Empirical Evaluation of Neutral Interactions in Host-Parasite Networks

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abstract: While niche-based processes have been invoked extensively to explain the structure of interaction networks, recent studies propose that neutrality could also be of great importance. Under the neutral hypothesis, network structure would simply emerge from random encounters between individuals and thus would be directly linked to species abundance. We investigated the impact of species abundance distributions on qualitative and quantitative metrics of 113 host-parasite networks. We analyzed the concordance between neutral expectations and empirical observations at interaction, species, and network levels. We found that species abundance accurately predicts network metrics at all levels. Despite host-parasite systems being constrained by physiology and immunology, our results suggest that neutrality could also explain, at least partially, their structure. We hypothesize that trait matching would determine potential interactions between species, while abundance would determine their realization.

Keywords: host-parasite network, neutrality, network structure, null model, species abundance distribution.

Introduction

Current theory on the structure of ecological networks is based on the assumption that biological traits are constraining interactions (Stouffer 2010), with defined niche dimensions such as body size (Williams et al. 2010; Krasnov et al. 2011; Eklof et al. 2013) or phenology (Colloca et al. 2010). Despite empirical support for this hypothesis, appropriate null models and alternative hypotheses are still needed to rigorously test the signature of trait-matching constraints on network structure (Gotelli and Graves 1996).

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Neutral theory of interactions posits that, in the absence of niche constraints, species abundance distributions will determine the structure of ecological networks (Bluethgen et al. 2008; Canard et al. 2012). Neutral interaction networks are more than simple random networks (e.g., Erdős-Rényi random graphs; Erdős and Rényi 1959) because interactions between species pairs are drawn from a biased distribution, where abundant species have a higher probability of interacting together (i.e., not all interactions are equally probable). Rare species are less likely to encounter and interact, thereby generating "neutral forbidden links" (as compared to "niche forbidden links" that are due to trait-based incompatibility between species; Jordano et al. 2003; Canard et al. 2012). As for competition theory, the neutral theory of interactions provides an intermediate hypothesis between random and trait-matching models (Gotelli and McGill 2006) and an appropriate benchmark against which the niche hypothesis should be tested (Bluethgen et al. 2008).

A hypothesis-testing approach requires evaluating the contribution of neutral interactions across network types to evaluate the support for the niche hypothesis. For instance, recent studies have shown that the structure of mutualistic networks is largely constrained by species abundance (Krishna et al. 2008; Vázquez et al. 2009; Verdú and Valiente-Banuet 2011; Chagnon et al. 2012). A good agreement between empirical data and neutral expectations was found for some components of network structure, such as nestedness (Krishna et al. 2008). The contribution of neutral interactions to the structure of antagonistic networks remains to be tested, however. The investigation of host-parasite networks is particularly appropriate to quantify the importance of neutrality in ecological interactions because these systems are hypothesized to be highly constrained by trait matching based on species

physiology and immunology (Flores et al. 2011; Poisot et al. 2011). In a previous study, Vasquez et al. (2005) revealed that abundance might be responsible for asymmetric interactions (i.e., the fact that a specialist species preferentially interacts with generalist and vice versa) in host-parasite networks, suggesting that neutral interactions could contribute significantly to their structure. We propose here to push this reasoning further and evaluate neutrality on all levels of network structure, from low-level properties such as pairwise interaction strength to the most aggregated properties such as connectance. Multiple metrics were considered in an effort to conduct the most comprehensive analysis of neutral theory, as suggested by McGill (2003).

There has been a rapid development of methods to parameterize niche models of interactions based on traits in recent years (Rohr et al. 2010; Williams et al. 2010; Eklof et al. 2013), but these have not been applied to host and parasites. For these rodent-ectoparasite systems, such as the rodents and ectoparasites we study here, some traits might be useful to predict interactions. For instance, host specificity is a parasite-specific attribute that varies significantly among parasite species but not among populations within parasite species (Krasnov et al. 2004). Furthermore, host specificity is to a large extent phylogenetically constrained and depends on key traits, such as spines and setae that anchor the ectoparasite within host hair to resist grooming, that evolve convergently in different lineages (Medvedev 2005). Previous works have shown niche conservatism in flea-mammal networks (Mouillot et al. 2006; Krasnov et al. 2012*b*), suggesting that closely related mammal species tend to share similar flea species due to inherited similarities in terms of physiology, immunology, or ecology.

Hosts provide two main resources for ectoparasites, blood for nutrition and a nest for the development of early life stages. The blood biochemical composition and the nesting microenvironment are heterogeneously distributed among mammal species and across lineages. For rodents, Gouy de Bellocq et al. (2006) found two types of cell-mediated immune responses. A prompt but relatively weak response was characteristic mainly of murine rodents, whereas a delayed but relatively strong response was typical of gerbilline rodents. This suggests that the two types of responses represent different antiparasitic strategies and are associated with some properties inherited from common ancestors. All of these traits contribute to behavioral and immunological defenses that ultimately determine ectoparasites' composition and abundance. It therefore seems reasonable to expect some trait-based processes to shape, at least partly, host–parasite webs. Trait-matching constraints should eventually scale up at the network level and influence its architecture. For instance, since close

relative mammal species tend to share similar flea species thanks to inherited similarities in terms of physiology, immunology, or ecology, we expect flea-mammal networks to be modular or compartmentalized (Krasnov et al. 2012*a*). In other words, phylogenetic constraints on trait distribution should make parasites interact with a set of hosts similar to that of their close relatives, thereby promoting the emergence of modules, where some species are highly connected with each other while having few connections to species in other modules.

Here we investigated the contribution of neutral interactions to the structure of host-parasite networks. The combination of different simulated species abundance distributions at the host and parasite levels could theoretically cover the wide range of degree distributions (i.e., the number of links per species) observed in empirical systems (Dunne et al. 2002). The neutral (abundance-based) expectation is that the interaction strength between a host and a parasite should be proportional to the product of their relative abundances. Conversely, the niche expectation (trait-based) is that interaction strength should be independent of abundance. The neutral expectation for pairwise interactions should also scale up to higher-level network properties such as interaction evenness, nestedness, and connectance. Such an integrative study does not exist yet. We used a data set of 113 host-parasite networks including quantitative interactions between ectoparasites (mites, fleas, and ticks) and small rodents at 13 localities in Slovakia. We compared the neutral expectations to observations for a range of metrics quantifying network structure, from pairwise species interactions to network levels. We conducted comparisons across the 113 networks and then refined our analysis by comparing neutral expectations to observations of the same local network recorded repeatedly over time. We found overall, contrary to our expectation, a good agreement between neutral expectations and empirical observations at all levels of organization.

Material and Methods

Neutral Model of Interactions

We considered a neutral model of bipartite interactions (Krishna et al. 2008; Canard et al. 2012) designed for hosts and parasites. The probability p_{ij} that a parasite species j encounters a host species i is simply the product of their relative abundances a, $p_{ij} = a_i a_j$. The expected neutral interaction strength b_{ij} is proportional to this probability. Consequently, both species abundance distributions (SADs) of hosts and parasites will impact the structure of such bipartite networks. Figure 1 illustrates that a combination of the most common SADs (the log series and
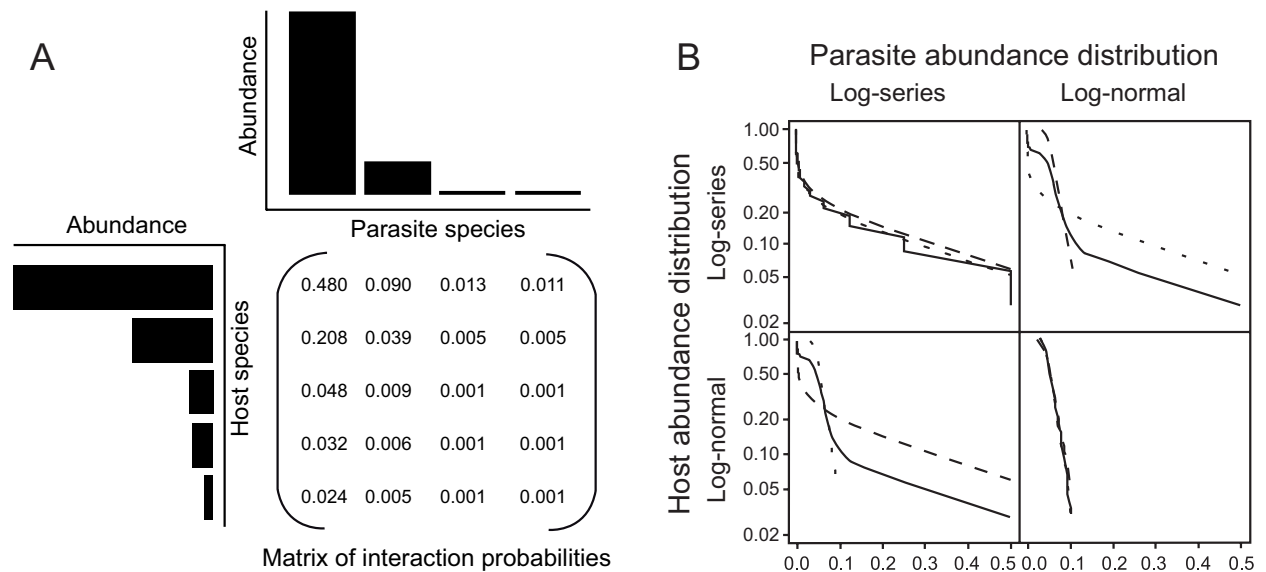
Figure 1: *A*, Schematic representation of the neutral theory of interactions. *B*, Linear-log plots of the cumulative degree distributions for parasites (dashed line), hosts (dotted line), and both combined (solid line) for different species abundance distributions.

the lognormal distributions) covers a wide range of degree distributions (here the cumulative distribution of the number of links per species; fig. 1*B*). The number of predicted interactions per species is more variable among species when the SADs have a higher proportion of rare species. The slope of the degree distribution increases if either one of the SADs tends to a log series (with a high proportion of rare species), meaning the distribution is skewed toward specialized parasites (i.e., parasites with low number of host species) and hosts of low vulnerability (i.e., hosts with elevated number of parasite species). The few species with elevated abundance increase the variance of the degree distribution because they experience a larger number of interactions than the rare species. On the other hand, a combination of lognormal SADs generates a less variable degree distribution, which is also less skewed toward specialists.

Empirical Data

We compared the neutral expectations to observations for several components of interaction networks using the empirical abundance distributions of hosts and parasites. We used 113 quantitative host-parasite networks of rodents and ectoparasites recorded in Slovakia from 1983 to 2001. Only 77 networks and only flea parasites were analyzed by Stanko et al. (2002). Interactions were recorded in 13 localities representing various habitats, including forests, grasslands, and mountains. Ten locations had between 2 and 33 replicated measurements (details in Stanko et al.

2002). The data set consists of 26 small mammalian species (from genera *Apodemus, Arvicola, Clethrionomys, Crocidura, Glis, Microtus, Muscardinus, Micromys, Mus, Neomys, Ondatra, Rattus, Sorex, Talpa*) and 61 ectoparasite species (mites, fleas, and ticks). Only some species of gamasid mites, which were collected on body hosts and clustered into groups of obligatory or facultative hematophages, were used in the evaluation (e.g., see Mašán and Fenďa 2010). Smaller mites of several families (e.g., Parasitidae, Macrochelidae, Ascidae, Rhodacaridae, Ameroseiidae) were excluded from the evaluation as they are associated only with nests. For each realization of the network (i.e., a network at a given locality at a given time), we used the total number of individuals recorded for a parasite species as a proxy for local abundance. Host abundance was evaluated as the number of host individuals trapped. We approximated the interaction strength b_{ij} as the total number of individual parasite species j collected over all host individuals of species i for each realization of the network.

Network Metrics

We considered quantitative metrics to describe network structure, except for modularity and nestedness, which are available only for binary networks (Tylianakis et al. 2009). Previous studies have shown that most metrics based on binary data are sensitive to the sampling effort (Goldwasser and Roughgarden 1997; Bersier et al. 1999; Martinez et al. 1999), while quantitative metrics are more robust (Banasek-Richter et al. 2004). To accurately understand each

component of our host-parasite networks, we chose to analyze network structure at three levels of organization: pairwise interactions, species, and network (table 1). The neutral model described above predicts pairwise interaction strength and is naturally the level to start the analysis. All pairwise interactions should combine and impact higher levels of network organization (species and network levels).

(1) *Pairwise interactions level.* We first compared the neutral expectations of interaction strength to the observations for all pairwise interactions. (2) *Species level.* We calculated a quantitative specialization index PDI (paired difference index; Poisot et al. 2011) that takes into account the strength of interactions. With this index, the highest interaction strength is used as a reference to which all other interaction strengths are compared. The PDI has a value of 0 when all interactions for a given parasite are equal (indicating a generalist) and positive when interactions are heterogeneously distributed (indicating a specialist). (3) *Network level.* We used the quantitative metrics of network structure developed by Bersier et al. (2002) adapted for hosts and parasites. These metrics are based on the measure of interaction strength (b_{ij}) between species i and j. Each species' diet and vulnerability is characterized by the diversity of its interaction strength. Metrics for binary data use the number of links to quantify the diversity of hosts or parasites, while their quantitative counterparts quantify this diversity using the Shannon entropy index (H_i). We calculated the quantitative directed connectance (C_q), which quantifies the proportion of interactions realized over all potential interactions. We also calculated the link density (L_d), quantifying the mean number of interactions per species, the mean vulnerability (V) of host species, and the mean generality (G) of parasite species in each network. We also considered the interaction evenness (IE) following Tylianakis et al. (2007) because it is more sensitive to differences in evenness. We characterized the network topology with two metrics quantifying specific elements of network structure: nestedness and modular-

Table 1: Summary of the network metrics considered in this study

Level	Metric	Definition	Formula	Reference
Pairwise interaction:				
b_{ij}	Interaction strength between host species i and parasite species j	No. of parasites i counted on the population of host j		
Species:				
PDI_i	Paired difference index of species i	Specialization of the species i	$PDI_i = \dfrac{\sum_j^{S_p} b_{i,max} - b_{ij}}{S_p - 1}$	Poisot et al. 2012*a*
Network:				
L	Number of interactions	Total no. of interactions in the network	$L = \frac{1}{2}\left(\sum_i n_i + \sum_j n_j\right)$	Bersier et al. 2002
L_d	Link density	Mean no. of interactions per species	$L_d = \frac{1}{2}\left(\frac{1}{S_h}\sum_i n_i + \frac{1}{S_p}\sum_j n_j\right)$	Bersier et al. 2002
C_q	Connectance	Proportion of interactions realized in the network	$C_q = \dfrac{L}{S_h + S_p}$	Bersier et al. 2002
G	Generality	Mean no. of interactions per parasite species	$G = \frac{1}{S_p}\sum_j n_j$	Bersier et al. 2002
V	Vulnerability	Mean no. of interactions per host species	$V = \frac{1}{S_h}\sum_i n_i$	Bersier et al. 2002
IE	Interaction evenness	Evenness of interactions in the network	$IE = \dfrac{-\sum_i\sum_j (b_{ij}/b_{..})\log_2(b_{ij}/b_{..})}{\log_2(S_p \times S_h)}$	Tylianakis et al. 2007
NODF	Nestedness	Measure of how many interactions realized by specialists are a subset of those realized by generalists	See Almeida-Neto et al. 2008 for a full description	Almeida-Neto et al. 2008
Q	Modularity	Compartmentalization of interactions in the network	$Q = \sum_{m=1}^{N}\left[\frac{I_m}{I} - \left(\frac{K_m^h K_m^p}{I^2}\right)\right]$	Barber 2007

Note: Variables: b_{ij} is the interaction strength between host species i and parasite species j; S_h and S_p are the number of host and parasite species, respectively; n_i and n_j are the reciprocal of the diversity of interactions for host species i and parasite species j, respectively; $b_{i,max}$ is the maximal interaction strength for host species i; $b_{..}$ is the sum of all the b_{ij} in the network; N is the number of modules in the network; I is the total number of interactions; I_m is the number of interactions between all the species within module m; and K_m^h and K_m^p are respectively the sum of the number of interactions of all the host and all the parasites in module m. NODF is defined in "Network Metrics."

ity. Nestedness quantifies how many interactions realized by specialized parasites are a subset of those realized by generalists (Bascompte et al. 2003). We calculated an index of nestedness called "NODF" that was developed by Almeida-Neto et al. (2008) using the function "nested-nodf" of the "vegan" package developed for R software (Team 2012). Modularity quantifies the compartmentalization of interactions in the network (Krause et al. 2003). Modules are defined as densely connected groups of species interacting little with other species outside of the module (e.g., May 1973; Rezende et al. 2009). Modularity was estimated using an index developed for bipartite networks (Barber 2007). This index was maximized with a simulated annealing algorithm following the method developed by Guimera and Amaral (2005).

Analysis

We compared the neutral expectations of each of the above metrics with observations using linear regression. Neutral interaction matrices were derived as described above using empirical abundances. We tested the hypothesis that there is a significant relationship between neutral predictions and observations, with an intercept of 0 and a slope of 1. Alternatively, the niche prediction is the absence of a significant relationship with an intercept corresponding to the average of the metric. We first analyzed the neutral-observed relationship across all 113 realized networks (referred to as "across-networks" analysis).

We took advantage of repeated measures of parasite-host interactions at some localities to refine our analysis. We performed linear regressions at each location, with each measurement considered a data entry (referred to as "within-networks" analysis). Under the niche hypothesis, we expect constant structure of the network despite temporal variations in species abundance. While the across-networks analysis could be potentially biased by an effect of specialization on abundance (e.g., if generalists are more abundant), the within-networks analysis should be independent because the specificity of ecological interactions should not vary over time. For this analysis, we retained only localities and species pairs having at least four measurements.

Results

Pairwise Interaction Level

We found a strong agreement between neutral expectations and observed interaction strengths b_{ij} across networks (average linear regression over all networks: $R^2 = 0.69$; table 2). However, there was considerable variation across networks in the strength of this relationship (fig. 2). The

within-network analysis revealed a similar, although weaker, relationship ($R^2 = 0.45$), with different results depending on the species pair considered (fig. 4B).

Species Level

The correspondence between the neutral and the observed PDI differed between network levels (table 2). Parasite PDI was better predicted than host PDI for all analyses (table 2; fig. 3C). The neutral-observed relationship was stronger for parasite species ($R^2 = 0.92$ and 0.81 for across- and within-networks analysis respectively, with more than 90% of regressions being significant; table 2; fig. 3C) than for host species ($R^2 = 0.34$ and 0.37 with fewer than half of the regressions being significant). There was considerable variation among species (fig. 4). Regressions for some species were always significant (e.g., the host *Apodemus flavicollis* or the parasite *Palaeopsylla soricis*), while they were never significant for others (e.g., the host *Apodemus sylvaticus* or the parasite *Hystrichopsylla talpae*).

Network Level

Network-level metrics were consistently well predicted by the neutral model, with the exception of nestedness (table 2). The correspondence between neutral expectations and observations was lower within networks than across networks but nevertheless significant for both. Best fits were obtained for the number of interactions L ($R^2 = 0.82$ and 0.80 for the across- and within-networks analysis, respectively) and the interaction evenness IE ($R^2 = 0.85$ and 0.78), but they were still good for connectance C_q ($R^2 = 0.75$ and 0.57) and generality G ($R^2 = 0.60$ and 0.17). However, weaker correspondence was found for the link density L_d, the vulnerability V, and the modularity Q (all $R^2 < 0.50$). The only exception was nestedness, which was found to be very different to neutral expectations, and largely overestimated ($R^2 = 0.00$ for both analyses).

Discussion

Do Neutral Interactions Mimic Empirical Host-Parasite Networks?

We investigated the contribution of neutral interactions to the structure of host-parasite networks. We first show that the neutral degree distribution is highly flexible and can thus reproduce various empirical network structures (fig. 1). Highly structured networks emerge in neutral communities despite random interactions among individuals because rare species are unlikely to encounter each other and thus interact, introducing "neutral forbidden links" in the network (Canard et al. 2012). We therefore com-

Table 2: Statistics of the linear regressions between empirical observations and neutral expectations

Level, data	Metric	Slope	Intercept	Adjusted R^2	Proportion of significant regressions
Pairwise interactions:					
Across	b_{ij}	1.2 (.2)	−1.3 (1.3)	.69 (.24)	1.00
Within	b_{ij}	.9 (1.6)	.9 (5.9)	.45 (.44)	.45
Species:					
Across	Parasite PDI	2.7 (1.6)	− 4.3 (6.2)	.92 (.15)	1.00
Within	Parasite PDI	1.5 (.8)	4.5 (15.6)	.81 (.18)	.93
Across	Host PDI	.6 (2.0)	29.4 (99.9)	.34 (.64)	.46
Within	Host PDI	1.1 (1.9)	15.0 (34.8)	.37 (.43)	.49
Network:					
Across	L	.6	4.9	.82	
	L_d	.5	1.2	.42	
	C_q	.7	0	.75	
	IE	1.2	−.2	.85	
	G	.5	.6	.60	
	V	.4	1.8	.37	
	NODF	.1	50	.00	
	Q	1.2	.2	.25	
Within	L	.7 (.1)	2.2 (3.4)	.80 (.10)	1.00
	L_d	.4 (.2)	1.3 (.9)	.23 (.33)	.43
	C_q	.6 (.1)	.1 (.1)	.57 (.16)	1.00
	IE	1.2 (.1)	−.2 (.1)	.78 (.17)	1.00
	G	.5 (.1)	.7 (.2)	.59 (.17)	1.00
	V	.4 (.2)	2.0 (1.3)	.19 (.33)	.29
	NODF	.2 (.4)	44.4 (32.0)	.00 (.10)	.00
	Q	1.7 (1.1)	.2 (.1)	.27 (.23)	.57

Note: Data are reported averages (SD in parentheses). The mean slope, intercept, adjusted R^2 are given for two analyses. In a first analysis, regressions were conducted across networks for species pairs, species, and network levels. In a second analysis, regressions were conducted within networks (over several repetitions over time) for species pairs, species, and network levels. We also report the proportion of regressions that were significant at $P < .05$. PDI = paired difference index; see text for other definitions.

pared the neutral expectations to observations for a range of metrics quantifying network structure. Our analysis revealed that pairwise interaction strength is accurately predicted by neutrality. We also found that neutrality accurately predicts higher-level network metrics (with particularly good fits for C_q, L, L_d, IE, and G metrics) but failed to predict the distribution of interactions within the network (with weak fits found for NODF and Q metrics). This contrast is particularly remarkable since the neutrality was good at predicting aspects related to the degree distribution but weak at predicting where these interactions were located in the host-parasite interaction matrix. We thus propose that the latter metrics were better indicators to discriminate neutral interactions from niche-based interaction than the former metrics were. While abundance-based interactions have been already proposed to explain nestedness in ecological networks (Krishna et al. 2008; Vázquez et al. 2009), we found that the abundance-based hypothesis overestimated nestedness and failed at predicting the natural variation of nestedness values.

Species abundance can vary both over time and space. We consequently studied the neutrality of interactions across and within networks, each analysis providing different information. We found that spatial variation in abundance, whatever the underlying process, is a robust predictor of pairwise interactions. The observation that abundance species are more generalist than rare species is only an agreement between neutral predictions and observations, not a proof of causality. The problem could obviously be flipped around, with generalist species being more abundant because they could interact with a larger quantity of potential hosts. A most comprehensive analysis would require the measurement of traits and the prediction of the interactions based on them. However this information is difficult to obtain, and new techniques are required to link traits to interactions. A strength of our study comes from repeated measures of parasite-host interactions at some localities. There are potentially several confounding spatially varying environmental factors that could explain an abundance-interaction relationship.
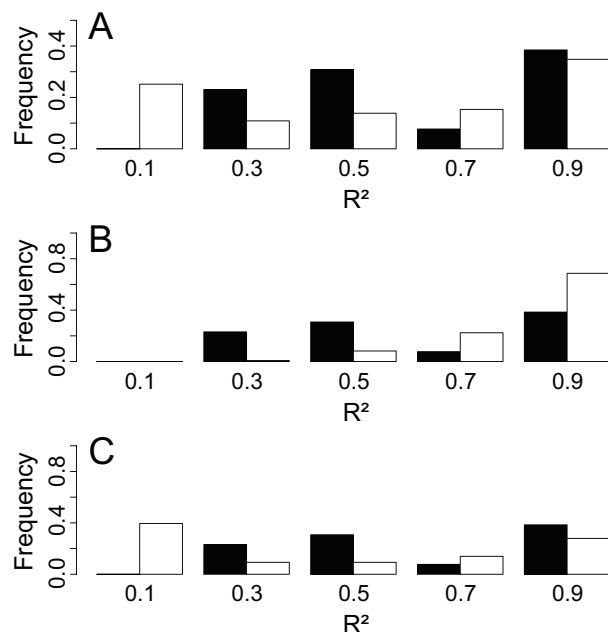
Figure 2: Histograms of R^2 values obtained for the linear regressions between neutral expectations and empirical observations of pairwise interaction b_{ij} (*A*), parasite species specialization PDI_{para} (*B*), and host species vulnerability PDI_{host} (*C*). Histograms are given for regressions across-network (black bars) and within-network (white bars) analyses. PDI = paired difference index.

There is also considerable spatial turnover in species composition among locations. Temporal variation in abundance at a single location is therefore a more stringent test of neutrality because only the abundance varies, not the traits. We found a similar support for neutrality for the within-network analysis.

The species-level metric we studied, quantifying specialization, was accurately predicted by the neutral model. The fit was lower for hosts than for parasites, suggesting that host vulnerability was more influenced by other features than abundance. In addition, we found marked differences among species. For instance, the specialization of the mouse *Apodemus flavicollis* was well explained by neutral interactions across the seven localities (all regressions were significant and exhibited a mean $R^2 > 0.9$; fig. 4*B*). In contrast, the specialization of some hosts, such as the shrew species *Sorex araneus* or the vole species *Microtus subterraneus*, were badly predicted by the neutral model. The distribution of goodness of fit was less variable for parasite species since neutrality consistently explained observed specialization values (fig. 4*B*) across mites (e.g., *Lealaps hilaris*), fleas (e.g., *Palaeopsylla soricis*, *Megabothris turbidus*), and ticks (e.g., *Ixodes ricinus*).

We expected this system to deviate more from neutrality than less constrained systems such as plant-mycorrhizae networks because host-parasite networks are hypothesized to be highly constrained by physiology and immunology (Chagnon et al. 2012). Our results nonetheless convincingly show that the strength of host-ectoparasite interactions are at least partly determined by species abundance distributions and consequently are more flexible and versatile than what is expected under a niche-based interaction hypothesis. Our findings are in agreement with studies on plant-pollinator networks showing very flexible interactions between insect and plant species over the season (Vázquez et al. 2009), highlighting the importance of opportunism in mutualistic interactions beyond trait-based mechanisms. Our interpretation might be particularly valid for systems where generalism provides an insurance against strong turnover in species composition (e.g., arthropod food webs on islands; Gravel et al. 2011). Our results provide a plausible explanation for the considerable turnover in network structure observed for host-parasite interactions (Poisot et al. 2012*b*).

Particularities, Limitations, and Opportunities

Hosts and parasites communities represent a particular type of interaction network because an individual parasite will interact with a single host at each stage of its life cycle, but the population altogether will sample an immense number of hosts. This situation differs from other systems where one individual will sample a large number of prey; for instance, a passerine bird will feed on thousands of insects, or a whale on millions of krill. If we consider a binary network of interactions, then it is very likely that a single whale will sample a much larger proportion of the prey diversity than a single parasite will do with host diversity. The whole parasite population will nonetheless sample most of the potential hosts. Theoretically, a binary matrix of interactions will be filled as the number of individuals tends to infinity, making neutral models of interactions useless. This problem vanishes when we consider quantitative metrics of interactions as we did in this study. If we put temporal variation in prey abundance aside, the proportion of a bird's diet filled by one particular insect species should be the same whether we consider a short sampling period (as we would do with the observation of stomach contents) or compile the diet over the year (as we would do with stable isotopes). The same should happen with parasites as we increase population size. This sampling effort effect has no impact on the signature of neutrality in interaction networks since the probability of an interaction depends on relative abundance and not absolute abundance. However the variance of interactions will shrink asymptotically with increasing population size (Poisot et al. 2012*a*).
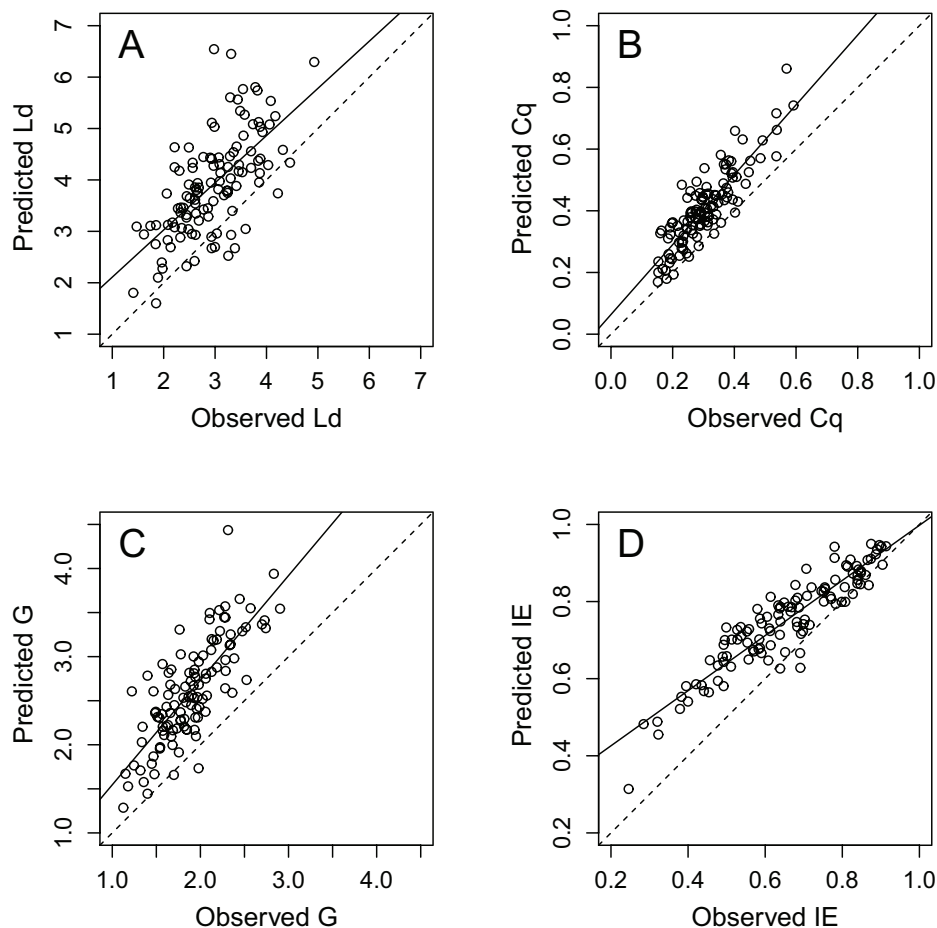
Figure 3: Linear regressions between neutral expectations and empirical observations of network-level structure indexes: link density L_d (*A*), connectance C_q (*B*), generality G (*C*), and interaction evenness *IE* (*D*). Each dot represents one of the 113 host-parasite networks, straight lines are regression lines, and dashed lines are the 1 : 1 relationships.

The study of ectoparasites introduces the question of how a density-dependent (or frequency-dependent) mechanism, such as transmission, could affect the structure of neutral interaction networks. If the parasites promote host spatial aggregation, then abundant hosts will have a probability of interactions biased in their favor relative to rare host species. We could also imagine similar phenomena with other organisms, for instance, with insects emitting pheromones promoting their aggregation. Some mycorrhizal fungi are also hypothesized to interact neutrally with their host (Chagnon et al. 2012). The enhanced performance of plants species following root infection will promote the growth of both the host and the fungi, thereby also impacting their interaction probabilities. However such density dependence is neutral in the sense that it is not more likely to happen for one species or another; it depends only on initial abundance. More generally, we intuit that any neutral density-dependence feedback,

whether positive or negative, will generate important priority effects. This promising hypothesis will require more thorough theoretical and empirical developments.

Our study reveals that the structure of host-ectoparasite networks depends, at least partly, on species abundances. Along with previous findings in mutualist networks, our results suggest that interactions between host and parasites exhibit some opportunism. The comparison between endoparasite versus ectoparasite networks could eventually provide significant knowledge in that regard. It is not obvious which one will be more neutral, as there are benefits for both endoparasite and ectoparasites to evolve generalization (neutrality) or specialization. Ectoparasites are potentially exposed to a much larger diversity of hosts and therefore neutral interactions might be more beneficial. They are also less exposed to the immune response of the host. Some gamasid mites that are considered to be obligatory hematophages do not exploit hosts directly. Many
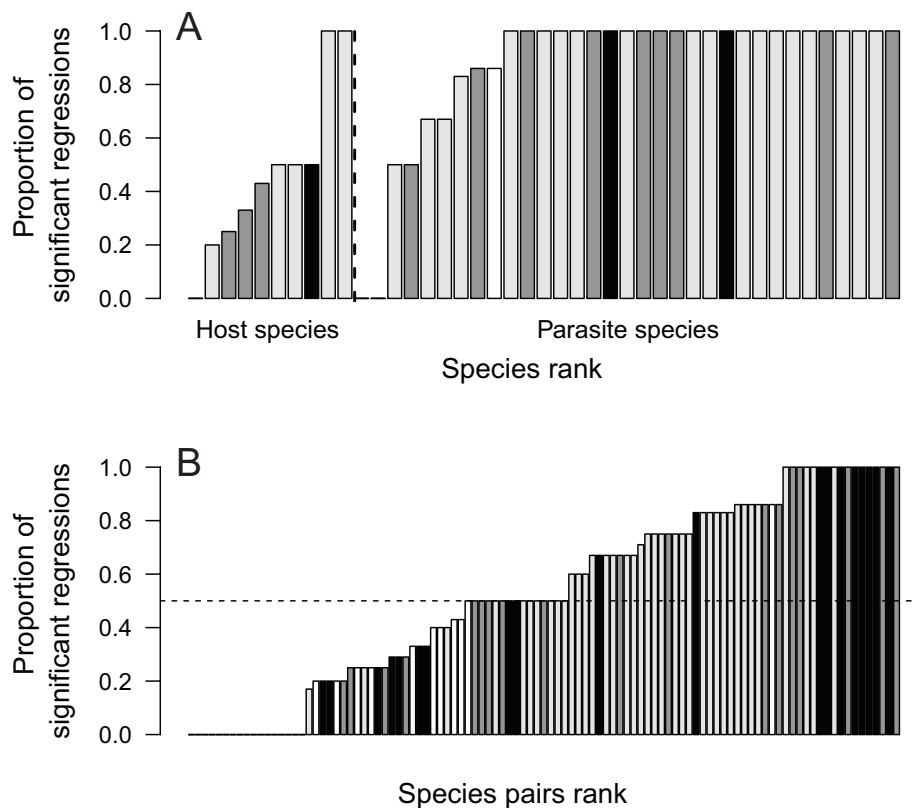
Figure 4: Proportion of significant regressions for repeated measurements (within-network analysis). Specialization (paired difference index [PDI]; *A*) and interaction strength between species pairs (b_{ij}; *B*). Colors represent the mean R^2 of significant regressions (black: $R^2 \geq 0.9$, dark gray: $0.9 > R^2 \geq 0.8$, gray: $0.8 > R^2 \geq 0.6$, white: $R^2 < 0.6$). Note that all significant regressions had an R^2 above 0.73 for parasite species PDI, 0.60 for host species PDI, and 0.35 for pairwise interaction strength.

mite species may obtain a host's blood via predation on other hematophages (e.g., larvae of ixodid ticks; Radovsky 1985). These mites may also satisfy their requirements by consuming dried blood on skin as well as dead lice or fleas that previously fed on host (e.g., Dowling 2006). On the other hand, endoparasites are required to find a suitable host at the transition between two stages, and obviously, generalists will have a higher probability of finding a suitable one (Gravel et al. 2011). What might be more discriminant is the distinction between obligate versus facultative parasites. The strength of coevolution between obligate parasites and their host is more susceptible to have imposed strong trait-matching constraints.

Methods should be developed to account for spatial and temporal fluctuations in abundance to better reveal the contribution of niche differentiation to network structure. Conversely, such methods could also be useful to reveal the role of interactions on variations in species abundance and extent of occurrence, an important issue in biogeography (Kissling et al. 2012). Instead of viewing the neutral theory of interactions in opposition to other niche-based hypotheses, we call for a continuum from niche to neutrality in interaction networks, just as for competitive systems (Gravel et al. 2006). A continuum theory of network structure posits that traits, or any biological feature, might constrain potential interactions between species, but relative abundance ultimately determines their realization. In other words, niches would determine potential links, among which abundance would filter out unrealizable links and determine the strength of interactions. Within this niche-neutral continuum perspective, our results suggest that the deviation of each pairwise interaction from the neutral expectation could be interpreted along the niche-neutral axis.

Implications of Neutral Interactions for Consumer-Resource Interactions

The idea of a neutral model of interactions is in apparent contradiction to classical consumer-resource theory, where ecological interactions drive abundance. However this interpretation is erroneous for two reasons. First, most con-

sumer-resource models consider a strong effect of abundance on the intensity of interactions. Traditional consumer-resource models such as the ones based on the Lotka-Volterra equation defines the interaction between two species with a mass-action assumption. The intensity of an interaction between species i and species j usually looks like $a_{ij}N_iN_j$, where a_{ij} is the per capita interaction coefficient. This model will be neutral when the a_{ij}s will be equal for all pairs of species; thus, any variation of interaction strength is dependent on variation in abundance. The second point is that consumer-resource interactions generate opposite predictions to our observations. In a typical host-parasite or predator-prey situation, we should expect that the abundance of the victim would decrease with the interaction strength while the one of the enemy would increase. In other words, we should expect that rare resources will have, overall, much more intense interactions with consumers than abundant resources would. Interestingly, we observed the opposite and abundant hosts were found to interact more with abundant parasites. These conflicting results should not be interpreted as a rejection of consumer-resource theory since our analysis was not designed with the purpose of testing this theory. Future theoretical work should be conducted to reconcile both the consumer-resource and neutral network theory.

Concluding Remarks

Neutrality is expected to occur within guilds, for instance, among plant species with similar soil affinities, while niche differentiation (environmental filtering) would take place among guilds (Purves and Pacala 2005; Hérault 2007). Similarly, neutrality is more likely to occur within species that share a similar set of traits that would potentially shape similar interactions. This hypothesis leads to interesting and testable predictions about the strength of interactions across a phylogeny, just as it was done for competitive systems (Kembel 2009). For instance, hosts within a genus should be interchangeable for a given parasite species, while not among families, through the conservatism of physiological and immunological responses (Mouillot et al. 2006). Similarly, we could think about different levels of organization within networks. Neutrality could occur within modules (Kondoh et al. 2010) while niche differentiation may act between modules, which could explain why nestedness and modularity metrics were so weakly explained by neutral interactions. New statistical methods will be required to better account for and partition the effects of trait matching and abundance to the structure of ecological networks.

The recently developed theory of neutral interactions will help to better understand spatial and temporal variation in network structure (Poisot et al. 2012a). For some predictions, we found bias or lower agreement with empirical observations. In particular, we observed that the fit between the neutral expectations and the observations was variable among the species or species pairs considered. Future work will have to quantify and study the origin of such differences. In conclusion, we advocate that both neutral and niche processes might constrain host-parasite networks, and the next challenge is to evaluate the relative magnitude of these two forces.

Acknowledgments

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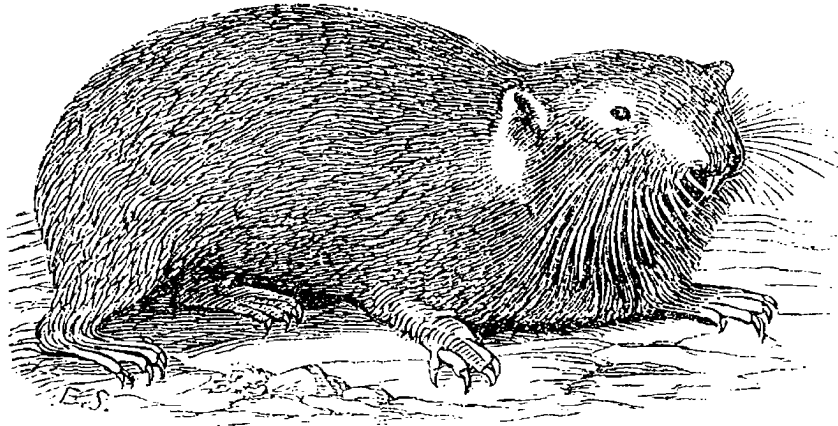
"The show'tl's food is the various vegetation of the locality, including shrubs, herbs, roots, etc. These it gathers in a hurried manner above ground, and drags them to the mouth of its burrow. It has been observed to ascend a bush two or three feet, cut off a limb quickly, and retreat with it to its hole. [...] I have known it to take possession of a field seeded down to red clover, forming numerous burrows, and seeming delighted to feed upon this herbage." From "The Sewellel or Show'tl" by S. K. Lum (*The American Naturalist*, 1878, 12:10–13).