

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

Elvira D’Bastiani^{1*}, Karla Magalhães Campião², Walter Antonio Boeger², Sabrina Borges Lino

Araújo³

¹Programa de Pós-Graduação em Ecologia e Conservação, Laboratório de Interações Biológicas - Setor de Ciências Biológicas, Caixa Postal 19031, CEP 81531-990, Curitiba, PR, Brasil.

²Departamento de Zoologia, Laboratório de Interações Biológicas - Setor de Ciências Biológicas, Caixa Postal 19031, CEP 81531-990, Curitiba, PR, Brasil.

³Departamento de Física, Laboratório de Interações Biológicas - Setor de Ciências Biológicas, Caixa Postal 19031, CEP 81531-990, Curitiba, PR, Brasil.

*Corresponding author: Elvira D’Bastiani, Programa de Pós-Graduação em Ecologia e Conservação, Laboratório de Interações Biológicas - Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba, Paraná 81531-980, Brazil. e-mail: elviradebastianii@gmail.com; Telephone: +55 41 996532860.

Abstract

Despite the great interest to quantify the structure of ecological networks, the influence of morphological, ecological and evolutionary characteristics of the species still remains poorly understood. One of the challenging issues in ecology is how the interaction opportunity influences and provides changes to the associations between species, and which effects these changes have on ecological systems. To explore topological patterns in host-parasite networks, we sampled endoparasites-anurans interactions in South America in order to determine whether the effect of the ecological opportunity affects our understanding of the topological structure of the interaction networks. To identify the effect of the ecological opportunity for interaction, we investigated interactions in environments with and without flood pulse, where presence would promote higher ecological opportunity of interaction. Moreover, we created three theoretical models with filters to test the influence of the ecological opportunity for interaction: random, phylogeny and host body size. We then calculated commonly used binary network metrics (connectance, nestedness and modularity) for the networks generated by the theoretical models. We demonstrated that the interaction ecological opportunity changes the structure of host-parasite networks, and was influenced mainly by phylogeny and body size of the host. Our results indicate that environments that offer greater opportunities for interaction between species present networks with the most connectance/nestedness and less modularity. Networks in environments that do not have such opportunities for interaction depict the opposite pattern. Our results indicate that the ecological opportunity of interaction is reflected in an increase in interaction associations between species and affect/change the organization of these interactive assemblages. From an epidemiological point of view, changes in the composition of parasitic species are associated with risks of invasions and emerging diseases. In part, emerging diseases are the result of processes such as those occurring during the flood pulse, in which climate change, travel, and global trade create opportunities for new species associations. Our results provide insight into the dynamics of incorporating a new resource, considering an evolutionary factor responsible for these changes in species composition.

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

59 Introduction

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.

In this study, we tested whether this structure is influenced by phylogeny and body size hosts and whether the periodic ecological opportunity of encounters influences the structure of an anuran-endoparasite (endoparasite-anuran) interaction network in environments with and without annual flood pulses. We used a database of anuran-endoparasite interactions to infer how the network structure of each environment can be explained by randomly sampled networks obtained under different theoretical models with filters: neutral, host phylogeny, and host body size. If phylogeny or body size imposes restrictions on species interactions, we expect to find compartments in the random networks. On the other hand, if there are no restrictions, networks would show nested patterns with interaction indirectly reflecting the abundance of species. We conclude that, among the filters analyzed, host body size and phylogeny greatly explain the observed host-endoparasite networks. However, similar networks of environments with cyclic flood pulse were not well explained by these filters, strongly suggesting that the increased opportunities provided by the environment can intensify encounters and promote and increase connectivity in the host-parasite local network.

Materials and Methods

To test for differences in ecological opportunity, we selected four parasite-host interaction networks compiled from literature data and described them using network metrics (nestedness, connectance, and modularity). Next, we sought to know if it was possible to explain their structure based on the phylogenetic characteristics and body size of the hosts analyzed. For this, we created theoretical models with filters (see below) and then compared the structure of the four networks analyzed with the networks generated by theoretical models to test the effect of the process of interaction of opportunity in different environments. See the methods for details.

133

134 **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

153 **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-

switching: Pantanal - Campião et al. [18], and Chaco - González and Inés [30] flood pulse. The Pantanal network was composed by 11 hosts and 16 parasites (Appendix S2) while the Chaco, by 35 and 46, respectively (Appendix S2) [18,30]. (ii) Two studies from environments without flood pulse, which potentially promote less ecological opportunity for host-switching: Atlantic Rainforest Graça et. [31], and Amazonian forest Bursey et al. [16]. The Atlantic Rainforest network was composed by 11 host and 15 parasites (Appendix S2), while the Amazonian forest by 43 and 16 respectively (Appendix S2) [31,16].

Theoretical models

To answer our questions, we chose to test the effect of random, phylogeny, and host body size to see the changing structure (ecological opportunity) of host-parasite networks in different environments. We chose phylogeny because it was revealed as a potential driver of parasitic diversity. Host species vary in their evolutionary time of exposure for parasites acquisition and sharing, therefore, suffering variable co-evolutionary constraints [32] which would influence the interactions and the structure of their networks' interaction. We also chose the host body size as it was a good predictor of the diversity of parasite species [17,42,53]. Large hosts can provide more space and resources, and possibly a greater breadth of niches for parasites. Moreover, larger hosts live longer and represent fewer ephemeral habitats than small species and are therefore also more exposed to parasites [61].

Three theoretical models with filters were created (random, phylogeny and body size of hosts models - Appendix S3), to test the influence of the ecological opportunity on the structure of host-parasite networks. Each model is characterized as a specific 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 $\pm 5\%$) 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

interactions database after each randomization, so that a species could be included in more than one random network. We then compared how well the filters explain the observed network (the comparison methods are detailed below). Unfortunately, it was not possible to impose on a similar real filter the ecological opportunity to evaluate the effect of interaction opportunity because we have no observation that refers to such a factor. Aquatic and terrestrial systems have different physical and chemical conditions, which seem to influence the biology and diversity of the organisms living in each of these habitats [75], that is why we assumed phylogenetic conservatism of the organisms living in each of these analyzed habitats. Given their aspects, we hypothesized that flood pulse environments are not as well explained by the filters (neutral, phylogeny, and host body size) as the other environments. We postulate that in environments without flood pulse the phylogenetic conservatism could be higher, that is, as it is an environment with few opportunities the species maintain their interactions over evolutionary time. If this is true, we expect that the networks will be better described by the phylogeny and body size models that are supposed to have their most preserved interactions. This is something we would not observe in the cyclic flood pulse because there is a constant change that interferes with this conservatism.

Data analysis

Network Metrics

We used the metrics nestedness, connectance, and modularity to characterize the structure of all networks. The nestedness was calculated using the metric proposed by Almeida-Neto et al. [6], to evaluate the presence of interactions that belong to subsets of other interactions. Therefore, a high nestedness value indicates a hierarchy of 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 Strauß [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:

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

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)

for each metric, from each random network of each theoretical model to the observed network in units of standard deviation:

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

where $\bar{Y}_{obs}$ is the standardized value of the observed network, $\bar{Y}_{rand}$ is the normalized value of the random network metric, and σ_{rand} the standard deviation of 1.000 values of $\bar{Y}_{rand}$. Subsequently, for a given metric and observed network, a unidirectional analysis of variance (ANOVA) was applied to evaluate whether there was a difference between these groups. Tukey's test [79] was used to determine the occurrence of differences between treatments. After measuring the difference, the distance averages between the real networks and each random network of each model was compared to verify which theoretical model best described the observed networks. When the metric and the observed network were fixed, we compared which model best explained the observed network. When the metrics and model were fixed, we compared which observed network was best explained by the models. All statistical analyses were performed using the "stats" package in the R software [22]. For all tests, we assumed the significance of $p < 0.05$.

Results

Structure of host-parasite interaction networks

Some of the random networks presented a range from smaller to greater number of parasite species than the observed networks (Fig. 1, 2, 3 - black bars, upper x axis - frequency of the number of parasites), except for the Amazon, whose smallest random network had at least twice more parasites than the observed network. Thus, by correcting the effect of network size, the theoretical models could not reach a network as small as that analyzed in the Amazon due to low parasitic richness analyzed in this

environment (Fig. 1, Fig. 2 and Fig. 3 - j to l). Despite our attempt to control the effect of network size by a standardization method, we were unable to ensure that the ratio of the metric and the number of parasites maintained the same linear tendency for such low numbers of parasites for Amazon. Therefore, the Amazonian simulations were removed from subsequent analysis.

The nestedness increases with the number of parasites in the network for the remaining three environments (Fig. 1, Appendix S6). Connectance and modularity were negatively correlated with the number of parasites in most simulated models (Fig. 2 and 3, Appendix S6), except for the connectance in simulated neutral models for the Pantanal ($R^2 = 0.01$, $p = 0.98$) and Atlantic Rainforest, which were not correlated ($R^2 = 0.002$, $p = 0.15$).

Fig. 1 Nestedness values according to the number of parasite species before standardization. The black dots indicate the nestedness value of random networks for three theoretical models. Grey dot - Pantanal (a, b, c), green dot - Chaco (d, e, f), orange dot - Atlantic Forests (g, h, i) and violet dot - Amazonian forest (j, k, l). The blue lines represent linear regression and the gray shadow represents standard deviation in random networks. The black bars indicate the frequency distribution of the random networks: right y axis - nestedness frequency, upper x axis - frequency of the number of parasites (details: Appendix S10 in Supporting Information).

Fig. 2 Connectance values according to the number of parasite species before standardization. The black dots indicate the connectance value of random networks for three theoretical models. Grey dot - Pantanal (a, b, c), green dot - Chaco (d, e, f), orange dot - Atlantic Forests (g, h, i) and violet dot - Amazonian forest (j, k, l). The blue lines represent linear regression and the gray shadow represents standard deviation over the random networks. The black bars indicate the frequency distribution of the random networks: right y axis - connectance frequency, upper x axis - frequency of the number of parasites (details: Appendix S10 in Supporting Information).

Fig. 3 Modularity values according to the number of parasite species before standardization. The black dots indicate the modularity value of random networks for three theoretical models. Grey dot - Pantanal (a, b, c), green dot - Chaco (d, e, f), orange dot - Atlantic Forests (g, h, i) and violet dot - Amazonian forest (j, k, l). The blue lines represent linear regression and the gray shadow represents standard deviation over the random networks. The black bars indicate the frequency distribution of the random networks: right y axis - modularity frequency, upper x axis - frequency of the number of parasites (details: Appendix S10 in Supporting Information).

Host body size and phylogeny models usually better describe the observed network than neutral models

The distance (D) between random networks and their respective observed network were significantly different among the models (Table 1). The body size model that better resembled the nestedness pattern was observed in the Pantanal and Chaco, while in the Atlantic Rainforest, it was the phylogeny model. The connectance values in the Atlantic Rainforest were better resembled by the neutral model, while in the Pantanal and Chaco were better resembled by the body size and phylogeny models, respectively. The modularity was better resembled by the phylogeny model in the Pantanal and Chaco networks, while modularity in the Atlantic Rainforest was best explained by the body size model (Table 1). Such results, with the exception for connectance in the Atlantic Rainforest, show that the body size and phylogeny of the hosts resemble better the network structure than neutral model.

Table 1. Analysis of variance (statistical significance test F_{2-2997}), Tukey Test between neutral models (N), 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
	Pantanal	2166.00*	P - N*	BS	12.56
			BS - N*	P	13.58
			BS - P *	N	15.46
Connectance	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
	Pantanal	166.50*	P - N*	P	- 5.15
			BS - N*	BS	- 5.33
			BS - P *	N	- 5.93
Modularity	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 ($\langle D \rangle$) between the observed network and the random networks. * = significant difference <0.01 .

335

336

337 **The theoretical models describe environments without flood pulse better**

338 **than the flood pulse environments**

339 The resemblance of the network metrics from randomly sampled networks to observed

340 networks environments with and without flooding for each metric presented different

341 distances (Table 2). All metrics pointed network structure of the Pantanal as the furthest

342 from the network structure of the theoretical models (statistics for support Table 2),

343 followed by the Chaco and the Atlantic Rainforest. This shows that the environment

344 without flood pulse is better described by the proposed models than the flood pulse

345 environments. All theoretical models pointed that Pantanal network is the most nested,

connected and less modular one followed by Chaco and Atlantic Rainforest (see the statistics for support test for each metric between random networks of the models and observed network - average distance value, $\langle D \rangle$, in Table 2).

Table 2. Analysis of variance (statistical significance test F_{2-2997}), Tukey Test between neutral (N), phylogeny (P) and body size (BS) theoretical models, for each metric and environment.

Metric	Model	ANOVA F_{2-2997}	Tukey HSD Environment	Environment	$\langle D \rangle$
Nestedness	N	4923*	Atlantic Rainforest - Chaco*	Pantanal	6.04
			Pantanal - Chaco*	Chaco	4.07
			Pantanal - Atlantic Rainforest *	Atlantic Rainforest	1.61
	P	5704*	Atlantic Rainforest - Chaco*	Pantanal	5.94
			Pantanal - Chaco*	Chaco	4.43
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	1.26
	BS	4840*	Atlantic Rainforest - Chaco*	Pantanal	5.85
			Pantanal - Chaco*	Chaco	3.21
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	1.48
Connectedness	N	39508*	Atlantic Rainforest - Chaco*	Pantanal	15.46
			Pantanal - Chaco*	Chaco	5.77
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	3.68
	P	27554**	Atlantic Rainforest - Chaco*	Pantanal	13.58
			Pantanal - Chaco*	Chaco	4.86
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	4.17
	BS	18577*	Atlantic Rainforest - Chaco*	Pantanal	12.56
			Pantanal - Chaco*	Chaco	5.68
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	4.62
Modularity	N	39508*	Atlantic Rainforest- Chaco*	Pantanal	-5.93
			Pantanal - Chaco*	Chaco	-4.53
			Pantanal - Atlantic Rainforest*	Atlantic Rainforest	-1.81
	P	27554*	Atlantic Rainforest - Chaco*	Pantanal	-5.15
			Pantanal - Chaco*	Chaco	-3.79
			Pantanal - Atlantic Rainforest *	Atlantic Rainforest	-1.68
	BS	18577*	Atlantic Rainforest - Chaco*	Pantanal	-5.33
			Pantanal - Chaco*	Chaco	-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 ($\langle D \rangle$) between the observed network and the random networks. *=significant difference <0.01 .

Discussion

The method we developed to infer how the structure of anuran-endoparasite interaction networks under different conditions of encounter opportunities could be described by theoretical models based on neutral, host phylogeny and host body filters. We found that the theoretical models described the network without flood pulse - i.e low ecological opportunity for interaction (Atlantic Rainforest) – better than the networks with cyclic flood pulse (Pantanal and Chaco). In addition, the networks of the three environments were best described by the theoretical models with phylogeny or host body size filters rather than the neutral filter. This result suggests that, in fact, the increased ecological opportunity for encounters provided by the environment increases connectivity through the incorporation of new host species in the repertoire of the parasites.

The topology patterns observed in the communities reflect the mechanisms that structure their respective networks. Some studies suggest randomness as an underlying mechanism for explaining the structure of parasitic communities [44,62]. However, the metrics we tested in our study did not indicate the neutral model as the main structuring mechanism for network topology, except for the connectance of the network in the Atlantic Rainforest. The interactions of the Atlantic Rainforest can be the result of random neutral encounters between individuals, whose probability is mediated by the relative abundances of the populations involved and by compatibility in the case of parasites.

In parasitic communities, the evolutionary history of the host acts as one of the determinants of the community structure [19,67]. Phylogenetic relationships function as a good proxy for describing ecological differences between hosts and host groups. This may indicate that these attributes are phylogenetically conserved, modulating interspecific barriers for parasite colonization among hosts [19,36], and outlining current interactions [26,64].

Many life-history traits are positively correlated with body size and therefore may have affected the structure and dynamics of ecological networks at multiple scales of biological organization, from the individual to the ecosystem [20,60,66,77]. Currently, the major challenge is to develop a body of theory that can explore the implications of body size on the structure and functioning of the host-parasite networks.

The metrics of the Atlantic Rainforest networks were more similar to the theoretical models than the Pantanal and Chaco networks (Fig. 1, 2, 3 and Table 2). These points to other potential factor(s), besides phylogeny and size, acting on the structure of the Pantanal and Chaco networks. Unlike the Atlantic Rainforest, the Pantanal and Chaco are environments marked by large annual floods. As we suggested, the presence of these floods promotes greater contact between aquatic and semi-aquatic species, thus increasing the ecological opportunity for the establishment of new host-parasite associations [2,4]. The encounters can lead to new associations by ecological fitting, i.e. the ability of organisms to adapt quickly to new resources due to their phenotypic flexibility, without genetic novelties [3,7,38].

Moreover, species may expand habitat use in response to the availability of new resources [49,78], which would be associated with the encounter of different hosts in this study. Some examples of habitat expansion (colonization and adaptation to new resources or other new selective ecological adjustment scenarios) arise directly from the events associated with the ecological opportunity [51]. Cyclical expansion of host-parasitic communities in the ecosystems subjected to annual flood pulses favors seasonal contact of infectious forms of parasites with hosts. The colonization of new host species should in fact generate more connected, more nested, and less modular networks (since modules are broken due to the new connections promoted by the 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

with these factors, all the observed networks had the same tendency; they were all more connected and less modular than predicted by the models, thus validating our results.

Acknowledgements

The authors would like to thank the Academic Publishing Advisory Center (Centro de Assessoria de Publicação Acadêmica, CAPA – www.capa.ufpr.br) of the Federal University of Paraná for assistance with English editing. EDB was supported by a Master degree fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

Author Contributions

KMC, WAB, SBLA and EDB originally formulated the idea. SBLA and EDB developed the mathematical models, conducted work and generated data analyses. EDB, SBLA, KMC and WAB wrote the manuscript.

Conflict of interest

The authors declare that they have no conflict of interests.

References

1. Adlard RD, Miller TL, Smit NJ. The butterfly effect: parasite diversity, environment, and emerging disease in aquatic wildlife. *Trends in Parasitology*. 2015;31(4):160-166.
2. Agosta SJ. On ecological fitting, plant–insect associations, herbivore host shifts, and host plant selection. *Oikos*. 2006;114(3):556-565.

3. Agosta SJ, Klemens JA. Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecology Letters*. 2008;11(11):1123-1134.
4. Agosta SJ, Janz N, Brooks DR. How specialists can be generalists: resolving the “parasite paradox” and implications for emerging infectious disease. *Zoologia*. 2010;27(2):151-162.
5. Agostinho AA, Thomaz SM, Minte-Vera CV, Winemiller KO. Biodiversity in the high Paraná river Floodplain. In: Gopal B, Junk WJ, Davis JA. Biodiversity in wetlands: assessment, function and conservation, Backhuys Publishers, Leiden; 2000. p. 89-118.
6. Almeida-Neto M, Guimaraes P, Guimaraes Jr PR, Loyola RD, Ulrich W. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*. 2008;117(8):1227-1239.
7. Araujo SB, Braga MP, Brooks DR, Agosta SJ, Hoberg EP, von Hartenthal FW, et al. Understanding host-switching by ecological fitting. *Plos One*. 2015;10(10):e0139225.
8. Bascompte J, Jordano, P, Melián CJ, Olesen JM. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*. 2003;100(16):9383-9387.
9. Bozelli RL. Composition of the zooplankton community of Batata and Mussura lakes and the Trombetas River, State of Pará, Brazil. *Amazoniana*. 1992;12:239-261.
10. Braga MP, Araujo SB, Agosta S, Brooks D, Hoberg E, Nylin S, et al. Host use dynamics in a heterogeneous fitness landscape generates oscillations in host range and diversification. *Evolution*. 2018;72(9):1773-1783.

11. Brooks DR, Hoberg EP. How will global climate change affect parasite-host assemblages? *Trends in parasitology*. 2007;23(12):571-574.
12. Brooks DR, León-Règagnon V, McLennan DA, Zelmer D. Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology*. 2006;87(sp7):S76-S85.
13. Brooks DR, Hoberg EP, Boeger WA, Gardner SL, Galbreath K, Herczeg D, et al. Finding them before they find us: informatics, parasites, and environments in accelerating climate change. *Comparative Parasitology*. 2014;81(2):155-165.
14. Brooks DR, Hoberg EP, Boeger WA. In the eye of the cyclops: the classic case of cospeciation and why paradigms are important. *Comparative Parasitology*. 2015;82(1):1-9.
15. Brooks DR, Hoberg EP, Boeger WA. The Stockholm paradigm: Climate change and emerging disease. 4th ed. University of Chicago Press, 2019.
16. Bursey CR, Goldberg SR, Parmelee JR. Gastrointestinal helminths of 51 species of anurans from Reserva Cuzco Amazónico, Peru. *Comparative Parasitology*. 2001;68(1):21-35.
17. Campiao KM, de Aquino Ribas AC, Morais DH, da Silva RJ, Tavares LER. How many parasites species a frog might have? Determinants of parasite diversity in South American anurans. *Plos One*. 2015;10(10):e0140577.
18. Campião KM, da Silva ICO, Dalazen GT, Paiva F, Tavares LER. Helminth parasites of 11 anuran species from the Pantanal Wetland, Brazil. *Comparative parasitology*. 2016;83(1):92-101.
19. Clark NJ, Clegg SM, Sam K, Goulding W, Koane B, Wells K. Climate, host phylogeny and the connectivity of host communities govern regional parasite assembly. *Diversity and Distributions*. 2018;24(1):13-23.

20. Cohen JE, Jonsson T, Müller CB, Godfray HCJ, Savage VM. Body sizes of hosts and parasitoids in individual feeding relationships. *Proceedings of the National Academy of Sciences*. 2005;102(3):684-689.
21. Combes C. *Parasitism: the ecology and evolution of intimate interactions*. University of Chicago Press, London. 2001.
22. Core Team. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0, URL <http://www.R-project.org/>. 2018.
23. Dallas T, Hall RJ, Drake JM. Competition-mediated feedbacks in experimental multispecies epizootics. *Ecology*. 2016;97(3):661-670.
24. Dormann CF, Strauss R. A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*. 2014;5(1):90-98.
25. Dormann CF, Gruber B, Fründ J. Introducing the bipartite package: analysing ecological networks. *Interaction*. 2008;1:0.2413793.
26. Dormann CF, Von Riedmatten L, Scherer-Lorenzen M. No consistent effect of plant species richness on resistance to simulated climate change for above-or below-ground processes in managed grasslands. *BMC Ecology*. 2017;17(1):23.
27. Erwin TL. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. *Taxonomy, phylogeny, and zoogeography of beetles and ants*. 1985;437-472.
28. Fecchio A, Pinheiro R, Felix G, Faria IP, Pinho JB, Lacorte GA, et al. Host community similarity and geography shape the diversity and distribution of haemosporidian parasites in Amazonian birds. *Ecography*. 2018;41(3):505-515.
29. Frost DR. *Amphibian Species of the World: an Online Reference*. Version 6.0. American Museum of Natural History, New York, USA. 2018.

30. González CE and Hamann MI. Checklist of nematode parasites of amphibians from Argentina. *Zootaxa*. 2015;3980(4):451-76.
31. Graça RJ, Oda FH, Lima FS, Guerra V, Gambale PG, Takemoto RM. Metazoan endoparasites of 18 anuran species from the mesophytic semideciduous Atlantic Forest in southern Brazil. *Journal of Natural History*. 2017;51(13-14):705-729.
32. Hadfield JD, Krasnov BR, Poulin R, Nakagawa S. A tale of two phylogenies: comparative analyses of ecological interactions. *The American Naturalist*. 2013;183(2):174-187.
33. Hoberg EP and Brooks DR. A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host-parasite systems. *Journal of Biogeography*. 2008;35(9):1533-1550.
34. Hoberg EP, Brooks DR. Beyond vicariance: integrating taxon pulses, ecological fitting, and oscillation in evolution and historical biogeography. The biogeography of host-parasite interactions. In Morand S, Krasnov BR (eds.) *The biogeography of host-parasite interactions*. Oxford University Press, 2010. p. 7:20.
35. Hoberg EP and Zarlenga DS. Evolution and biogeography of *Haemonchus contortus*: linking faunal dynamics in space and time. In: Gasser RB and Von Samson, *Advances in Parasitology. Haemonchus contortus and Haemonchosis - Past, Present and Future Trends*. 2016. P. 1-30.
36. Huang S, Bininda-Emonds OR, Stephens PR, Gittleman JL, Altizer S. Phylogenetically related and ecologically similar carnivores harbour similar parasite assemblages. *Journal of Animal Ecology*. 2014;83(3):671-680.

37. Janz N, Nylin S, Wahlberg N. Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC evolutionary biology*. 2006;6(1):4.
38. Janzen DH. On ecological fitting. *Oikos*. 1985;45:308-310.
39. Jones KE, Patel NG, Levy MA, Storeygard A, Balk D, Gittleman JL, et al. Global trends in emerging infectious diseases. *Nature*. 2008;451(7181):990-993.
40. Joppa LN and Williams R. Modeling the building blocks of biodiversity. *Plos One*. 2013;8(2):e56277.
41. Junk WJ, Bayley PB, Sparks RE. The flood pulse concept in river-floodplain systems. *Canadian special publication of fisheries and aquatic sciences*. 1989;106(1):110-127.
42. Kamiya T, O'Dwyer K, Nakagawa S, Poulin R. What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews*. 2014;89(1):123-134.
43. Krasnov BR, Fortuna MA, Mouillot D, Khokhlova IS, Shenbrot GI, Poulin R. Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *The American Naturalist*. 2012;179(4):501-511.
44. Krishna A, Guimaraes Jr PR, Jordano P, Bascompte J. A neutral-niche theory of nestedness in mutualistic networks. *Oikos*. 2008;117(11):1609-1618.
45. Lafferty KD, Kuris AM. Trophic strategies, animal diversity and body size. *Trends in Ecology & Evolution*. 2002;17(11):507-513.
46. Lafferty KD. The ecology of climate change and infectious diseases. *Ecology*. 2009;90(4):888-900.

47. Leung TLF and Koprivnikar J. Nematode parasite diversity in birds: the role of host ecology, life history and migration. *Journal of Animal Ecology*. 2016;85(6):1471–1480.
48. Locke SA, McLaughlin JD, Marcogliese DJ. Predicting the similarity of parasite communities in freshwater fishes using the phylogeny, ecology and proximity of hosts. *Oikos*. 2013;122(1):73-83.
49. MacArthur RH, Diamond JM, Karr JR. Density compensation in island faunas. *Ecology*. 1972;53(2):330-342.
50. Mácová A, Hoblíková A, Hypša V, Stanko M, Martinů J, Kvičerová J. Mysteries of host switching: Diversification and host specificity in rodent-coccidia associations. *Molecular phylogenetics and evolution*. 2018;127:179-189.
51. Malcicka M, Agosta SJ, Harvey JA. Multi level ecological fitting: indirect life cycles are not a barrier to host switching and invasion. *Global change biology* 2015;21(9):3210-3218.
52. May RM. Stability and complexity in model ecosystems. Princeton University Press. v. 6. 1974.
53. Morand S. (Macro-) Evolutionary ecology of parasite diversity: From determinants of parasite species richness to host diversification. *International Journal for Parasitology: Parasites and Wildlife*. 2015;4(1):80-87.
54. Morse SS, Mazet JA, Woolhouse M, Parrish CR, Carroll D, Karesh WB, et al. Prediction and prevention of the next pandemic zoonosis. *The Lancet*. 2012;380(9857):1956–1965.
55. Navaud O, Barbacci A, Taylor A, Clarkson JP, Raffaele S. Shifts in diversification rates and host jump frequencies shaped the diversity of host

- range among Sclerotiniaceae fungal plant pathogens. Molecular ecology. 2018;27(5):1309-1323.
56. Nylin S, Janz N. Butterfly host plant range: an example of plasticity as a promoter of speciation? Evolutionary Ecology. 2009;23(1):137-146.
57. Nylin S, Agosta S, Bensch S, Boeger WA, Braga MP, Brooks DR, et al. Embracing colonizations: a new paradigm for species association dynamics. Trends in ecology & evolution. 2018;33(1):4-14.
58. Olesen JM, Bascompte J, Dupont YL, Jordano P. The modularity of pollination networks. Proceedings of the National Academy of Sciences. 2007;104(50):19891-19896.
59. Patella L, Brooks DR, Boeger WA. Phylogeny and ecology illuminate the evolution of associations under the Stockholm Paradigm: *Aglaiogyrodactylus* spp. (Platyhelminths, Mongenoidea, Gyrodactylidae) and species of Loricariidae (Actinopterygii, Siluriformes). Vie et Milieu-Life and Environment. 2017;67(2):91-102.
60. Peters RH. The Ecological Implications of Body-Size, Cambridge University Press. 1983.
61. Poulin R. Species richness of parasite assemblages: evolution and patterns. Annual review of Ecology and Systematics. 1997;28(1):341-358.
62. Poulin R. Parasites and the neutral theory of biodiversity. Ecography. 2004;27(1):119–123.
63. Ramalho WP, Machado IF, Vieira LJS. Do flood pulses structure amphibian communities in floodplain environments? Biotropica. 2018;50(2):338-345.

64. Rezende EL, Albert EM, Fortuna MA, Bascompte J. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters*. 2009;12(8):779-788.
65. Rigaud T, Perrot-Minnot MJ, Brown MJ. Parasite and host assemblages: embracing the reality will improve our knowledge of parasite transmission and virulence. *Proceedings of the Royal Society B: Biological Sciences*. 2010;277(1701):3693-3702.
66. Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL. Effects of body size and temperature on population growth. *The American Naturalist*. 2004;163(3):429-441.
67. Scordato ES and Kardish MR. Prevalence and beta diversity in avian malaria communities: Host species is a better predictor than geography. *Journal of Animal Ecology*. 2014;83(6):1387-1397.
68. Stigall AL. When and how do species achieve niche stability over long time scales? *Ecography*. 2014;37(11):1123-1132.
69. Stigall AL, Bauer JE, Lam AR, Wright DF. Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record. *Global and Planetary Change*. 2017;148:242-257.
70. Streicker DG, Turmelle AS, Vonhof MJ, Kuzmin IV, McCracken GF, Rupprecht CE. Host phylogeny constrains cross-species emergence and establishment of rabies virus in bats. *Science*. 2010;329(5992):676-679.
71. Thomaz SM, Bini LM, Bozelli RL. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*. 2007;579(1):1-13.
72. Thomaz SM, Roberto MDC, Bini LM. Caracterização limnológica dos ambientes aquáticos e influência dos níveis fluviométricos. In *A planície de inundação do*

671 alto rio Paraná: aspectos físicos, biológicos e socioeconômicos. Maringá:
672 EDUEM. 1997. p. 73-102.

673 73.Wells K, Gibson DI, Clark NJ. Global patterns in helminth host specificity:
674 phylogenetic and functional diversity of regional host species pools matter.
675 Ecography. 2019;42(3):416-427.

676 74.Wells K, O'Hara RB, Morand S, Lessard JP, Ribas A. The importance of
677 parasite geography and spillover effects for global patterns of host–parasite
678 associations in two invasive species. Diversity and Distributions.
679 2015;21(4):477-486.

680 75.Vermeij GJ, Dudley R. Why are there so few evolutionary transitions between
681 aquatic and terrestrial ecosystems?. Biological Journal of the Linnean Society.
682 2000;70(4):541-554.

683 76.Wolfe ND, Dunavan CP, Diamond J. Origins of major human infectious
684 diseases. Nature. 2007;447(7142):279.

685 77.Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, et
686 al. Body size in ecological networks. Trends in ecology & evolution.
687 2005;20(7):402-409.

688 78.Wright SJ. Density compensation in island avifaunas. Oecologia.
689 1980;45(3):385–389.

690 79.Zar JH. Biostatistical Analysis, (4th ed.). Prentice-Hall, Upper Saddle River, NJ,
691 USA. 1999. p. 931.

Figures

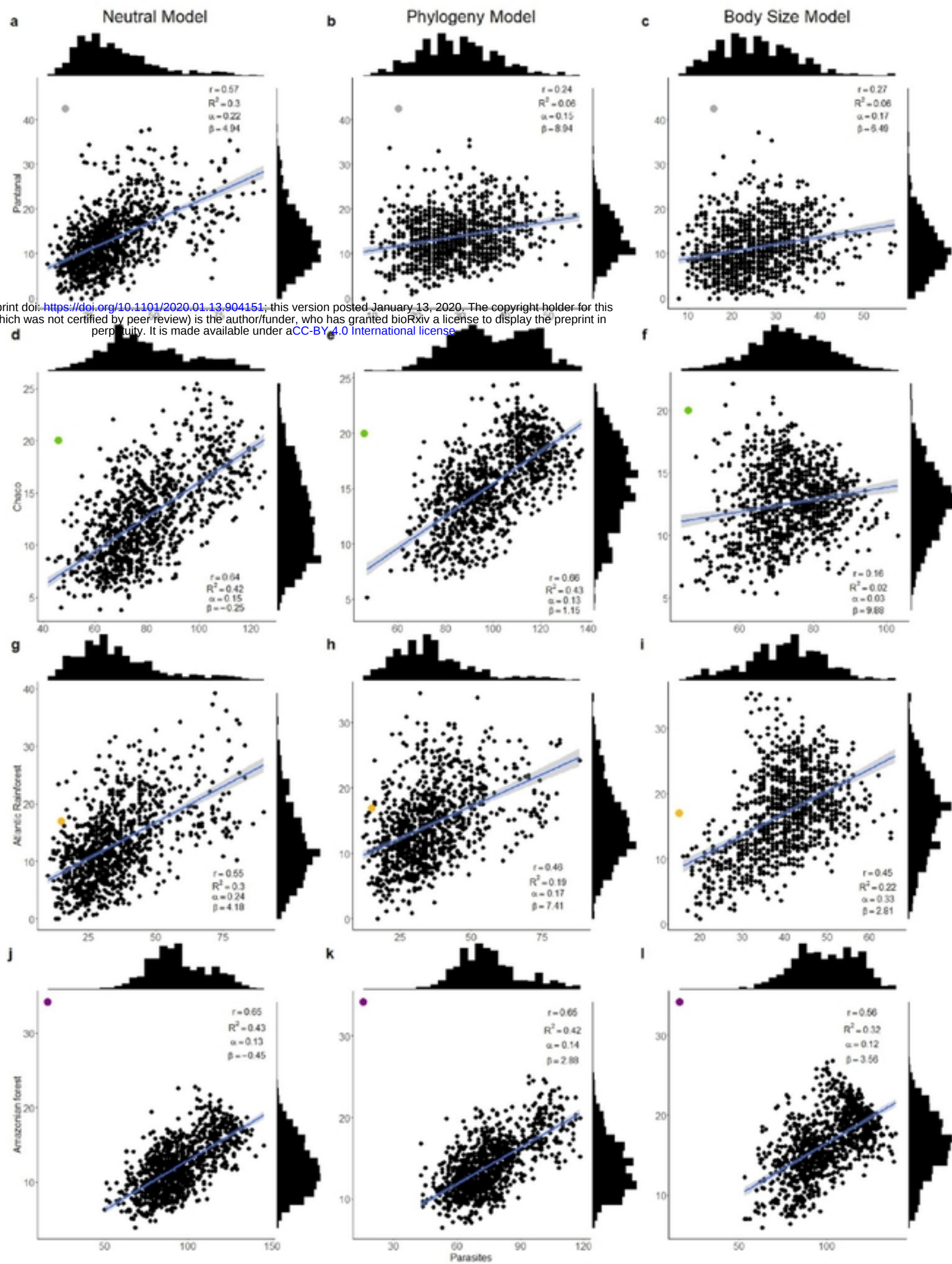


Fig. 1

bioRxiv preprint doi: <https://doi.org/10.1101/2020.01.13.904151>; this version posted January 13, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

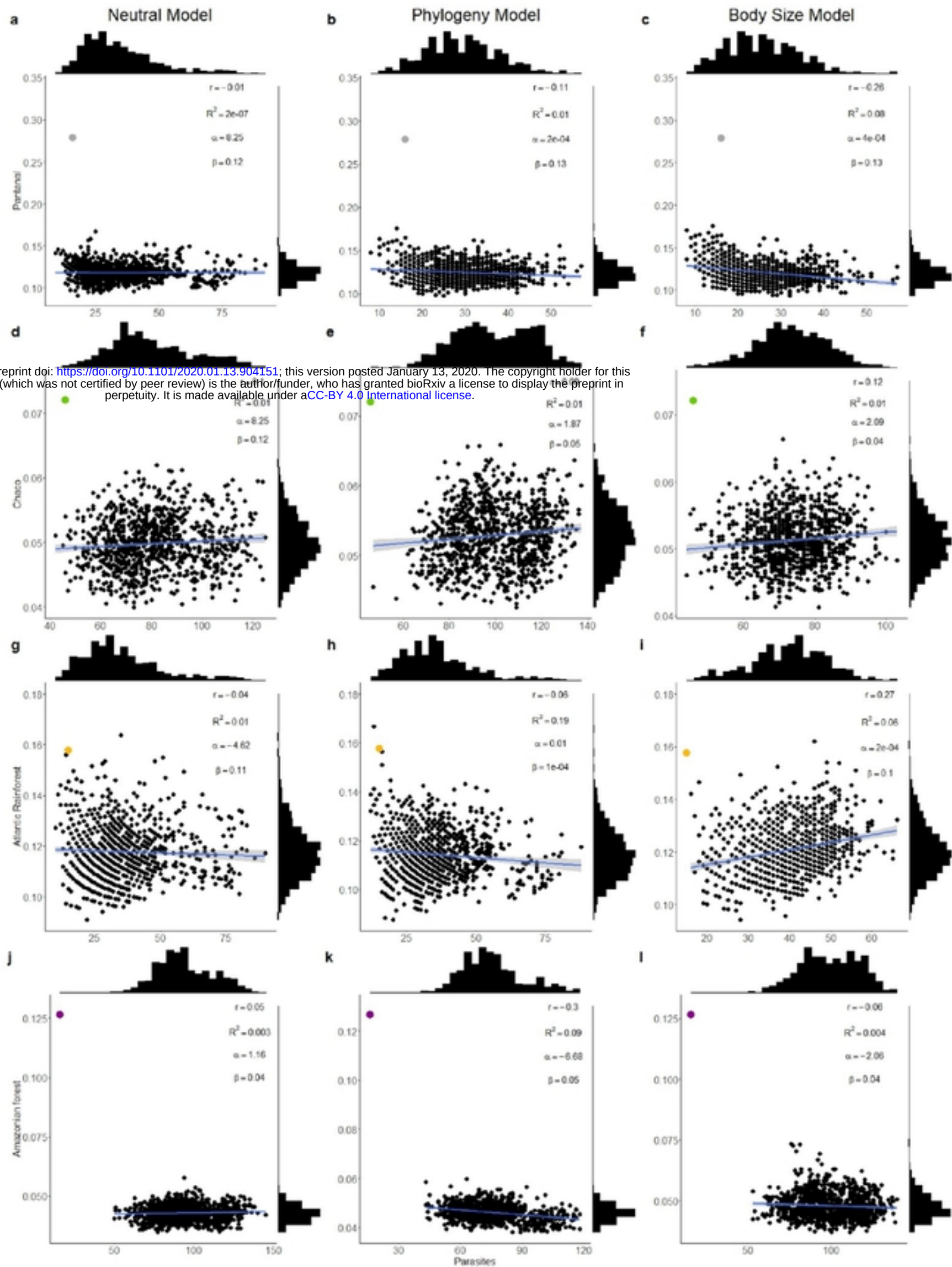


Fig. 2

bioRxiv preprint doi: <https://doi.org/10.1101/2020.01.13.904151>; this version posted January 13, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

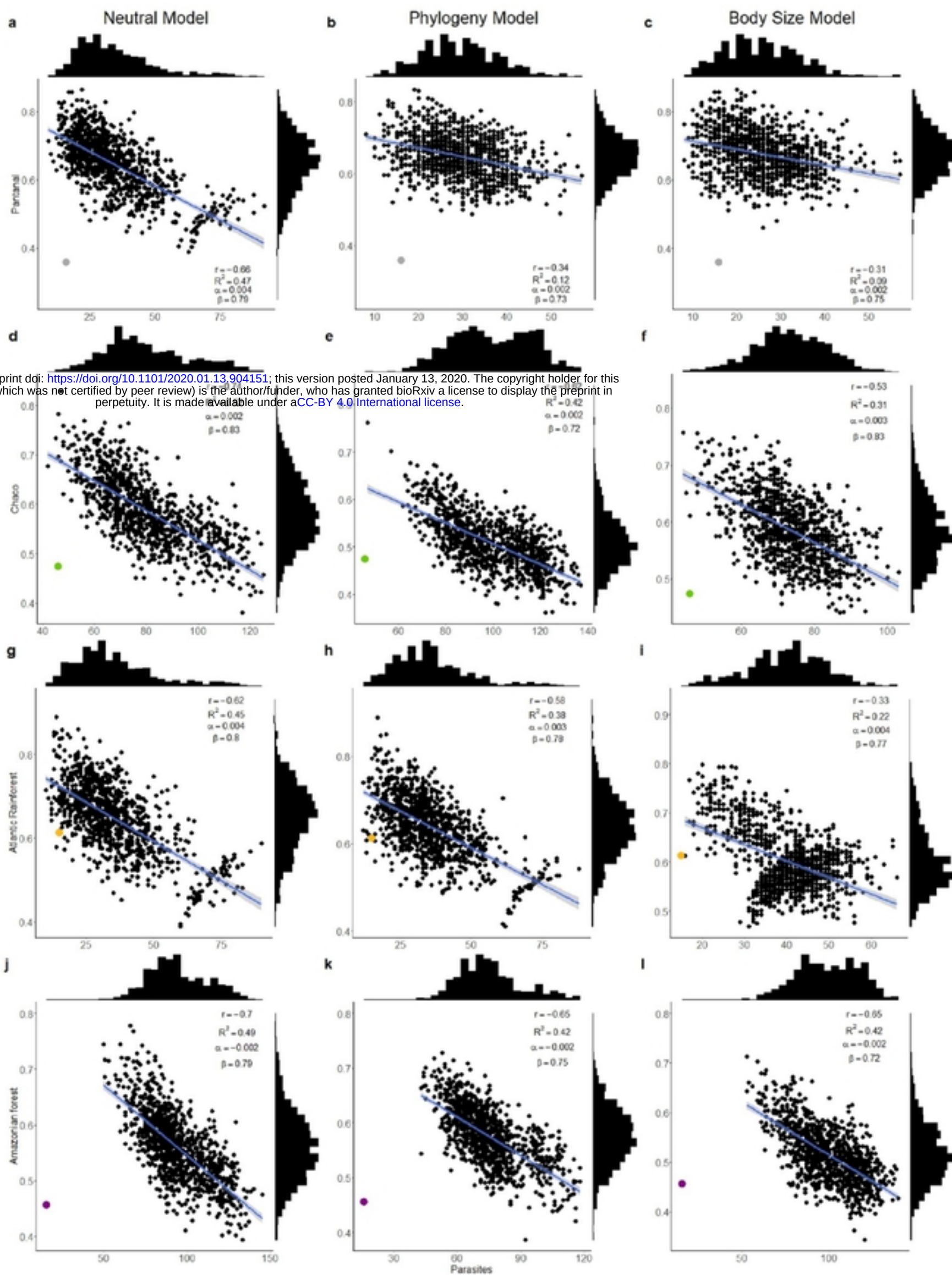


Fig. 3