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Are there general rules governing parasite diversity? Small mammalian hosts and gamasid mite assemblages

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ABSTRACT

Parasite biodiversity varies on several scales, and in particular among different host species. Previous attempts at finding relationships between host features and the diversity of the parasite assemblages they harbour have yielded inconsistent results, suggesting strongly that any patterns might be taxon-specific. Here, we examined the potential of three host characteristics (host body mass, basal metabolic rate, and area of the geographical range) as determinants of parasite diversity in one group of ectoparasites, gamasid mites (superfamily Dermanyssoidea), using data from 63 species of small mammalian hosts. Our analyses used three measures of parasite diversity (species richness, the Shannon diversity index, and average taxonomic distinctness), and controlled for sampling effort and phylogenetic influences. Although several significant relationships were observed, they depended entirely on which diversity measure was used, or on which host taxon was investigated (insectivores vs. rodents and lagomorphs). In addition, the present results on patterns of mite diversity were not consistent with those of an earlier study involving roughly the same host taxa and the same biogeographical area, but a different group of ectoparasites, i.e. fleas. Thus, there appears to be no universal determinant of parasite diversity, and associations between host features and parasite diversity probably evolve independently in different host–parasite systems.

Keywords
Basal metabolic rate, body mass, geographical range, diversity, hosts, parasites.

INTRODUCTION

Parasites represent an integral part of global biodiversity. Moreover, parasites form a large proportion of the diversity of life, and parasitism is possibly more common than any other feeding strategy (Sukhdeo & Bansemir, 1996). In addition, parasites play important roles in the regulation of populations and communities of their hosts (e.g. Poulin, 1998; Combes, 2001). Therefore, it is not surprising that the number of attempts to explain patterns of parasite diversity among host species as well as within host species and among geographical regions has increased greatly in recent years. Indeed, different host species harbour different number of parasite species, though the reasons why are not always clear (e.g. Caro *et al.*, 1997; Poulin & Morand, 2000, 2004; Krasnov *et al.*, 2004a). The host body is the ultimate habitat for the majority of parasites. Consequently, variation in host body characteristics has often been considered as a primary factor determining among-host variation in parasite diversity (Caro *et al.*, 1997; Feliu *et al.*, 1997; Morand & Poulin, 1998; Morand & Harvey, 2000; Arneberg, 2002; Krasnov *et al.*, 2004a).

In particular, host body size and basal metabolic rate (BMR) have been considered as important factors affecting parasite diversity. The reasons why a correlation between parasite diversity and host body mass is expected are rather straightforward. Larger hosts are expected to sustain richer parasite assemblages because they provide more space and a greater variety of niches and, thus, can provide different parasite species with an opportunity for spatial niche diversification. Metabolic rate is also expected to correlate positively with parasite diversity because hosts exposed to diverse infections should invest in higher BMR as a compensation for a costly immune response (Morand & Harvey, 2000), although some researchers have argued that the cost of the immune response is an energy cost above that of the BMR (Degen, 1997). Alternatively, instead of being seen as a consequence of parasitism, high BMR might itself lead to greater parasite diversity: following the metabolic theory of ecology (see Brown *et al.*, 2004), the higher rates of processing of energy and materials associated with high BMR can provide the resources needed to support a rich parasite assemblage. However, studies aimed at finding relationships between these host body parameters

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and parasite diversity have produced contradictory results that vary among both host and parasite taxa. For example, Arneberg (2002) found a positive relationship between strongylid nematode species richness and body mass of their mammalian hosts, but only following a correction for the effect of host population densities. A positive correlation between host body size and parasite richness was reported in other studies for mammalian (Gregory *et al*., 1996; Vitone *et al*., 2004) as well as for fish hosts (Guégan *et al*., 1992; Guégan & Morand, 1996). In contrast, other studies of ecto- and endoparasites of various host taxa did not find any relationship between host body size and parasite diversity (Poulin, 1995; Morand & Poulin, 1998; Clayton & Walther, 2001; Krasnov *et al*., 2004a). Similar contradictions arise when the effect of host BMR on parasite diversity is considered. A positive relationship between these parameters for intestinal helminths parasitic in mammals was found by Morand & Harvey (2000), but not even a weak association between parasite diversity and host BMR was reported for fleas exploiting small mammals by Krasnov *et al*. (2004a).

Another host-related factor that has been repeatedly considered as an important determinant of parasite diversity is the size of the host's geographical range. A positive correlation between these two parameters is expected merely because hosts with larger geographical ranges presumably encounter more parasite species. Indeed, this pattern was found in parasite assemblages of rodents (Feliu *et al*., 1997 for gastrointestinal helminths; Krasnov *et al*., 2004a for fleas), although it was not supported by a study of birds and their lice (e.g. Clayton & Walther, 2001).

The complete lack of consistency among the results mentioned above suggests that, perhaps, no universal pattern exists in the relationship between host body size, BMR, or geographical range and parasite diversity. The effect of host-related parameters on parasite diversity can be either parasite taxon-specific or host taxon-specific, or even host/parasite association-specific. If this is the case, then the weak (if any) relationships between host parameters and parasite diversity reported in the studies in which several parasite taxa exploiting a particular host taxon were pooled together are not surprising (e.g. Watve & Sukumar, 1995). A variety of patterns in the relationships between host-related factors and parasite diversity among parasite taxa can mask each other. In addition, different measures of parasite diversity may have different sensitivity to host-related factors (Poulin, 2004).

To achieve the required level of analysis when host-related factors and parasite diversity are studied, it is necessary to compare patterns in the relationships between these parameters among parasite taxa within a host taxon as well as within a parasite taxon among host taxa. Here, we studied the relationships between diversity of haematophagous gamasid mites belonging to the superfamily Dermanyssoidea and body mass, BMR, and geographical range size of their small mammalian hosts from the Northern Palaeoarctic. Previously, we examined the effect of these parameters on flea species richness and found that none of the host body characteristics correlated with species richness of flea assemblages, whereas flea species richness increased with an increase in the size of the host's geographical range (Krasnov *et al*., 2004a). In the present study, the analyses are done in approximately the same way and the hosts are more or less the same, providing a good basis for comparisons between flea and mite assemblages. Fleas are obligate haematophages, whereas the interspecific variation in the ecology and feeding mode of gamasids is huge, as they include soil-dwelling and nidicolous predators, and facultative and obligatory vertebrate ecto- and endoparasites (see Radovsky, 1985 for review). Nevertheless, here we focused on haematophagous mites collected from host bodies. These mites use their hosts both as food sources and as dispersal vehicles, and, thus, the association between these mite species and their hosts is assumed to be very intimate (Radovsky, 1985). Consequently, we expected to find patterns between host-related parameters and mite diversity similar to those found for fleas. In addition, in this study we used diversity measures other than mere species richness. In particular, we applied a measure of diversity that takes into account the taxonomic affinities of the various mite species (Clarke & Warwick, 1998, 1999; Warwick & Clarke, 2001). This measure places the emphasis on the taxonomic distance between mite species exploiting a host species rather than on their number, providing a different and complementary perspective on mite diversity.

MATERIALS AND METHODS

Data set

Data on mites collected from host bodies were obtained from published surveys and unpublished data that reported mite distribution and abundance on small mammals (Insectivora, Lagomorpha and Rodentia) in 26 different regions of the Northern Palaeoarctic (see Appendices S1 & S2 in Supplementary Material). These sources reported data on number of mite species found on a particular small mammal species in a particular location. We used only those sources where sampling effort (the number of examined hosts) and number of individuals of each mite species were reported. In all studies most rodents and shrews were captured using snap traps, shrews were also captured using pitfall traps, sciurids and lagomorphs were hunted, whereas moles were captured using mole traps. Each trapped animal was placed in an individual cloth bag and transported to the laboratory where its fur was thoroughly combed using a toothbrush, and all dislodged mites were collected.

Data on BMR were obtained from various sources (see Appendix S1 in Supplementary Material). Metabolic rate in these sources was expressed either as O_2 consumption per unit time or in energetic units. To ensure the consistency of the data we converted all data into energetic units, assuming 20.08 kJ per mL O_2 (Degen, 1997). Data on mean body mass were obtained from Silva & Downing (1995) and various additional sources. In total, we used data on mite assemblages and body mass and metabolic characteristics of 45 rodent, 2 lagomorph, and 16 insectivore species, from which 70 mite species were collected. Ubiquitous commensal species such as *Mus musculus* and *Rattus norvegicus*, as well as *Ondatra zibethicus* which was introduced to the Palaeoarctic, were excluded from the analyses of the relationship between diversity of mite assemblages and the size of the host geographical range.

Diversity estimates

For each host species, we estimated three measures of mite species diversity as follows: (1) the number of mite species found on a host species, or species richness, corrected for sampling effort (see below); (2) mite species diversity estimated with the Shannon diversity index (Magurran, 1988, 2004); and (3) average mite taxonomic distinctness (Δ^+) and the variance in taxonomic distinctness (Λ^+) of the mite species present (see below). Measures of mite diversity were averaged across regions for each host species that occurred in more than one region. We chose to use the Shannon index because it is the most widely used estimate of diversity (Magurran, 1988, 2004). In addition, this index assumes that individuals are randomly sampled from a large population (Pielou, 1975), which seems to be a reasonable assumption for arthropod ectoparasites on small mammals (Krasnov *et al*., 2004c).

When mite species are placed within a taxonomic hierarchy, the average taxonomic distinctness is the mean number of steps up to the hierarchy that must be taken to reach a taxon common to two species, computed across all possible species pairs (Clarke & Warwick, 1998, 1999; Warwick & Clarke, 2001; Poulin & Mouillot, 2003, 2004). The greater the taxonomic distinctness between mite species, the higher the number of steps needed, and the higher the value of the index Δ^+. Taxonomic distinctness is used as a surrogate for genetic or phylogenetic distances among mites; although the latter measures would provide a better representation of the overall differences between mites, the respective data are not yet available for this taxon. Using the taxonomic classification of Bregetova (1956), Radovsky (1985), and Halliday (1998), all mite species were fitted into a taxonomic structure with four hierarchical levels above species, i.e. genus, subfamily, family, and superfamily (Dermanyssoidea) (see Appendix S2 in Supplementary Material). We restricted our use of taxonomic levels to these basic ones because they are the only ones available for all mite taxa included here. The maximum value that the index Δ^+ can take is thus 4 (when all mite species belong to different families), and its lowest value is 1 (when all mite species belong to the same genus). However, as the index cannot be computed for hosts exploited by a single mite species, we assigned a Δ^+ value of 0 to these host species, to reflect their extremely species-poor mite assemblages. The variance in Δ^+, Λ^+, provides information on any asymmetries in the taxonomic distribution of mite species in assemblages (Clarke & Warwick, 1998, 1999; Warwick & Clarke, 2001; Poulin & Mouillot, 2003); it can only be computed when an assemblage comprises a minimum of three species (it always equals zero with two species). To calculate Δ^+ and Λ^+, DM and RP developed a computer program using Borland C + + Builder 6.0 (available at http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2).

Estimates of parasite diversity may be biased if some hosts are studied more intensively than others (Morand & Poulin, 1998). To ensure that variation in between-host sampling effort did not bias estimates of mite diversity, we regressed each estimate of mite diversity against the number of hosts examined in log–log space. Mite species richness and Shannon diversity appeared to be strongly affected by sampling effort ($r^2 = 0.36$, $F = 34.3$ and $r^2 = 0.42$, $F = 44.0$, respectively, $P < 0.001$ for both). Each value of richness or diversity was therefore substituted by its residual deviation from a linear regression on the number of hosts examined.

Both Δ^+ and Λ^+ were unaffected by sampling effort ($r^2 = 0.03$, $F = 1.7$ and $r^2 = 0.01$, $F = 0.6$, respectively, $P > 0.40$ for both). However, the number of mite species exploiting a host species was significantly positively correlated with both Δ^+ and Λ^+ ($r^2 = 0.21$, $F = 16.7$ and $r^2 = 0.24$, $F = 19.0$, respectively, $P < 0.0001$ for both), indicating that these measures were influenced by the number of species in a host's mite assemblage. Therefore, in the subsequent analyses Δ^+ and Λ^+ were corrected for the mite species richness in an assemblage, using residuals. In addition, Δ^+ and Λ^+ did not covary with each other ($r = 0.03$, $N = 61$, $P > 0.05$).

Host-related factors

BMR was significantly correlated with body mass ($r^2 = 0.63$, $F = 65.7$, $P < 0.001$). Consequently, we controlled BMR for body mass, using residuals from linear regression in a log–log space.

The size of the entire geographical range for each host species included in the analysis was calculated from a polygon distribution map constructed using ARCVIEW 3.2. Maps for mammals were based on published reports (Sokolov & Orlov, 1980; Panteleev *et al*., 1990; Zhang *et al*., 1997).

Data analysis

We regressed estimates of mite diversity against host-related parameters (body mass, BMR, geographical range size) separately for (1) rodents and lagomorphs (there were only two lagomorph species in our data set, and rodents and lagomorphs are sister-groups) and (2) insectivores using both conventional regressions and the method of independent contrasts that allows to control for the confounding effect of phylogeny (Felsenstein, 1985). We used a phylogeny of hosts derived from various sources (see Krasnov *et al*., 2004a,b for details). To compute independent contrasts, we used the PDAP:PDTREE program (Garland *et al*., 1993; Midford *et al*., 2005) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison & Maddison, 2006). We regressed standardized contrasts of the dependent variables against the standardized contrasts of the independent variables using regressions forced through the origin (see Garland *et al*., 1992 for details).

In addition, we used a multivariate approach for the subset of 28 rodent and nine insectivore species for which all three host-related parameters were available. We analysed each estimate of mite diversity against all host-related parameters using multiple stepwise regressions (forward procedure) separately for rodents and insectivores. Multiple regressions of independent contrasts were forced through the origin. This multivariate approach produced results very similar to those of separate regressions. Here we only report the results of separate regressions as these analyses were based on the larger data set comprising all 63 host species.

Table 1 Summary of linear regressions of the measures of mite assemblage diversity against host-related parameters across 45 rodent, two lagomorph and 16 insectivore species. Only the results of significant regressions (using at least one method) are presented

Host taxon	Mite diversity measure	Host-related parameter	Conventional statistics				Method of independent contrasts	
			r^2	F	P	Slope ± SE	r	P
Rodentia and Lagomorpha	Species richness	Body mass	0.10	5.1	0.03	−0.11 ± 0.05	−0.32	0.03
	Shannon diversity	BMR	0.18	6.5	0.01	0.80 ± 0.31	0.48	0.006
	Δ^+	Geographical range	0.12	5.8	0.02	−0.07 ± 0.03	−0.31	0.04
	Λ^+	BMR	0.24	8.9	0.005	−0.16 ± 0.05	−0.63	0.001
Insectivora	Shannon diversity	Body mass	0.46	11.9	0.003	0.72 ± 0.21	0.50	0.04
	Λ^+	Body mass	0.32	6.6	0.02	0.15 ± 0.05	0.20	0.46

We did not use an adjustment of the alpha level for multiple comparisons (e.g. Bonferroni adjustment). These methods have been increasingly criticized by statisticians and ecologists in recent years, because they often lead to the incorrect acceptance of the false null hypothesis (Rothman, 1990; Perneger, 1998, 1999; Moran, 2003; Garcia, 2004). In fact, the Bonferroni procedure may be on its way out in ecological sciences (Nakagawa, 2004).

RESULTS

A summary of the regressions of the measures of mite assemblage diversity against three host-related parameters (body mass, BMR, and geographical range) is presented in Table 1. Illustrative examples with host body mass and mite species richness (for rodent/lagomorph hosts) or Shannon diversity of mite assemblages (for insectivore hosts) are presented in Figs 1 and 2, respectively.

In rodent and lagomorph hosts, the species richness of mite assemblages correlated negatively with host body mass (Table 1) and was not affected by either of the two other host parameters ($r^2 = 0.004–0.07$, $F = 0.1–0.2$ for conventional regressions and $r = 0.01–0.16$ when using independent contrasts, $P > 0.38$ for all). Shannon diversity of mite assemblages significantly increased with an increase of host BMR (Table 1). The taxonomic distinctness of mite assemblages, Δ^+, and its variance, Λ^+, significantly decreased with an increase of either host geographical range or its BMR (Table 1). No relationship between the latter three measures of mite diversity and any other host-related parameter was found ($r^2 = 0.003–0.07$, $F = 0.1–2.9$ for conventional regressions and $r = –0.05–0.29$ for the method of independent contrasts, $P > 0.06$ for all). Nevertheless, a positive relationship between Λ^+ and the size of the host's geographical range was marginally significant ($r^2 = 0.07$, $F = 2.9$, $P = 0.09$ for conventional regression and $r = 0.29$, $P = 0.06$ when using independent contrasts).

In insectivores, the Shannon diversity of mite assemblages increased with an increase of body mass (Table 1), though this relationship is somewhat dependent on a few outliers (see Fig. 2). The same was true for the variance in taxonomic distinctness, Λ^+, when its relationship with body mass was analysed using conventional statistics, whereas a correlation between these two parameters was not supported by the method of independent contrasts (Table 1). No significant relationship between any other pair of mite- and host-related parameters was found ($r^2 = 0.003–0.14$, $F = 0.01–1.6$ for conventional regressions and $r = –0.19–0.11$ for the method of independent contrasts, $P > 0.09$ for all).

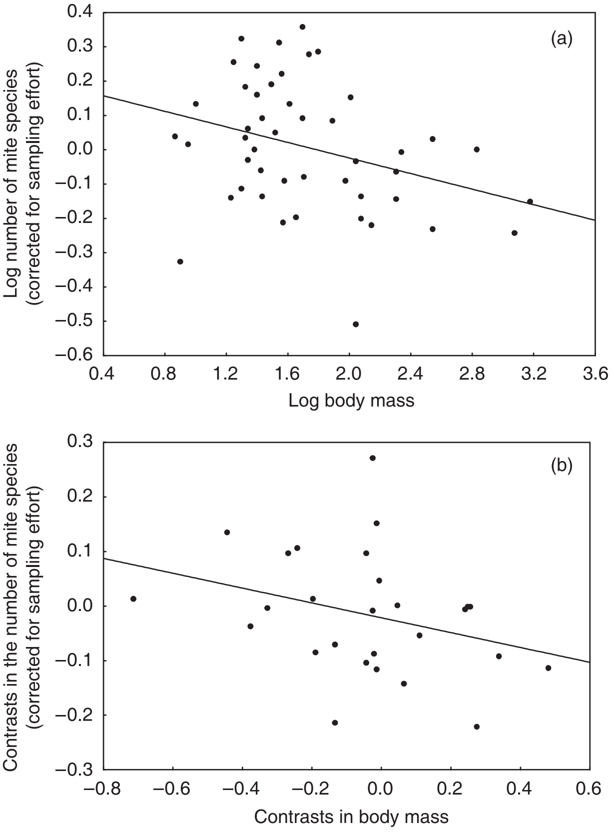

Figure 1 Relationship between mite species richness (corrected for host sampling effort) and host body mass across 45 rodent and two lagomorph species. (a) conventional regression; (b) method of independent contrasts.

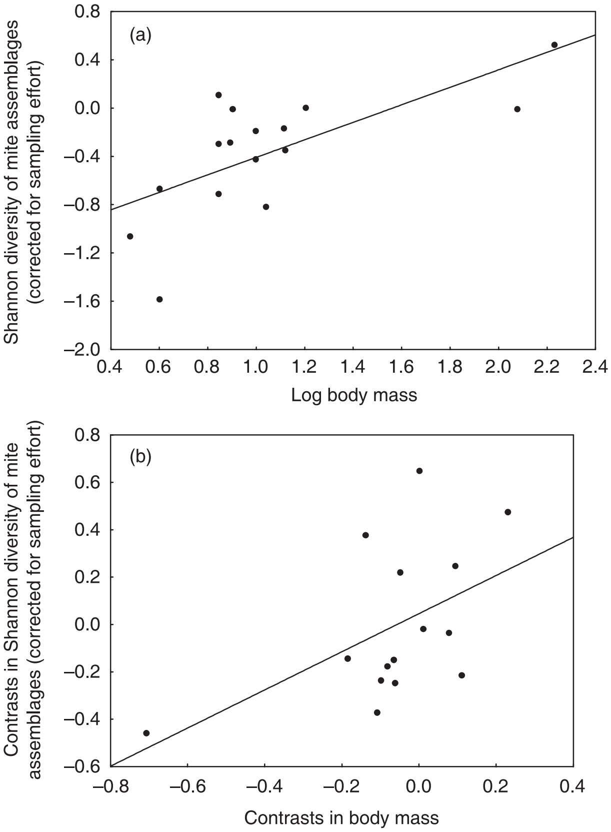

Figure 2 Relationship between Shannon diversity of mite assemblages (corrected for host sampling effort) and host body mass across 16 insectivore species. (a) conventional regression, (b) method of independent contrasts.

DISCUSSION

The main results of this study are that (1) different diversity measures capture different aspects of parasite diversity, as they display different relationships with host-related factors; (2) interspecific patterns of diversity for the same parasite taxon may differ among host taxa (diversity of mites in rodents vs. insectivores); and (3) the same host characteristics of the same host taxon may have different influences on the diversity of different parasite taxa [diversity of mites (this study) vs. diversity of fleas (Krasnov *et al*., 2004a) in rodents].

Diversity measures and parasite diversity

The most popular measure of species diversity employed in the vast majority of studies is mere species richness. Although this measure when applied to some parasites has been shown to be sensitive to some host characters (see Poulin & Morand, 2000, 2004 for review), this was not the case for mite species richness in insectivores. However, other measures of species diversity (e.g. the Shannon diversity of mite assemblages that takes into account not only the number of mite species but also their relative abundances) appeared to be correlated with some parameters of insectivore hosts. This strongly supports the notion of Poulin (2004) that the use of alternative measures may reveal diversity patterns that would not be detectable using the number of species only. For example, a measure that incorporates information on the taxonomic affinity of mite species (Δ^+) allowed the detection of a relationship between mite diversity and rodent/lagomorph host geographical range. This relationship was not identified using other diversity measures. It should be noted, however, that an earlier study of intestinal helminth assemblages in mammalian hosts did not find any relationship between parasite taxonomic distinctness and host features (Poulin & Mouillot, 2004).

Difference in mite diversity patterns among host taxa

The results of this study demonstrate sharp differences in mite diversity patterns between rodent/lagomorph and insectivore hosts. First, larger rodents harboured less diverse mite assemblages, whereas the opposite was true with insectivores. This result contradicts the common view of a host size/parasite diversity pattern as a particular case of the species–area relationship, which is one of the most pervasive ecological patterns observed in free-living organisms in support of the theory of island biogeography (see review in Rosenzweig, 1995). Indeed, why do mites on insectivore hosts behave according to this theory, whereas mites on rodent hosts do not? The answer to this question may lie in ecological differences between rodents and insectivores. In particular, the permanence of shelters (burrows and/or nests) in rodents and *Ochotona* lagomorphs is stronger than that in insectivores, at least in those from our data set (Kucheruk, 1983; Dolgov, 1985). Consequently, mites of insectivore hosts might depend more strongly on their host's body than mites of rodent/lagomorph hosts. For the latter, the main habitat might not be the host body per se but rather its burrow/nest. As a result, mite diversity might be related to the degree of complexity of the host burrow/nest rather than to its body size. Nevertheless, the relationship between mite species richness and rodent/lagomorph body size appeared to be negative. The reason for this might be a difference in the frequency of nest sanitation by relatively small and relatively large rodents. Larger rodents in our data set are mainly represented by social species with highly developed digging abilities (ground squirrels, great gerbils) for which nest sanitation and/or burrow changing behaviour is an important antiparasitic adaptation (Kucheruk, 1983; Hart, 1990), whereas this is less of a characteristic for small solitary rodents (mice and voles; but see Schmid-Holmes *et al*., 2001). In addition, some burrowing mammals, including rodents, are known to incorporate into their nests plant material that may have biocidal or fumigant properties (Hart, 1990; Hemmes *et al*., 2002). This may impede the re-colonization of a burrow by mites. An alternative explanation for the negative relationship between rodent/lagomorph body mass and mite species richness may be related to 'Eichler's rule' (host genera with higher number of species are expected to harbour a higher diversity of parasites; see Guégan *et al*., 1992). Indeed, most of the largest host species (except *Spermophilus*) from our data set either belong to monotypic genera (*Ondatra*, *Arvicola*, *Rhombomys*), or to genera represented in the Palaeoarctic by a few species only (see Appendix S1). As a result, mite species richness in these hosts is expected to be less than that in hosts belonging to more diverse taxa (*Apodemus*, *Microtus*, etc.). However, no indication of this trend was found in insectivores.

Second, rodents with higher BMR harboured more diverse mite assemblages than rodents with lower BMR, whereas no relationship between mite diversity and BMR was found in insectivores. On the one hand, the positive correlation between mass-independent BMR and mite diversity in rodents can be due to a higher energy allocation to the immune system in hosts with richer mite assemblages (Morand & Harvey, 2000). The likely reason for this is the high energy cost of maintaining a competent immune system and mounting an immune response (Sheldon & Verhulst, 1996). Furthermore, the variance in taxonomic distinctness of mite assemblages decreased with an increase of BMR, suggesting that hosts with higher BMR have taxonomically less asymmetric mite assemblages. A high value of Λ^+ suggests that one main branch in the taxonomic tree of the parasite species contributes proportionally more species to the list than other branches (Warwick & Clarke, 2001; Poulin & Mouillot, 2003). Consequently, mite assemblages in hosts with higher BMR are characterized by approximately equal number of mite species from different lineages. This supports the idea that higher BMR can be considered as a compensation for a costly immune response in hosts exposed to diverse parasite attacks (Morand & Harvey, 2000). Nevertheless, the cross-resistance of a host against closely related ectoparasites has been repeatedly reported (e.g. McTier *et al*., 1981). However, cross-resistance is due to the similarity of salivary components within a parasite taxon (Mans *et al*., 2002). This may not be the case for gamasid mites because parasitism in different lineages of this taxon is thought to have arisen independently (Radovsky, 1985). On the other hand, the lack of relationship between mite diversity and BMR in insectivores suggests that the above-mentioned mechanism is not universal. In addition, insectivores have generally very high BMR for various reasons other than parasites (see Degen, 1997). This can explain, at least partly, why insectivores that harbour either rich or poor mite assemblages do not differ in their mass-independent BMR. Also, the relatively small number of insectivore species in our data set may be a reason why no relationship between host BMR and mite diversity could be detected. The relatively low power of host BMR as a predictor of mite diversity found for rodents ($r^2 = 0.18$) supports this explanation.

Third, we found a general lack of relationship between mite diversity and the size of the host's geographical range, except for a weak negative correlation involving Δ^+ of mite assemblages in rodent/lagomorph hosts. The association between host geographical range and parasite diversity has been reported for some host–parasite systems, but not for others (e.g. Feliu *et al*., 1997 vs. Clayton & Walther, 2001). Host geographical range is expected to affect parasite diversity because of the acquisition of new parasites via host-switching in hosts with broad geographical ranges that may overlap with more other host species than narrowly distributed hosts (Gregory, 1990; Poulin & Mouillot, 2004). However, this appeared not to be the case for gamasid mites. Broadly distributed rodent hosts harboured less taxonomically diverse mite assemblages, which could be a result of losing rather than acquiring certain mite lineages with an expansion of the geographical range. A mite lineage can be lost due to, for example, unsuitability of the microclimate of a host burrow for some mite lineages in some regions (because of their sensitivity to temperature and moisture; see Krantz, 1978) as well as some unknown or even random factors.

Mite and flea diversity

A comparison of the present results with those of Krasnov *et al*. (2004a) on the effect of rodent host features on diversity of fleas suggests that these relationships vary among parasite taxa within the same host taxon. The diversity of fleas (assessed as species richness only) was affected little by parameters of the host body and to a much greater extent by parameters related to the host environment, whereas the opposite was true for gamasid mites. The reasons for this difference undoubtedly lie in differences in life history and the type of association with hosts between these two arthropod taxa. On the one hand, imago fleas are obligate haematophages, whereas the gamasids considered in this study are either obligatory or facultatively parasitic. Although this suggests that host body parameters should be more important for fleas than for mites, the results of this study point to the opposite direction. On the other hand, preimaginal fleas are almost never parasitic (larvae feed on various kinds of organic matter), whereas not only imago but also nymphal stages of many parasitic dermanyssoid mites feed on host blood (e.g. Radovsky, 1969, 1985), and some mite species spend their entire life cycle on the host body (Zemskaya, 1969). The dependence of both imago and preimaginal stages on the host body can be, at least in part, responsible for the tighter association between host body features and parasite diversity for mites than for fleas.

Host features and parasite diversity

This and previous studies that attempted to link host characters with parasite diversity have failed to find universal predictors of parasite diversity. Furthermore, the predictive power of the relationships between host features and parasite diversity found in this as well as other studies appeared to be rather low. This supports the notion of Poulin (2004) that macroecological patterns of parasite diversity are often less clear-cut than those found for free-living species. The main reason for this might be the conceptual difference between the habitat of free-living species and the habitat (= host) of parasites. The hosts are not submissive victims of parasites, they resist their exploitation by parasites and are, thus, under strong selection to evolve antiparasite defenses (Morand & Poulin, 2000). Therefore, parasite diversity of a host is the net result of the regional pool of parasite species and the negative responses of a host to this pool (Poulin, 2004).

In conclusion, relationships between host features and parasite diversity seem to be specific for each parasite–host association. In particular, this may result in weak or no relationships between host features and parasite diversity when different parasite taxa are pooled together for analysis. This is because the differential patterns of relationships between host characters and diversity of different parasite taxa can mask or even nullify each other when not considered separately.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Data on diversity of mite assemblages and metabolic characteristics in 63 small mammal species.

Appendix S2 Data on regions where small mammal and mite surveys have been carried out.

This material is available as part of the online article from:
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