Species abundance and the distribution of specialization in host–parasite interaction networks

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Summary

1. Recent studies have evaluated the distribution of specialization in species interaction networks. Species abundance patterns have been hypothesized to determine observed topological patterns. We evaluate this hypothesis in the context of host–parasite interaction networks.

2. We used two independent series of data sets, one consisting of data for seven sites describing interactions between freshwater fish and their metazoan parasites and another consisting of data for 25 localities describing interactions between fleas and their mammalian hosts. We evaluated the influence of species abundance patterns on the distribution of specialization in these host–parasite interaction networks with the aid of null models.

3. In parallel with recent studies of plant–animal mutualistic networks, our analyses suggest that host–parasite interactions in these systems are highly asymmetric: specialist parasites tend to interact with hosts with high parasite richness, whereas hosts with low parasite richness tend to interact mainly with generalist parasites.

4. The observed distribution of specialization was predicted by a null model that assumed that species-specific probabilities of being assigned a link during the randomization process were roughly proportional to their relative abundance. Thus, abundant hosts tend to harbour richer parasite faunas, with a high proportion of rare specialists.

Key-words: abundance, asymmetric specialization, host–parasite interactions, network structure, null models.

Introduction

Degree of specialization is an important aspect of species interactions that can have profound ecological and evolutionary consequences (Brown 1984; Thompson 1994; Waser *et al*. 1996; Vázquez & Simberloff 2002). Although a particular species may interact with many other species in a community, not all interactions will be equally important; arguably, specialized interactions are more likely to be ecologically or evolutionarily

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relevant for interacting species than less specific interactions (Thompson 1994). For this reason, it is difficult to think of a discussion of species interactions that does not involve, under one of its many labels (specificity, mono/polyphagy, mono/polylecty, niche breadth), the idea of specialization.

Specialization in host–parasite interactions has usually been seen either from the perspective of the parasites or from that of the hosts. An apparent generalization of these studies is that the frequency distribution of numbers of host species exploited by a parasite species is highly right-skewed, with most parasite species exploiting one or a few host species (Gregory, Keymer & Harvey 1991; Poulin 1992); likewise, the distribution of interactions is also right-skewed

from the host perspective, with most host species harbouring few parasite species and only a few host species harbouring many parasites (Poulin 1995). A similar pattern has also been observed in food webs and in plant–animal mutualistic networks (Waser *et al.* 1996; Memmott, Martinez & Cohen 2000; Montoya & Solé 2002; Jordano, Bascompte & Olesen 2003; Vázquez & Aizen 2003), which suggests that a right-skewed distribution of links per species is a general feature of species interaction networks.

Albeit informative and interesting, considering specialization for hosts or parasites separately provides only a limited picture of the complex pattern of interaction and its potential dynamic consequences. Much insight can be gained by considering simultaneously the distribution of specialization between the two interacting groups. Such a perspective has led to important recent findings in the study of other ecological (Melián & Bascompte 2002; Bascompte *et al.* 2003; Vázquez & Aizen 2004) and nonecological (Pastor-Satorras, Vázquez & Vespignani 2001; Maslov & Sneppen 2002; Newman 2002, 2003) networks. In the particular case of ecological interaction networks, it has been shown that nodes with few links ('specialists') tend to associate with nodes with many links ('generalists'), leading to a nested pattern of species interactions in which a core of generalists interacts frequently and presumably strongly among themselves and many specialists interact asymmetrically with generalists (Melián & Bascompte 2002; Bascompte *et al.* 2003; Vázquez & Aizen 2004). One explanation for this apparently pervasive pattern is that the number of links per species is determined by the underlying interspecific abundance distribution, so that rare species tend to have fewer links than abundant species, which in turn results in rare specialists interacting mostly with abundant generalists (Vázquez & Aizen 2004, 2005). If true, this hypothesis means that topological patterns in species interaction networks can be predicted if the relative abundance of interacting species is known. To our knowledge, no study to date has evaluated this hypothesis.

The few previous studies that have attempted to analyse interaction patterns considering both the hosts' and the parasites' perspectives have found contradictory results. Poulin (1997) analysed the relationship between regional parasite richness in Canadian freshwater fishes and mean parasite specialization; he found that parasites of hosts harbouring richer parasite faunas tended to be more specialized than those of hosts with poorer parasite faunas. In contrast, Valtonen *et al.* (2001) found evidence for the opposite pattern in fishes of the north-eastern Baltic Sea and their metazoan parasites: hosts with poor parasite faunas tended to harbour more specialized parasite species than hosts with richer faunas. Although important for their pioneering approach, both studies have major limitations. Poulin's (1997) study was based on regional accounts of the number of parasite genera per host species, which may not provide a good picture of the patterns of interac-

tions among species in local communities. The study by Valtonen *et al.* (2001) suffered from the limitation that it was studying two sets of marine and freshwater host species coexisting in brackish waters in the Bothnian Bay, a result of the recent decrease in water salinity in this area; the very limited exchanges between the two sets of host species mean that the entire community represents a mixture of two separate interaction networks, and it is unclear how this mixture affected the observed patterns. In addition, Valtonen *et al.* used nestedness analysis to evaluate patterns of interaction, and the particular measure of nestedness used by them is problematic, both because it looks at nestedness only from the host perspective (i.e. whether parasite faunas of different host species exhibit a nested pattern), and because it assigns equal weight to any unexpected presence or absence of interactions (see Cutler 1991; Atmar & Patterson 1993).

Here we describe the distribution of specialization in host–parasite interaction networks from two series of data sets: the first one describes interactions between metazoan parasites and their fish hosts in seven freshwater lakes and rivers in Canada; the second one describes interactions between fleas and their mammalian hosts in 25 sites in Eurasia and North America. We used null model analyses to evaluate the hypothesis that the distribution of specialization in these host–parasite interaction networks is the result of the underlying distribution of abundance among species.

Materials and methods

DATA SETS

Canadian freshwater fish and their metazoan parasites

Data on host use by parasites were obtained from seven Canadian freshwater systems, either large lakes or rivers, in which most fish species have been surveyed for parasites (Table 1). Only fish species for which at least five individuals have been examined per locality were included, because we judged that estimates of parasite infection levels were inaccurate for smaller samples. All species of internal and external metazoan parasites were included in the analyses. These include the following groups: nematodes, acanthocephalans, cestodes, trematodes, monogeneans, leeches, copepods and branchiurans. When a species of internal worm occurred among sampled fish as both larval and adult forms, the two forms were treated as functionally distinct species; this convention is justified because larval and adult worms often have different modes of transmission, infect different fish species, and different organs within fish. Species composition of both the host and the parasite faunas of the different lakes and rivers overlapped to some extent, because some species have continental-wide distributions; still, they can be viewed as independent systems, because patterns of host use will partly depend on local conditions (e.g. local

Table 1. Data sets on fish and their metazoan parasites from freshwater Canadian systems included in the study. Data are available through the Interaction Web Database (http://www.nceas.ucsb.edu/interactionweb)

Location	No. of species of		Source
	Hosts	Parasites	
Aishihik Lake, Yukon Territory	7	29	Arthur, Margolis & Arai (1976)
Cold Lake, Alberta	10	40	Leong & Holmes (1981)
Lake Huron and Manitoulin Island, Ontario	33	97	Bangham (1955)
McGregor River, British Columbia	14	51	Arai & Mudry (1983)
Parsnip River, British Columbia	17	53	Arai & Mudry (1983)
Smallwood Reservoir, Labrador	6	25	Chinniah & Threlfall (1978)
Lake of the Woods, Ontario	31	144	Dechtiar (1972)

composition of host and parasite species and the characteristics of the abiotic environment). Species with no interactions were excluded from the analyses.

Following Combes (2001), we define parasite infrapopulation as the set of individuals of parasite species *i* coexisting on an individual of host species *j*, and xenopopulation as the set of individuals of a parasite species *i* inhabiting a population of host species *j*. The number of infrapopulations was estimated as the number of sampled host individuals of species *j* examined in a particular study times the prevalence of parasite species *i* on that particular host. The number of xenopopulations in host species *j* was estimated as the number of parasite species infecting it, whereas the number of xenopopulations of parasite species *i* is defined as the number of host species it infects. Because it represents the occurrence of an interspecific interaction, the concept of xenopopulation is equivalent to that of a 'link' used in the food web or plant–animal mutualistic literature.

Host sample size was used as a surrogate of host abundance. However, for the Canadian fish data, host sample size provides only a rough approximation of species abundance, because fish were collected for a parasite survey and not specifically to measure their relative abundance. Thus, in this case host sample size is likely to underestimate the abundance of abundant species. In addition to data on number of sampled hosts, one data set (Cold Lake) also included independent information on host abundance, which allowed us to examine more directly the influence of the distribution of abundance among host species on the observed patterns of interaction. Parasite abundance was in turn estimated as the number of infrapopulations observed for each parasite species on any host species.

Fleas and their mammalian hosts

Data on host use by parasitic fleas were obtained from 25 field surveys carried out in distinct geographical regions (Table 2). Only mammalian species for which at least 10 individuals have been examined per locality were included, because estimates of parasite infection level are inaccurate for smaller samples. Single findings of a flea species on a host species or in a region were considered accidental and were not included in the

analyses. As with the Canadian fish–metazoan parasite data, the species composition of both mammals and fleas of the different regions overlapped to some extent, because several of the species have broad geographical distributions; still, they can be viewed as independent systems, as patterns of host use will, to some extent, depend on local conditions.

Small mammals (orders Insectivora, Rodentia and Lagomorpha) were obtained mainly by trapping, and thus the numbers of each species caught and examined for fleas provide rough estimates of the relative abundance of most host species. The total numbers of fleas of each species found on each host species were available for all surveys. From these data we could thus obtain flea abundance (the mean number of fleas of a given species per host individual in a given host species). Thus, this information allowed us to evaluate directly the effect of abundance on the structure of the interaction network.

It is important to mention that there are a few mammalian host species for which sample size data may not be an accurate estimate of their relative abundance. *Marmota* spp. were a target for the Anti-Plague service in Central Asia and thus sampling effort on this species was disproportionally high compared with its abundance. On the other hand, *Talpa europea* (which is trapped using specific traps with a unique design), *Sciurus vulgaris* and *Eutamias* spp. (which are rather hunted than trapped) and *Pygeretmus pumilio* (folivorous species rarely entering standard traps; Shenbrot *et al.* 1995) seem to be undersampled. Nevertheless, these animals represent only a minor part of the data set and are absent from most of our study regions.

QUANTIFICATION OF INTERACTION SPECIALIZATION

For the analyses, each host–parasite interaction network was represented as a binary interaction matrix, in which rows represent host species and columns represent parasite species. In these matrices, a cell *ij* containing a '1' indicates an interaction between parasite species *i* and host species *j* (i.e. a xenopopulation), while a cell with a '0' indicates no interaction. The number of 'links' per species, that is, total number of species with

Table 2. Data on small mammals and fleas from the 25 regions used in the analyses. Numbers in parentheses represent the total numbers of sampled individuals. Data are available from B. R. Krasnov upon request

| Location | No. of species of | | Source |
	Hosts	Fleas	
Adzharia, southern Caucasus	12 (8391)	20 (1756)	Alania *et al*. (1964)
Akmolinsk region, northern Kazakhstan	8 (264)	19 (1789)	Mikulin (1959b)
Altai mountains	19 (1473)	9 (1949)	Sapegina, Lukyanova & Fomin (1981)
California	8 (1543)	17 (2254)	Davis *et al*. (2002)
Central Yakutia	6 (535)	17 (770)	Elshanskaya & Popov (1972)
Dzhungarskyi Alatau, Kazakhstan	15 (5230)	22 (5224)	Burdelova (1996)
East Balkhash desert, Kazakhstan	11 (473)	35 (7272)	Mikulin (1959a)
Idaho	12 (3898)	28 (10 709)	Allred (1968)
Kabarda, northern Caucasus	9 (1642)	21 (1755)	Syrvacheva (1964)
Khabarovsk region, southern Russian Far East	8 (6607)	21 (5226)	Koshkin (1966)
Kustanai region, north-western Kazakhstan	18 (159)	14 (735)	Reshetnikova (1959)
Mongolia	5 (1741)	20 (18 593)	Vasiliev (1966)
Moyynkum desert, Kazakhstan	12 (45 443)	31 (260 720)	Popova (1967)
Negev desert, Israel	13 (1230)	11 (4882)	Krasnov *et al*. (1997) and unpublished data
North Asian Far East	14 (1667)	16 (1405)	Yudin, Krivosheev & Belyaev (1976)
North Kyrgyzstan	14 (4750)	31 (6858)	Shwartz, Berendiaeva & Grebenyuk (1958)
North New Mexico	20 (8706)	31 (23 693)	Morlan (1955)
Novosibirsk region, southern Siberia	20 (1912)	28 (4311)	Violovich (1969)
Pavlodar region, eastern Kazakhstan	7 (78)	11 (317)	Sineltschikov (1956)
Selenga region, central Siberia	7 (978)	11 (990)	Pauller, Elshanskaya & Shvetsova (1966)
Slovakia	13 (9932)	22 (20 884)	Stanko *et al*. (2002)
Tarbagatai region, eastern Kazakhstan	12 (316)	30 (1525)	Mikulin (1958)
Turkmenistan	14 (235 968)	36 (908 815)	Zagniborodova (1960) and unpublished data
Tuva	13 (3145)	28 (28 758)	Letov *et al*. (1966)
Volga-Kama region	20 (33 380)	31 (33 770)	Nazarova (1981)

which a given species was observed interacting (*s*) was obtained from the binary interaction matrix as the sum of the rows or columns for hosts and parasites, respectively; thus, low *s* means high specialization, whereas large *s* means generalization. Average *s* of interaction partners (*p*) was used as a measure of degree of specialization of all species interacting with a given species; thus, a species with low *p* interacts with species that are relatively specialized, whereas a species with high *p* interacts with generalists (see Vázquez & Simberloff 2002; Vázquez & Aizen 2004).

NULL MODELS

We used simple computer algorithms written in Matlab (MathWorks 1999) to randomize host–parasite interactions in the data sets; these algorithms are based on those used in previous analyses of plant–pollinator interactions (Vázquez & Aizen 2003, 2004). Briefly, the number of filled cells originally observed in the interaction matrix was distributed among species of hosts and parasites using Monte Carlo simulations, with the sole requirement that each species had at least one interaction (i.e. the criterion for inclusion of host and parasite species in the data sets). Connectance (i.e. the number of filled cells over the total number of cells in the matrix) in the randomized data sets was the same as in the original data sets.

We used two null models. In null model 1, interactions were randomly distributed among pairs of host

and parasite species; all host or parasite species had the same probability of interacting, thus assuming neutrality at the species level (i.e. all species are equal, regardless of their characteristics). This model thus assumed that species of hosts and parasites interact randomly, regardless of their identity or relative abundance. This model can be considered a benchmark for comparison, in the sense that it allows comparison of an observed pattern with a pattern lacking nonrandom structure. Conversely, in null model 2 interactions were assigned proportionally to a species' relative abundance, so that species with greater relative abundance had a higher probability of being assigned an interaction than rarely interacting species. Model 2 thus allowed us to evaluate the hypothesis that the distribution of specialization in host–parasite interaction networks is an epiphenomenon of the underlying species abundance distribution. Because data on host sample size for the Canadian fish data sets are only a rough estimate of host abundance (see *Data sets: Canadian freshwater fish and their metazoan parasites*), we also ran null model 2 using the independent estimates of host abundance available for the Cold Lake data set.

To study the distribution of specialization among interacting hosts and parasites, we overlapped the *s*–*p*-values from each of 1000 randomized interaction matrices, and used the 99% least extreme values of *p* for each category of *s* as boundaries of the distribution generated by the null model (the 'null space'). We then compared the *s*–*p*-values obtained for real networks
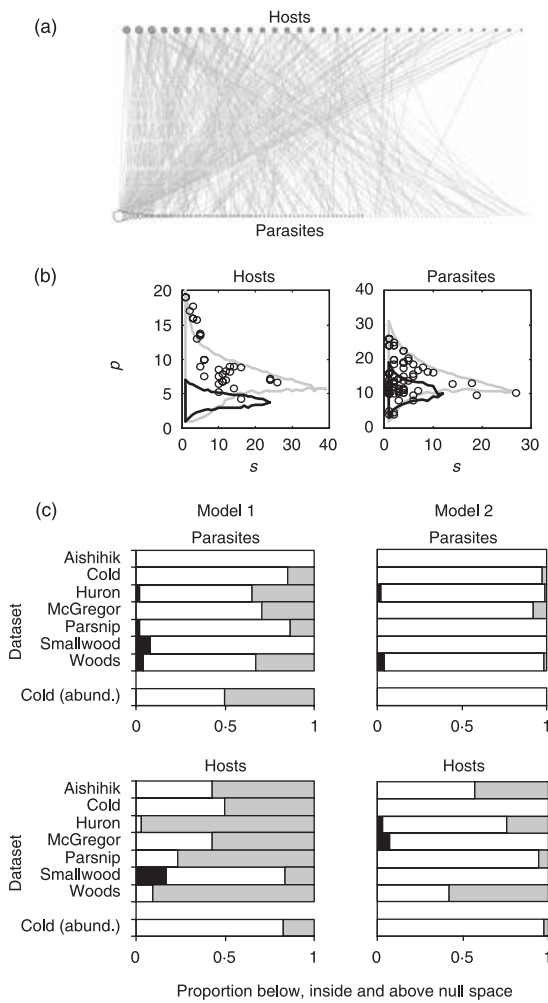
Fig. 1. Distribution of specialization in interaction networks of Canadian fish and their metazoan parasites. (a) An example of a network for Lake Huron. White circles (bottom) are parasite species; grey circles (top) are host species (circle diameter proportional to species abundance; species arranged in decreasing order of importance). Lines represent interspecific interactions ('links') between parasite and host species. (b) Degree of specialization (s) vs. average specialization of interaction partners (p) for Lake Huron. Circles: observed s–p-values; black lines: null space for model 1; grey lines: null space for model 2. (c) Summary of results of null model analyses for all data sets. Horizontal bars are proportion of host (upper row) and parasite (lower row) species below (black), inside (white) and above or to the right of (grey) null space of models 1 and 2. Results of model 2 for Cold Lake when probability of hosts of acquiring interspecific interactions during randomization was proportional to their abundance are given at the bottom of each chart.

with the null space. Species with observed s–p combinations falling above or to the right of the null space are regarded as more asymmetrically specialized than expected from the null model, either because they are specialists interacting with extreme generalists or because they are extreme generalists themselves (which implies that they interact with at least some specialists); conversely, species falling under the lower limit of the null space (i.e. in the lower-left corner of the s–p graph) would be more symmetrically specialized

than expected from the null model. For each data set, we counted the number of species below, within, and above the null space.

Results

A comparison of the observed distribution of s- and p-values calculated for each species with that predicted by null model 1 (Figs 1 and 2) suggests that host–parasite interactions tend to be asymmetrically specialized: a substantial proportion of species are above or to the right of the null space of this null model, away from the lower-left corner of symmetric specialization. Thus, most parasite species are specialists interacting with generalist hosts (i.e. hosts that interact with several to many parasite species), or are generalists themselves; this pattern of interaction results in most species being away from the lower-left corner of the graph, which indicates that most species are not reciprocally specialized on specialists. There are exceptions to this pattern (some parasite species do fall at the lower-left corner of the graph, below the null space of null models; Figs 1 and 2), but it is true for a majority of species. Similarly, most host species are either parasitized by few generalist parasites or are themselves 'generalists' (i.e. they have rich parasite faunas).

Null model 2 (which assumes abundant species have a higher probability of interspecific interactions than rarer species) explains the observed distribution of specialization better than null model 1 (which assumes that interactions occur randomly among species; Figs 1 and 2). Thus, the occurrence of asymmetric specialization of host–parasite interactions observed in the data sets is partly explained by the fact that abundant parasite and host species tend to interact with more species than rare species. The good fit of this model is a direct result of the positive correlation between species abundance and their number of interspecific interactions ('links'), so that abundant species tend to be more generalized than rare species (Appendix I).

As we mentioned above, an important caveat of our analysis for the Canadian fish data is that host sample sizes are only a rough surrogate of host abundance (see *Data sets: Canadian freshwater fish and their metazoan parasites*). However, for Cold Lake (the only data set for which we had independent estimates of host abundance), host abundance and sample size are indeed positively correlated, so that abundant hosts tend to be sampled more frequently than rare hosts (Pearson's correlation coefficient for log-transformed variables: $r = 0.84$). This correlation implies that the sampling artefact resulting from the researcher's sampling bias (sampling some host species more intensely than others biases estimates of parasite species richness) can also occur as an ecological process if parasites 'sample' abundant hosts more frequently than rare hosts. Following Guégan & Kennedy (1996), we use path analysis to propose a causal model relating host abundance, host sample size and parasite richness
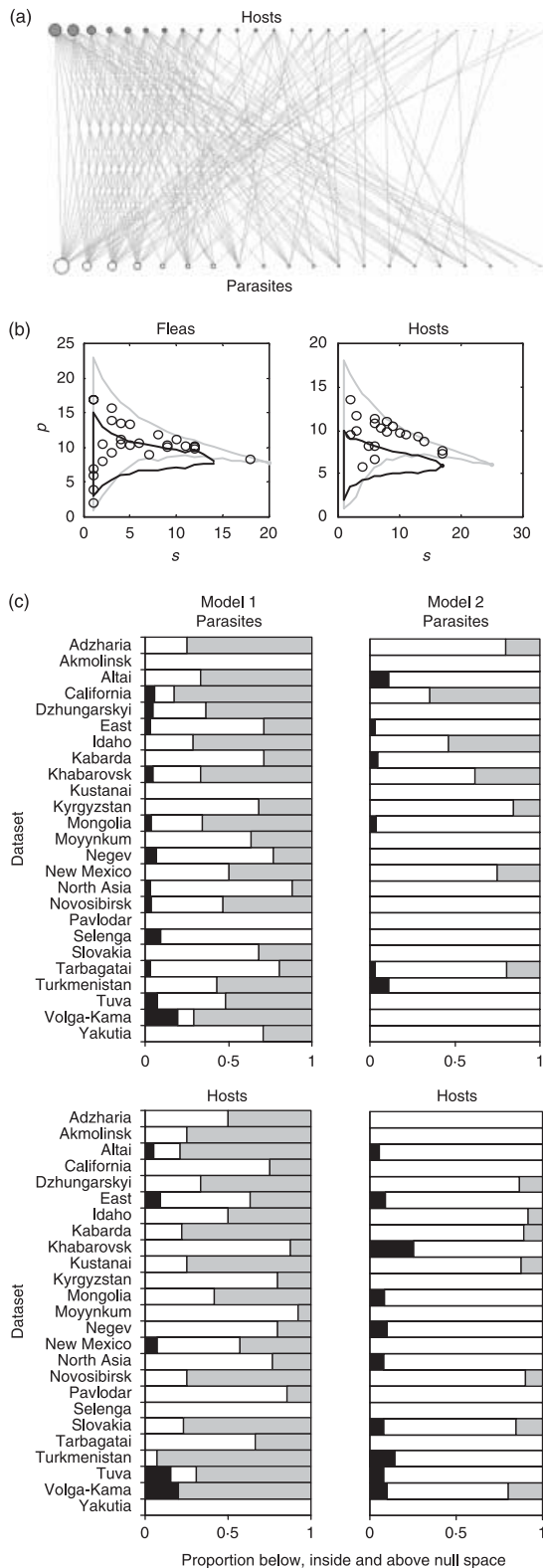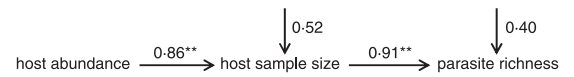
Fig. 3. Path analysis relating logarithms of host abundance, sample size and parasite richness for Cold Lake (fish–metazoan interactions). Horizontal arrows are causal effects of one variable on another; vertical arrows indicate unexplained variability of endogenous (dependent) variables. Numbers next to arrows are magnitudes of path coefficients (statistical significance: **$P < 0.01$).

(Fig. 3). As indicated by path coefficients (which typically vary between 1 and −1, these extremes representing strong positive and negative effects, respectively; Mitchell 2001), there are strong, positive effects of abundance on host sample size and of host sample size on parasite richness. With path analysis it is also possible to calculate the indirect effect of host abundance on host–parasite richness as the product of the path coefficients linking abundance with sample size and sample size with parasite richness (Mitchell 2001): $0.86 \times 0.91 = 0.78$. This means that even when accounting for sampling effort, the effect of abundance on host–parasite richness is substantially high. Furthermore, incorporating host abundance in null model 2 for the Cold Lake data set, so that the probability of hosts of acquiring interspecific interactions during the randomization process was proportional to their abundance, yields results similar to those obtained when host sample size was used instead as a surrogate of abundance (Fig. 1c). This result further supports the conclusion that abundant host species tend to harbour a higher number of parasite species than rare host species, and that many of the parasites of abundant host species are themselves specialists.

Discussion

Our results suggest that patterns of interaction among metazoan parasites and their fish hosts and among fleas and their mammalian hosts interacting at local communities are highly asymmetric: specialist parasites tend to parasitize host species with high parasite richness, whereas host species with low parasite richness tend to be parasitized by generalists. These findings parallel previous results in plant–animal mutualistic networks (Bascompte *et al*. 2003; Vázquez & Aizen 2004). Taken together, this evidence suggests asymmetric specialization could be a general feature of species interactions. Furthermore, our results are consistent with the hypothesis that this pattern of interaction is a consequence of the fact that abundant species tend to have more links than rare species. Thus, the observed structure in these interaction networks could be an epiphenomenon of the underlying species abundance distribution.

It is important at this point to digress briefly to consider causality. Showing that a model fits the data well is not a demonstration that the mechanism assumed by

Fig. 2. Distribution of specialization in interaction networks of small mammals and their parasitic fleas. (a) An example of a network for Novisibirsk. (b) Degree of specialization (*s*) vs. average specialization of interaction partners (*p*) for Novisibirsk. (c) Summary of results of null model analyses for all data sets. Conventions as in Fig. 1.

the model actually operates, because a given pattern can usually result from more than one model (McGill 2003). In this paper we have assumed that the direction of causality is abundance → specialization; however, the opposite direction is also possible, i.e. specialization → abundance. The first causal scheme allows abundance to be determined by any factor or combination of factors, and makes no assumption about the intrinsic degree of specialization of species: they simply interact with other species as they encounter them, which means that they will encounter abundant species more often than rare ones. This is what our null model assumes, and the results indicate that it is a reasonable model. Conversely, the second causal scheme assumes that species have an intrinsic degree of specialization, and that abundance is determined by the degree of specialization on this particular type of interaction, regardless of other components of the species' niche. Given these alternatives and the limitations of our approach, all we can say at this point is that our results strongly suggest that the distribution of abundance of hosts and parasites is linked to the distribution of specialization in host–parasite interactions, and that we favour the former causal scheme as a simpler explanation of the observed patterns.

Another important question is whether patterns exhibited by these host–parasite networks could be the result of sampling artefacts. Previous studies have suggested that the observed distribution of interspecific interactions among species could be partly a result of sampling artefacts (Guégan & Kennedy 1996; Goldwasser & Roughgarden 1997; Poulin 1998; Martinez *et al*. 1999; Combes 2001; Vázquez & Aizen 2003, 2004, 2005). In particular, the positive correlation between host sample size and parasite richness suggests that the detection probability of parasite species is higher in host species with higher sample sizes (see also Poulin 1998; Combes 2001). However, because in our data sets abundant hosts tend to be sampled more often, our results suggest that the same kind of 'bias' could be occurring in nature, in the sense that parasites 'sample' abundant hosts more often than rare ones. Furthermore, our path analysis for the Cold Lake data set suggests that even when the sampling effect is considered separately from host abundance the indirect effect of host abundance on parasite richness is substantially high. Thus, we conclude that our results are consistent with the hypothesis that observed patterns of interaction in host–parasite interaction networks partly result from the distribution of abundance among species.

Provided that the observed patterns are real and not solely the result of sampling artefacts, our finding of asymmetric specialization in host–parasite interactions opens intriguing possibilities about the coevolution of host–parasite interactions. Because specialist parasites rely on only one or a few host species, hosts are likely to represent strong selective agents for the parasites; and because generalist hosts are parasitized by many para-site species, the selective importance of each parasite species should be relatively small. In contrast, selection coming from each of the many host species of generalist parasites is likely to be weak; however, because many of these hosts are likely to be 'specialists' (i.e. parasitized by few species), the selective pressure of each of these parasite species on the host is likely to be relatively high. Thus, asymmetric specialization could also lead to selective asymmetry (Dawkins & Krebs 1979), whereby specialists are strongly selected by generalists but not vice versa.

Although our network approach provides new insights about the ecology of host–parasite interactions, it is important to acknowledge its limitations. We have used binary networks for our analyses, in which interactions between pairs of species are represented as either present or absent. This approach overlooks much of the complexity of host–parasite interactions. Arguably, some interactions are more important than others, for example in terms of prevalence and intensity of infection, or in terms of impact of the interaction to the host. Future studies should attempt to go beyond these simplifications and evaluate whether incorporating some of the complexities of real interactions change the conclusions reached in the present analysis.

Acknowledgements

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Appendix I

Correlations between the logarithms of species abundance and the number of links. The number of host species (*n*), Pearson's correlation coefficient (*r*) and its associated probability value (*P*) are given for each correlation. *P*-values significant at α = 0·05 are highlighted in bold.

Interaction type	Data set	Hosts			Parasites		
		n	*r*	*P*	*n*	*r*	*P*
Fish–parasite	Aishihik	7	0·83	**0·0210**	29	0·74	**< 0·0001**
	Cold (host sample size)	10	0·91	**0·0002**	40	0·61	**< 0·0001**
	Cold (host abundance)	9	0·75	**0·0209**			
	Huron	33	0·75	**< 0·0001**	97	0·70	**< 0·0001**
	McGregor	14	0·71	**0·0047**	47	0·73	**< 0·0001**
	Parsnip	17	0·76	**0·0004**	49	0·58	**< 0·0001**
	Smallwood	6	0·39	0·4434	25	0·35	0·0912
	Woods	31	0·75	**< 0·0001**	144	0·76	**< 0·0001**
Mammal–flea	Adzharia	12	0·75	**0·0046**	20	0·89	**< 0·0001**
	Akmolinsk	8	0·68	0·0660	19	0·83	**< 0·0001**
	Altai	19	0·61	**0·0056**	9	0·92	**0·0005**
	California	8	0·73	**0·0405**	17	0·13	0·6089
	Dzhungarskyi	15	0·79	**0·0004**	22	0·81	**< 0·0001**
	East Balkhash	11	0·69	**0·0189**	35	0·37	**0·0280**
	Idaho	12	0·77	**0·0037**	28	0·99	**< 0·0001**
	Kabarda	9	0·64	0·0657	21	0·83	**< 0·0001**
	Khabarovsk	8	0·59	0·1232	21	0·12	0·5983
	Kustanai	8	0·54	0·1688	14	0·90	**< 0·0001**
	Kyrgyzstan	5	0·85	0·0700	19	0·67	**0·0017**
	Mongolia	12	0·89	**0·0001**	29	0·91	**< 0·0001**
	Moyynkum	13	0·47	0·1091	11	0·75	**0·0080**
	Negev	20	0·76	**< 0·0001**	30	0·19	0·3176
	New Mexico	14	0·63	**0·0168**	16	0·53	**0·0351**
	North Asia	13	0·51	0·0761	34	0·39	**0·0227**
	Novosibirsk	20	0·83	**< 0·0001**	28	0·83	**< 0·0001**
	Pavlodar	7	0·72	0·0672	11	0·57	0·0689
	Selenga	7	0·64	0·1247	11	0·76	**0·0071**
	Slovakia	13	0·68	**0·0098**	22	0·85	**< 0·0001**
	Tarbagatai	12	0·35	0·2597	31	0·35	0·0532
	Turkmenistan	14	0·83	**0·0002**	37	0·92	**< 0·0001**
	Tuva	13	0·42	0·1569	27	0·54	**0·0036**
	Volga-Kama	20	0·73	**0·0003**	31	0·71	**< 0·0001**
	Yakutia	6	0·80	0·0557	17	0·79	**0·0001**