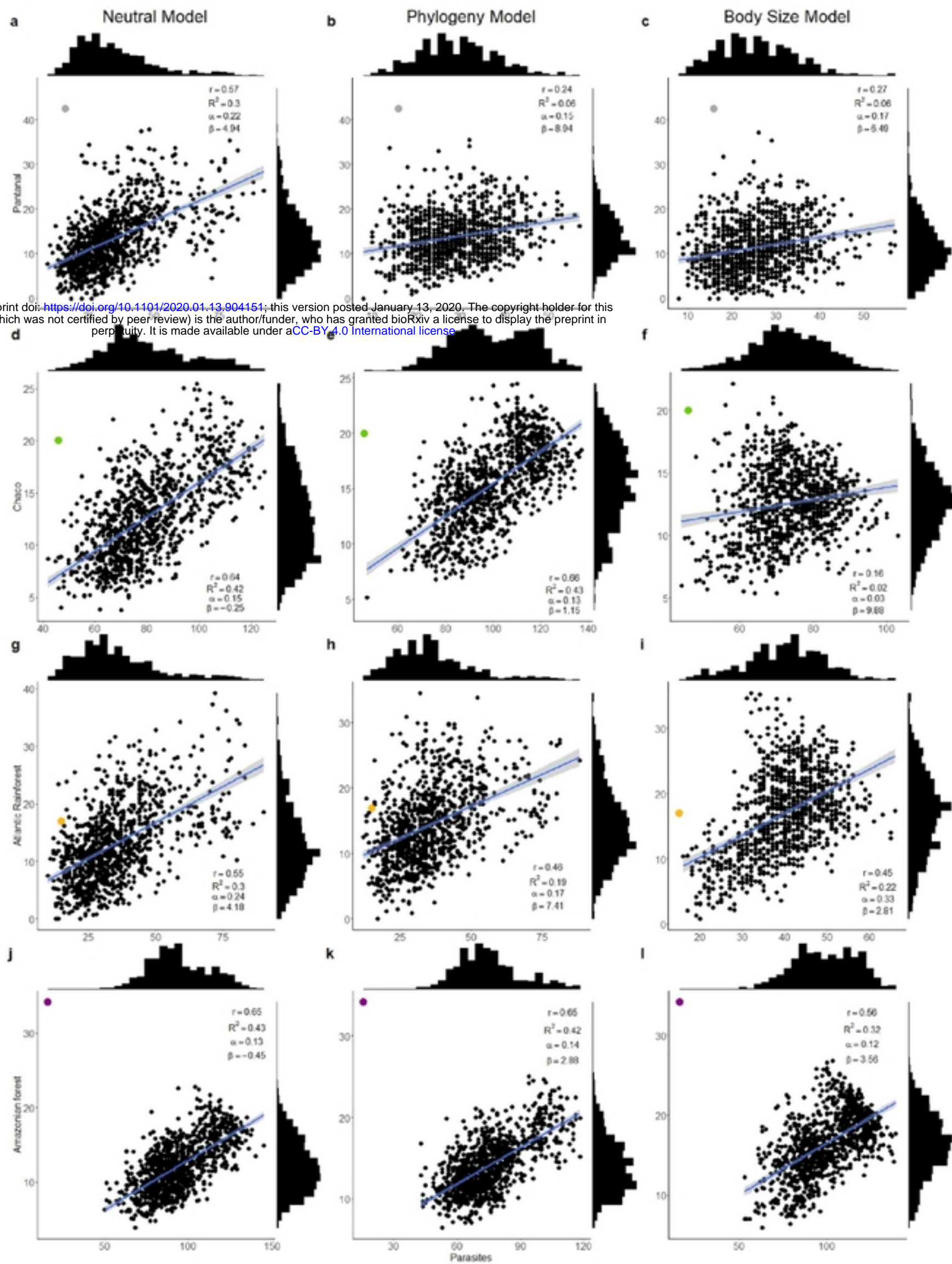
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Figures

Fig. 1

Fig. 2

Fig. 3