

Covariance in species diversity and facilitation among non-interactive parasite taxa: all against the host

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SUMMARY

Different parasite taxa exploit different host resources and are often unlikely to interact directly. It is unclear, however, whether the diversity of any given parasite taxon is indirectly influenced by that of other parasite taxa on the same host. Some components of host immune defences may operate simultaneously against all kinds of parasites, whereas investment by the host in specific defences against one type of parasite may come at the expense of defence against other parasites. We investigated the relationships between the species diversity of 4 higher taxa of ectoparasites (fleas, sucking lice, mesostigmatid mites, and ixodid ticks), and between the species richness of ectoparasites and endoparasitic helminths, across different species of rodent hosts. Our analyses used 2 measures of species diversity, species richness and taxonomic distinctness, and controlled for the potentially confounding effects of sampling effort and phylogenetic relationships among host species. We found positive pairwise correlations between the species richness of fleas, mites and ticks; however, there was no association between species richness of any of these 3 groups and that of lice. We also found a strong positive relationship between the taxonomic distinctness of ecto- and endoparasite assemblages across host species. These results suggest the existence of a process of apparent facilitation among unrelated taxa in the organization of parasite communities. We propose explanations based on host immune responses, involving acquired cross-resistance to infection and inter-specific variation in immunocompetence among hosts, to account for these patterns.

Key words: ectoparasites, endoparasites, rodents, species diversity, taxonomic distinctness.

INTRODUCTION

Interactions between species within a community include a variety of direct and indirect relations with species exerting positive or negative effects on each other (Martin and Martin, 2001). Furthermore, facilitation and competition may operate among the same species either simultaneously or with the strength of each process varying in time or space (Callaway and King, 1996; Callaway and Walker, 1997; Levine, 1999), with consequences on community organization. Recently, the many advantages of using parasites to search for rules that govern community organization have become clear. These advantages include the ease of obtaining replicated samples, the similar trophic and spatial niche of different parasite species, and the simultaneous presence on a host of several closely related parasites.

As a result, the number of studies of community organization in parasitic organisms has increased considerably (see Combes, 2001).

Depending on the presence or absence of inter-specific interactions, both isolationist and interactive parasite communities can be distinguished (Holmes and Price, 1986; Bush *et al.* 1997). It is commonly accepted that interactive communities are those that comprise parasite species belonging to the same guild, e.g. sharing the same trophic level, whereas parasite species in isolationist communities, though sharing a host, do not exploit the same resources (Poulin, 1998). Nevertheless, interactions, although rather indirect than direct, between parasite species belonging to different guilds are also possible. These interactions could be mediated via host defence mechanisms. Indeed, in contrast to the habitats of free-living organisms, the habitat of parasites (host) defends itself from exploiters (parasites) on ecological time-scales. For example, suppression of a host defence system by one parasite species could lead to greater opportunities for another parasite species to survive and, thus, to facilitation among parasite

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species. Alternatively, the triggering of host defence systems by one parasite species could lead to concomitant fitness decrease in another parasite species. An example of the latter is provided by the phenomenon of cross-resistance of a host against closely-related parasites. For instance, cross-resistance to closely-related species of parasites has been repeatedly reported mainly for haematophagous arthropods (McTier, George and Bennet, 1981; Njau and Nyiando, 1987; Khokhlova *et al.* 2004*a, b*) but also for protozoans (Leemans *et al.* 1999) and gastrointestinal helminths (Smith and Archibald, 1969). However, haematophagy evolved independently in different taxa of arthropods and, thus, it is commonly accepted that chemical mediators occurring in their saliva are different (Ribeiro, 1987, 1996; Jones, 1996). Therefore, cross-resistance is expected against closely-related species but not against parasites belonging to different taxa (Mans, Louw and Neitz, 2002).

Activation of an immune response and even maintenance of a competent immune system is an energetically demanding protective process that requires trade-off decisions among competing energy demands for growth, reproduction, thermoregulation, work, and immunity (Sheldon and Verhulst, 1996). In other words, the trade-offs occur between defence against parasites and other concurrent needs of the organism (Sheldon and Verhulst, 1996). Empirical evidence suggests that such costs can be relatively high (e.g., Moret and Schmid-Hempel, 2000; Bonneaud *et al.* 2003). Development of immune responses and investment into immune defences should thus depend on the pattern of parasite pressure (see Combes, 2001 and references therein). For example, it could depend on the frequency and probability of parasite attacks (Martin *et al.* 2001; Tella, Scheuerlein and Ricklefs, 2002). Consequently, if the probability of attacks by parasites of one taxon is higher than that by parasites of other taxa, a host should develop those immune responses that are most effective against parasites belonging to a taxon whose attacks are most probable (Khokhlova *et al.* 2004*b*). Given (a) the likelihood of cross-resistance against parasites belonging to the same taxon, and (b) the likelihood of a trade-off between mounting multiple immune responses and investment in other functions, negative relationships between the species diversity of different parasite taxa within the same host individual or population would be expected. A host that effectively withstands the attacks of, for example, flea parasites and is able to eliminate some or even most of them could thus be more prone to the attacks by, for example, various mite or tick species. Furthermore, these negative relationships could be expected in relation to both different taxa of parasites that share spatial and trophic level (e.g., haematophagous ectoparasites) and different taxa of parasites that belong to different guilds (e.g., ectoparasitic arthropods and gastrointestinal helminths). This is

because the defence properties of a host against various parasites are based on the same morphological, biochemical and energetic resources (immune system).

On the other hand, also because of the common basis of defence resources, suppression of host defence system due to parasitism by one parasite taxon could facilitate parasitism by other parasite taxa, not necessarily belonging to the same guild. In this case, the species diversity of parasites of different taxa exploiting the same host individual or population would be positively correlated.

However, in spite of extensive investigations of community organization of parasites over the last 2 decades, most studies only considered interactions (direct or mediated via host) within the same parasite taxon or spatial and/or trophic guild (see Poulin, 1998; Combes, 2001 and references therein). One of the reasons for this is a scarcity of data on parasites belonging to different taxa and/or guilds collected from the same hosts in the same locality at the same time, especially for terrestrial hosts. Studies that aim to investigate the composition of communities of both ecto- and endoparasites in terrestrial hosts are especially rare.

Here we studied species diversity of 4 higher taxa of haematophagous ectoparasites [fleas (Siphonaptera), sucking lice (Anoplura), mesostigmatid mites (Mesostigmata) and ixodid ticks (Ixodidae)] and 4 higher taxa of gastrointestinal helminths [flukes (Trematoda), tapeworms (Cestoda), roundworms (Nematoda) and thorny-headed worms (Acanthocephala)] in a variety of rodent hosts sampled in different localities of the world (Europe, Asia, North and South America and Africa). The aim of this study was to compare species diversity (a) between parasite taxa sharing space and resources (different taxa of haematophagous parasites) and (b) between parasite taxa that do not share space and resources (ectoparasites and endoparasites) among different host species. We asked (a) whether there are relationships between the species diversity of different parasite taxa within the same host; and (b) whether these relationships (if any) are negative or positive. The occurrence of relationships would advocate interactivity of the parasite community even if it is composed of parasites from different spatial and resource guilds. Negative relationships between the species diversities of any 2 parasite taxa would suggest a trade-off between host defence mechanisms aimed at different parasites, whereas positive relationships would suggest host-mediated facilitation among different parasites.

In addition, rather than taking the mere number of parasite species as a measure of species diversity, we also applied a measure that takes into account the taxonomic or phylogenetic affinities of the various parasite species (Clarke and Warwick, 1998, 1999; Poulin and Mouillot, 2004). This measure places the

emphasis on the taxonomic distance between parasite species exploiting a host rather than on their number.

MATERIALS AND METHODS

Data set

Data on ecto- and endoparasite species richness were obtained from published studies that simultaneously sampled either more than one of ectoparasite taxa (fleas, lice, mesostigmatid mites and ticks) or at least one ectoparasite taxon and at least one taxon of gastrointestinal helminths and reported data on the number and identity of parasite species found on a particular rodent species in a particular location (see Appendix, Table A1 and Table A2). We used only those sources where sampling effort (the number of examined hosts) was reported. In total, we used data on 80 rodent species for the analyses concerning ectoparasite taxa and 20 rodent species for the analysis concerning ecto- versus endoparasites.

Estimates of parasite species richness may be biased if some hosts are studied more intensively than others (Morand and Poulin, 1998). Consequently, unequal study effort among host species may result in confounding variation in estimates of parasite species richness. To ensure that variation in sampling effort did not bias estimates of species richness, we regressed the number of parasite species found against the number of hosts examined. Parasite richness appeared to be strongly affected by sampling effort ($r^2=0.17-0.27$, $F=14.1-29.9$, $N=20-80$; $P<0.001$ for all). Each value of parasite richness was then substituted by its residual deviation from a linear regression of the number of parasite species found against the number of hosts examined in the ln-ln space. This provided a measure of parasite richness that is independent of sampling effort.

Measures of parasite species diversity

We used 2 measures of parasite species diversity (a) the number of parasite species found on a host species, or species richness, corrected for sampling effort (residuals of the linear regression against number of hosts examined) and (b) average taxonomic distinctness (Δ^+) of the parasite species present. When these parasite species are placed within a taxonomic hierarchy, the average taxonomic distinctness is the mean number of steps up the hierarchy that must be taken to reach a taxon common to 2 parasite species, computed across all possible pairs of parasite species (Clarke and Warwick, 1998, 1999; Warwick and Clarke, 2001; Poulin and Mouillot, 2004). The greater the taxonomic distinctness between parasite species, the higher the number of steps needed, and the higher the value of the index Δ^+ (see details in Poulin and Mouillot, 2004). All parasite species included here were fitted into a taxonomic structure with a different number of hierarchical levels above

species, namely 8 for fleas (subgenus or species group, genus, tribe, subfamily, family, superfamily, infraorder, and order), 4 for lice (genus, family, suborder and order), 5 for mites (genus, family, superfamily, cohort and suborder), 4 for ticks (subgenus, genus, subfamily and family) and 7 for gastrointestinal helminths (genus, family, order, subclass, class, phylum and subkingdom). The sources for taxonomic classification were Smit (1982) and Medvedev (1998) for fleas, Durden and Musser (1994) for sucking lice, Bregetova (1956), Halliday (1998) and Salmane (2001) for mesostigmatid mites, Camicas *et al.* (1998) and Horak, Camicas & Keirans (2002) for ticks, and Dailey (1996) for helminths. When ectoparasites of different taxa were considered together (for the analysis of species diversity between ectoparasitic and endoparasitic assemblages), they were fitted into a taxonomic structure with 12 hierarchical levels above species (subgenus or species group, genus, tribe, subfamily, family, superfamily, cohort, infraorder or suborder, order, class and phylum). The maximum value that the index Δ^+ can take is thus 4–12 (when all parasite species belong to different suborders/subfamilies-classes, respectively), and its lowest value is 1 (when all parasite species belong to the same subgenus or species group). However, since the index cannot be computed for hosts exploited by a single parasite species, we assigned a Δ^+ value of 0 to these host species, to reflect their extremely species-poor parasite assemblages. To calculate Δ^+ , DM and RP have developed a computer program using Borland C++ Builder 6.0 (available at <http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2>). To compare taxonomic distinctness among different parasite taxa we scaled Δ^+ values to range between 1 and 100, regardless of the number of taxonomic levels. Instead of giving each step up the taxonomic tree a length value of 1 unit, we gave it a length of $100/n$, where n was the maximum number of steps or taxonomic levels.

Across host species, the number of ectoparasite species of a particular ectoparasite taxon exploiting a host species was significantly positively correlated with Δ^+ for this taxon (Pearson product-moment correlations, $r=0.68-0.88$, $N=38-74$; respectively, $P<0.05$ for all), indicating that this measure is influenced by the number of species in a host's parasite assemblage. However, Δ^+ values for the assemblage of combined ectoparasite taxa or intestinal helminths were not affected by the number of species in an assemblage ($r=-0.01$ and $r=0.39$, respectively; $N=20$, $P>0.05$ for both). Therefore, in the subsequent analyses Δ^+ was corrected for the parasite species richness in an assemblage when necessary.

Data analyses

To examine if the species diversity of an assemblage of a particular parasite taxon within a host species is

Table 1. Pearson's correlation coefficients (r) for all pairwise associations of species richness (SR) and taxonomic distinctness ($\Delta+$) between assemblages of four higher ectoparasite taxa found on the same host species

(Both parameters were controlled for confounding variables (sampling effort in the case of SR, and number of species in the case of $\Delta+$). In parentheses: value of r after removal of 11 host species for which fewer than 10 individuals were examined. * $P < 0.01$.)

Taxon 1	Taxon 2	SR	$\Delta+$
Fleas	Lice	0.08 (0.08)	-0.27 (-0.27)
	Mesostigmatid mites	0.31* (0.32*)	0.10 (0.17)
	Ticks	0.47* (0.48*)	0.07 (0.10)
Lice	Mesostigmatid mites	-0.03 (-0.03)	-0.21 (-0.22)
	Ticks	0.10 (0.10)	0.06 (0.06)
Mesostigmatid mites	Ticks	0.37* (0.36*)	0.18 (0.13)

associated with that of another parasite taxon, we correlated species richness (corrected for sampling effort) and taxonomic distinctness (corrected for the species richness of a parasite assemblage if necessary) between each pair of ectoparasite taxa as well as between the entire ectoparasite assemblage and the entire assemblage of gastrointestinal helminths using Pearson's product-moment correlations. Because we examined the correlations of the same ectoparasite taxa in different combinations, we avoided an inflated Type I error by performing Bonferroni adjustments of alpha. Significance was only recorded at the adjusted level.

Treating host species as statistically independent data points in a comparative study may be invalid as it can introduce bias in the analysis (Harvey and Pagel, 1991). To control for the effects of phylogeny, we used the method of independent contrasts (Felsenstein, 1985). We used a phylogeny of rodents derived from various sources (see Krasnov *et al.* 2004). To compute independent contrasts, we used the PDAP:PD TREE program (Garland *et al.* 1993; Midford, Garland and Maddison, 2004) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison, 2004). Procedure of the method of independent contrasts followed Garland, Harvey and Ives (1992). Regressions were forced through the origin as is standard practice with contrasts, because of the arbitrariness associated with the sign of independent contrasts (see Garland *et al.* 1992 for details).

RESULTS

Comparison among ectoparasite taxa

Different host species supported a different number of ectoparasites belonging to different taxa. The number of flea species per host species ranged from 1 to 19 with a median value of 2. Published surveys used in this study reported no flea species for 5 of 80 rodents

(*Akodon azarae*, *Nectomys squamipes*, *Bolomys lasiurus*, *Oryzomys subflavus*, and *Spermophilus beltingi*). Lice were found on 38 of 80 rodent hosts only. Species richness of these ectoparasites ranged from 1 (30 of 38 hosts) to a maximum of 3 species (4 of 38 hosts) with a median of 1. Of 80 rodent species, 68 were parasitized by mesostigmatid mites with the number of species ranging from 1 to 21 with a median of 4. Ticks were found on 55 of 80 rodents. Tick species richness varied from one to 12 with a median of 2. The species richness of flea assemblages on a host species varied significantly across geographical regions (Palaeartic, Nearctic, Neotropical and Afrotropical: ANOVA, $F_{3,71} = 4.0$, $P < 0.05$) being highest in the Palaeartic. However, this significance disappeared when 3 of 27 Palaeartic species that had the richest flea assemblages (*Alticola argentata*, *Cricetulus migratorius* and *Microtus arvalis*) were excluded from the analysis ($F_{3,68} = 2.6$, $P > 0.05$). On the contrary, species richness of the assemblages of other ectoparasite taxa did not differ among regions (ANOVAs, $F_{3,34-64} = 0.6-2.3$, $P > 0.05$ for all). The same was true for taxonomic distinctness of the assemblages of any ectoparasite taxon (ANOVAs, $F_{3,34-71} = 1.1-1.3$, $P > 0.05$ for all).

Numbers of species of most ectoparasite taxa on the same host (controlled for sampling effort) were significantly positively correlated with one another (Table 1; see Fig. 1 for the illustrative example with fleas and ticks). However, this was not the case for lice. The number of louse species was not correlated with the number of species of any other ectoparasite taxon (Table 1). Taxonomic distinctness ($\Delta+$) was not correlated among the assemblages of different ectoparasitic taxa (Table 1). The results did not change after exclusion from the analyses of 11 host species for which fewer than 10 individuals were examined (Table 1).

Comparisons of species richness among ectoparasitic taxa using the method of independent

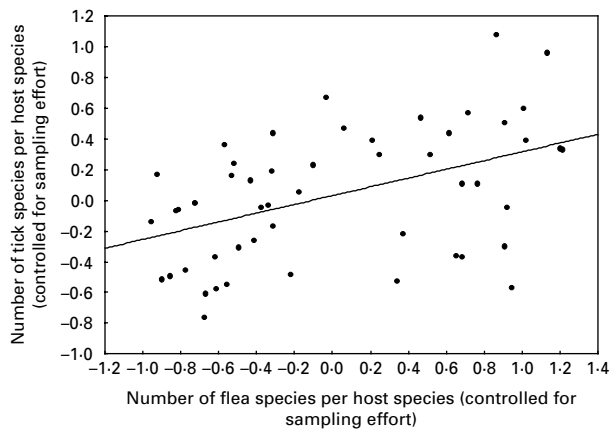


Fig. 1. Relationships between the number of tick species and the number of flea species on the same host species among 52 rodent species.

contrasts yielded essentially the same results as those of conventional analyses. Species richness but not taxonomic distinctness was significantly positively correlated among the assemblages of fleas, mites and ticks (Table 2), whereas neither the number of louse species nor the taxonomic distinctness of their assemblages were correlated with those of other ectoparasites (Table 2). The results did not change after exclusion from the analyses of 11 host species for which fewer than 10 individuals were examined, as was the case with conventional statistics (Table 1). An illustrative example with mites and ticks is shown in Fig. 2. The correlation remained significant ($r=0.30$, $P<0.05$) after removal of one data point from the bottom left corner (contrast between *Neotoma floridana* and *Neotoma fuscipes*) and two data points from the upper right corner (contrast between *Alticola argentata* and *Alticola streltzovi* and contrast between *Microtus arvalis* and *Microtus ochrogaster*).

Comparison between ectoparasite and endoparasites assemblages

Neither species richness nor taxonomic distinctness of ectoparasite and endoparasite assemblages in a host species differed significantly among geographical regions (ANOVAs, $F_{2,17}=0.2-1.3$, $P>0.05$ for all). The species richness of ectoparasite assemblages was not correlated with that of the assemblage of gastrointestinal helminths on the same host species when their relationship was analysed using both conventional statistics and the method of independent contrasts ($r=0.26$, $N=20$ and $r=0.27$, $N=19$, respectively, $P>0.05$ for both). In contrast, the correlation between the taxonomic distinctness of ectoparasite assemblages and that of endoparasites was highly significantly positive when both conventional analysis and the method of independent contrasts were used ($r=0.82$, $N=20$ and $r=0.83$, $N=19$, respectively $P<0.01$; see Fig. 3 for independent contrasts). Correlations remained significant after the

exclusion of 2 host species for which fewer than 10 individuals were examined ($r=0.81$, $N=18$ for conventional analysis and $r=0.84$, $N=17$ for independent contrasts; $P<0.01$ for both). In addition, the correlation between independent contrasts in taxonomic distinctness of ectoparasite assemblages and independent contrasts in taxonomic distinctness of assemblages of gastrointestinal helminths remained significant, albeit weaker, when the two right upper points (Fig. 3) were removed ($r=0.47$, $N=17$, $P<0.05$); these points represented the contrasts between *Spermophilus armatus* and *Spermophilus beldingi* and between *Geomys bursarius* and *Perognathus parvus*.

DISCUSSION

The results of this study demonstrated that, in general, the species diversities of different parasite taxa in the same host species are positively interrelated. This appeared to be true among parasites that use the same space and resource in their host (fleas, mites and ticks) as well as between parasites belonging to completely different spatial and trophic guilds (ectoparasites and gastrointestinal helminths). These results, combined with an earlier demonstration that the species richnesses of different groups of endoparasitic helminths covary among their vertebrate hosts (Poulin and Morand, 2004, pp. 75–79), provide strong evidence of apparent facilitation (*sensu* Levine, 1999) among different parasite taxa.

The existence of relationships between species diversities of different parasite taxa (even those from different guilds) suggests that the host represents an important force shaping parasite communities. Moreover, positive correlations between species diversities among 3 ectoparasite taxa and between ecto- and endoparasites advocate host-mediated facilitation among different parasites. A host that is unable to resist attacks from multiple flea species appears to be also unable to resist attacks from multiple mite and tick species. When the diversity of unrelated taxa of free-living organisms co-varies positively across localities, the general explanation usually invokes intrinsic differences in rates of colonization and extinction among localities (Gaston, 1996). It is thus possible that intrinsic properties of the various host species could lead to some hosts accumulating parasites of all taxa at a high rate. In this context, our results are more likely due to some biochemical or physiological properties of a host rather than to its ecological characteristics. Indeed, the depth and degree of complexity of a rodent burrow system can determine the relative richness of flea and mite assemblages (Kucheruk, 1983) because pre-imaginal development in many species occurs off-host. In most ixodid ticks, though, questing larvae and nymphs (adult ticks of most species parasitize mainly large mammals) do not depend on the

Table 2. Pearson's correlation coefficients (r) for all pairwise associations of species richness (SR) and taxonomic distinctness ($\Delta+$) between assemblages of four higher ectoparasite taxa found on the same host species using the method of phylogenetically independent contrasts

(Both parameters were controlled for confounding variables (sampling effort in the case of SR, and number of species in the case of $\Delta+$). In parentheses: value of r after removal of 11 host species for which fewer than 10 individuals were examined. * $P < 0.01$.)

Taxon 1	Taxon 2	SR	$\Delta+$
Fleas	Lice	0.03 (0.04)	-0.29 (-0.29)
	Mesostigmatid mites	0.49* (0.48*)	-0.07 (-0.03)
	Ticks	0.58* (0.59*)	0.08 (0.11)
Lice	Mesostigmatid mites	0.28 (0.29)	-0.21 (0.22)
	Ticks	0.31 (0.31)	0.12 (0.12)
Mesostigmatid mites	Ticks	0.50* (0.43*)	0.17 (0.16)

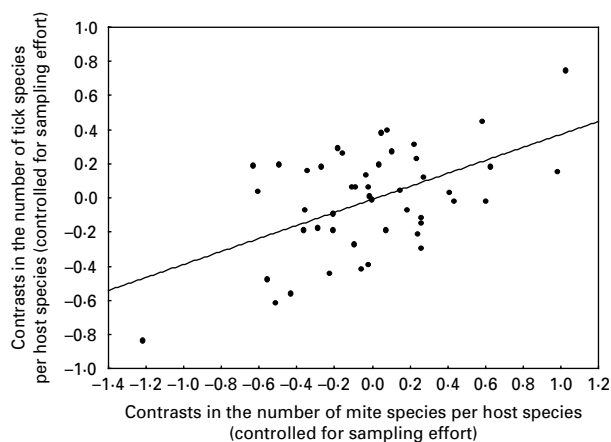


Fig. 2. Relationships between the number of tick species and the number of mesostigmatid mite species on the same host species among 55 rodent species using independent contrasts.

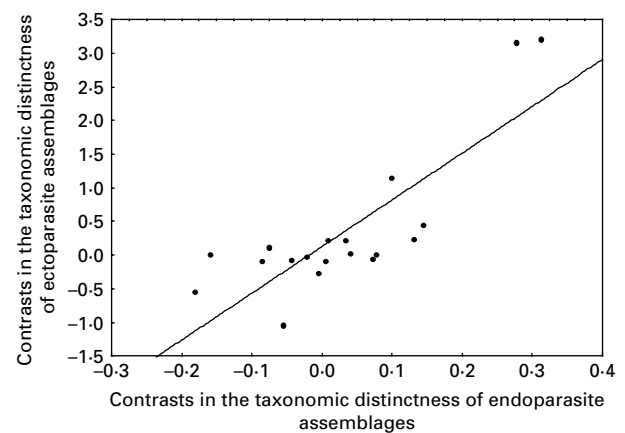


Fig. 3. Relationships between the taxonomic distinctness of ectoparasite and endoparasite assemblages among 20 rodent species using phylogenetically independent contrasts.

host's burrow but crawl up the stems of grass or perch on the edges of leaves on the ground and wait for a host passing by.

On the other hand, a host species that is able to resist attacks from many species of one parasite taxon appears to be able also to resist attacks from many species of other parasite taxa. This suggests some level of cross-resistance against distantly related parasites. In particular, rodent species that are exploited by only a few flea species appeared also to be exploited by only few mite and tick species. Although many chemical mediators that are contained in the saliva of different ectoparasite lineages are different (Ribeiro, 1996), some salivary anti-clotting, anti-platelet and vasodilatory substances can be quite similar among taxa. Indeed, cross-immunity between distantly-related parasite taxa has been reported. For example, rabbits infested with mites *Prosoptes cuniculi* produce antibodies reactive to both mite and tick extracts (den Hollander and Allen, 1986). However, the occurrence of cross-immunity seems to depend on both parasite and host taxon. For

example, guinea pigs demonstrated cross-immunity between different ticks of the genus *Dermacentor* but not between ticks of the genera *Dermacentor* and *Amblyomma* (McTier *et al.* 1981). Rabbits demonstrated cross-resistance between 2 *Hyalomma* ticks (Kumar and Kumar, 1996), but not between *Rhipicephalus* and *Ixodes* (Rechav, Heller-Haupt and Varma, 1989). Cross-immunity between 2 *Rhipicephalus* species was reported for rabbits (Njau and Nyindo, 1987), but not for guinea pigs (Rechav *et al.* 1989). Nevertheless, close homology of saliva proteins was found in closely related argasid ticks (Mans *et al.* 2002) but not in closely-related sand flies (Warburg *et al.* 1994). Thus, some still unknown factors determine cross-resistance patterns in different host-parasite systems.

Species richness of anopluran lice was not correlated with that of any other ectoparasite taxon, whereas their taxonomic distinctness was sometimes even negatively, albeit not significantly, correlated with that of other taxa. The number of louse species on a host species was low independently of the species

richness of any other parasite taxon. Indeed, the vast majority of host species harboured a single louse species only. Furthermore, taxonomic distinctness of louse assemblages was always low (in average across hosts, 12.4 ± 4.0 compared with 54.4 ± 4.3 , 41.7 ± 2.8 and 48.8 ± 5.3 for fleas, mites and ticks, respectively) regardless of whether the $\Delta+$ of other ectoparasite taxa is high or low. In other words, some ectoparasite taxa (e.g., lice) could be constrained in their taxonomic diversity, whereas this is not the case for other taxa. Constraints in louse taxonomic diversity can be explained by the extremely high host specificity of lice and their extremely low dispersal capacity. Another explanation can be that sucking lice were under-sampled in at least part of the reported surveys. This is likely the case because these insects are small, usually attach to the hair bases next to the host skin and, thus, cannot be easily brushed off the host.

The positive relationships among species diversities of the assemblages of different ectoparasites as well as between ecto- and endoparasites could arise also from immunodepression in a host subjected to multiple immune challenges from a variety of parasite species. The occurrence of a positive correlation in terms of taxonomic distinctness rather than in terms of number of species between ecto- and endoparasite assemblages strengthens this explanation. Immunity is an energetically and/or nutritionally demanding process (Lochmiller and Deerenberg, 2000). Indeed, relationships between parasitism, immunity and reproduction observed in wild birds and mammals strongly support a high energy cost of the immune system (Norris, Anwar and Read, 1994; Demas and Nelson, 1998; Ilmonen *et al.* 2003). The difference between defence mechanisms against haematophagous ectoparasites versus intestinal helminths is much sharper than that between defence mechanisms against different ectoparasite taxa (see Wakelin, 1996; Wikel, 1996). Maintaining several different means of defence is likely more costly than mounting one specific type of defence (Taylor, Mackinnon and Read, 1998). As a result, the effectiveness of energy allocation to immune defence decreases as the diversity of attack types increases (Jokela, Schmid-Hempel and Rigby, 2000). Jokela *et al.* (2000) argued that in cases when the diversity of attacks is high and, thus, the effectiveness of defence is low, the optimal strategy is to tolerate damage. Consequently, a host subjected to attacks from multiple parasite species is forced to give up its defence and to surrender. This can be one of the reasons explaining why hosts that are exploited by taxonomically diverse assemblages of haematophagous arthropods, also harbour assemblages of gastrointestinal helminths of high taxonomic distinctness.

Another, not necessarily alternative, explanation for the observed patterns is that host species can differ also in their intrinsic ability to defend themselves against parasites using their immune system.

Different, sometimes even closely related, rodent species have been shown to have different abilities to mount both humoral and cell-mediated immune responses (Klein and Nelson, 1998*a, b*). As a result, a rodent with lower intrinsic immunocompetence can be exploited by a higher number of parasite species compared with more immunocompetent species.

Finally, the results of this study do not support suggestions of strong direct or host-mediated competitive exclusion between different parasite species or lineages (Waage, 1979; Rozsa, 1993), although such competition undoubtedly occurs (Barker and Close, 1990; Patrick, 1991; Combes, 2001). Instead, our results suggest host-mediated facilitation among species of different taxa within parasite assemblages of rodent hosts. Because a host is not only a resource but also a competitor for a parasite (Combes, 2001), the relationships among different parasite lineages in a host species represent a sort of apparent facilitation, i.e. positive interactions mediated by a shared competitor (Levine, 1999). Apparent facilitation is considered as an important process in communities of both free-living (Levine, 1999) and parasitic (Cox, 2001; Krasnov *et al.* 2005) organisms.

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APPENDIX

Table A1. Data on rodents and their ectoparasites included in the analyses of parasite species diversity among higher ectoparasite taxa

Species	Number of examined individuals	Number of parasite species	Source
<i>Aethomys chrysophilus</i>	46	7	Braack <i>et al.</i> 1996
<i>Akodon arviculoides</i>	11	8	Lopes, Linardi and Botelho, 1989
<i>Akodon azarae</i>	17	4	Nava, Lareschi and Voglino, 2003
<i>Akodon montensis</i>	4	7	Barros-Battesti <i>et al.</i> 1998
<i>Akodon serrensis</i>	14	8	Barros-Battesti <i>et al.</i> 1998
<i>Allactaga elater</i>	51	11	Sartbaev, 1975
<i>Alticola argentata</i>	201	29	Sartbaev, 1975
<i>Alticola streltzevi</i>	800	18	Shubin, 1959
<i>Ammospermophilus leucurus</i>	14	11	Jenkins and Grundmann, 1973

Table A1. (Cont.)

Species	Number of examined individuals	Number of parasite species	Source
<i>Apodemus uralensis</i>	1334	52	Sartbaev, 1975
<i>Arvicanthis niloticus</i>	6	3	Oguge, Rerieya and Ondiaka, 1997
<i>Arvicola terrestris</i>	1103	37	Letova, Emelyanova and Letov, 1963
<i>Bolomys lasiurus</i>	4	4	Lopes <i>et al.</i> 1989
<i>Callosciurus erythraeus</i>	105	3	Shinozaki <i>et al.</i> 2004
<i>Clethrionomys glareolus</i>	65	16	Bugmyrin <i>et al.</i> 2003
<i>Clethrionomys rutilus</i>	309	22	Elshanskaya and Popov, 1972
<i>Cricetulus barabensis</i>	6	11	Shvedko, 1958
<i>Cricetulus migratorius</i>	133	40	Sartbaev, 1975
<i>Dryomys nitidula</i>	127	6	Sartbaev, 1975
<i>Ellobius talpinus</i>	113	14	Sartbaev, 1975
<i>Eutamias sibiricus</i>	5	8	Elshanskaya and Popov, 1972
<i>Geomys bursarius</i>	144	4	Bartel and Gardner, 2000
<i>Gerbillus andersoni</i>	240	9	Lehmann, 1992
<i>Glaucomys volans</i>	70	9	Pung <i>et al.</i> 2000
<i>Holochilus brasiliensis</i>	7	5	Nava <i>et al.</i> 2003
<i>Lasiopodomys brandti</i>	171	21	Vasiliev, 1966
<i>Lemniscomys striatus</i>	7	5	Oguge <i>et al.</i> 1997
<i>Marmota baibacina</i>	266	16	Sartbaev, 1975
<i>Marmota sibirica</i>	1458	7	Vasiliev, 1966
<i>Mastomys natalensis</i>	14	6	Oguge <i>et al.</i> 1997
<i>Meriones erythrouros</i>	152	25	Sartbaev, 1975
<i>Meriones tamariscinus</i>	502	35	Sartbaev, 1975
<i>Microtus arvalis</i>	416	43	Sartbaev, 1975
<i>Microtus fortis</i>	277	7	Garbuzov, 1958
<i>Microtus gregalis</i>	846	46	Sartbaev, 1975
<i>Microtus ochrogaster</i>	59	9	Ritzi and Whitaker, 2003
<i>Microtus oeconomus</i>	5	11	Elshanskaya and Popov, 1972
<i>Mus musculus</i>	461	20	Sartbaev, 1975
<i>Napaeozapus insignis</i>	101	5	Whitaker, 1963a
<i>Nectomys squamipes</i>	11	2	Bossi, Linhares and de Godoy Bergallo, 2002
<i>Neofiber alleni</i>	25	3	Smith, Whitaker and Layne, 1988
<i>Neotoma cinerea</i>	30	19	Cudmore, 1986
<i>Neotoma floridana</i>	47	12	Durden <i>et al.</i> 1997
<i>Neotoma fuscipes</i>	35	12	Cudmore, 1986
<i>Ochrotomys muttali</i>	46	12	Durden <i>et al.</i> 2004
<i>Oligoryzomys delticola</i>	10	8	Lareschi <i>et al.</i> 2003
<i>Oligoryzomys flavescens</i>	8	6	Nava <i>et al.</i> 2003
<i>Ondatra zibethica</i>	85	4	Garbuzov, 1958
<i>Oryzomys nigripes</i>	9	6	Barros-Battesti <i>et al.</i> 1998
<i>Oryzomys palustris</i>	11	2	Kollars, Durden and Oliver, 1997
<i>Oryzomys russatus</i>	139	6	Bossi <i>et al.</i> 2002
<i>Oryzomys subflavus</i>	10	5	Lopes <i>et al.</i> 1989
<i>Oryzomys utiaritensis</i>	33	14	Lopes <i>et al.</i> 1989
<i>Oxymycterus rufus</i>	29	8	Lareschi <i>et al.</i> 2003
<i>Oxymycterus rutilans</i>	4	4	Linardi <i>et al.</i> 1991
<i>Pedetes capensis</i>	118	7	Anderson and Kok, 2003
<i>Perognatus parvus</i>	183	3	O'Farrel, 1975
<i>Peromyscus gossypinus</i>	64	9	Durden <i>et al.</i> 2000
<i>Peromyscus leucopus</i>	60	10	Ritzi and Whitaker, 2003
<i>Peromyscus maniculatus</i>	28	7	Ritzi and Whitaker, 2003
<i>Proechimys iheringi</i>	75	3	Bossi <i>et al.</i> 2002
<i>Rattus turkestanicus</i>	391	21	Sartbaev 1975
<i>Reithrodontomys megalotis</i>	24	2	Kollars <i>et al.</i> 1997
<i>Scapteromus aquaticus</i>	22	5	Nava <i>et al.</i> 2003
<i>Sciurus carolinensis</i>	14	3	Kollars <i>et al.</i> 1997
<i>Sciurus niger</i>	87	6	Coyner, Wooding and Forrester, 1996
<i>Sciurus vulgaris</i>	11	4	Sartbaev, 1975
<i>Sicista tianschanica</i>	195	21	Sartbaev, 1975
<i>Sigmodon hispidus</i>	23	7	Durden <i>et al.</i> 2000
<i>Spermophilus armatus</i>	14	17	Jenkins and Grundmann, 1973
<i>Spermophilus beldingi</i>	12	1	Jenkins and Grundmann, 1973
<i>Spermophilus fulvus</i>	668	5	Sartbaev, 1975
<i>Spermophilus lateralis</i>	24	17	Jenkins and Grundmann, 1973
<i>Spermophilus relictus</i>	176	8	Sartbaev, 1975

Table A1. (Cont.)

Species	Number of examined individuals	Number of parasite species	Source
<i>Spermophilus townsendi</i>	25	7	Jenkins and Grundmann, 1973
<i>Spermophilus undulatus</i>	39	9	Elshanskaya and Popov, 1972
<i>Spermophilus variegatus</i>	61	14	Jenkins and Grundmann, 1973
<i>Synaptomys cooperi</i>	15	9	Ritzi and Whitaker, 2003
<i>Tatera leucogaster</i>	46	9	Braack <i>et al.</i> 1996
<i>Zapus hudsonius</i>	956	9	Whitaker, 1963b

Table A2. Data on rodents and their ecto- (EC) and endoparasites (EN) included in the analyses of parasite species diversity between ectoparasites and endoparasites

Species	Number of individuals examined		Number of species		Source
	EC	EN	EC	EN	
<i>Alticola streltzevi</i>	800	200	18	3	Shubin, 1959
<i>Ammospermophilus leucurus</i>	14	135	11	9	Jenkins and Grundmann, 1973
<i>Ammospermophilus nelsoni</i>	500	37	3	4	Hawbecker, 1959
<i>Arvicanthis niloticus</i>	6	6	3	3	Oguge <i>et al.</i> 1997
<i>Clethrionomys glareolus</i>	65	65	16	10	Bugmyrin <i>et al.</i> 2003
<i>Cricetulus barabensis</i>	63	63	11	4	Letov <i>et al.</i> 1966
<i>Geomys bursarius</i>	144	144	4	8	Bartel and Gardner, 2000
<i>Glaucomys volans</i>	70	70	9	5	Pung <i>et al.</i> 2000
<i>Lemniscomys striatus</i>	7	7	5	4	Oguge <i>et al.</i> 1997
<i>Mastomys natalensis</i>	14	14	6	5	Oguge <i>et al.</i> 1997
<i>Napaeozapus insignis</i>	101	113	5	4	Whitaker, 1963a
<i>Perognatus parvus</i>	183	38	3	3	O'Farrel, 1975
<i>Rattus norvegicus</i>	255	255	4	7	Stojcevic, Mihajilevic and Marunculic, 2004
<i>Sciurus niger</i>	87	119	6	11	Coyner, Wooding and Forrester, 1996
<i>Spermophilus armatus</i>	14	35	17	6	Jenkins and Grundmann, 1973
<i>Spermophilus beldingi</i>	12	12	1	4	Jenkins and Grundmann, 1973
<i>Spermophilus lateralis</i>	24	100	17	6	Jenkins and Grundmann, 1973
<i>Spermophilus townsendi</i>	25	12	7	2	Jenkins and Grundmann, 1973
<i>Spermophilus variegatus</i>	61	154	14	17	Jenkins and Grundmann, 1973
<i>Zapus hudsonius</i>	956	956	10	7	Whitaker, 1963b

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