Searching for general patterns in parasite ecology: host identity versus environmental influence on gamasid mite assemblages in small mammals

B. R. KRASNOV[1,2]*, N. P. KORALLO-VINARSKAYA[3], M. V. VINARSKI[4], G. I. SHENBROT[1,2], D. MOUILLOT[5] *and* R. POULIN[6]

[1] *Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 84490 Midreshet Ben-Gurion, Israel*
[2] *Ramon Science Center, P.O. Box 194, 80600 Mizpe Ramon, Israel*
[3] *Laboratory of Arthropod-Borne Viral Infections, Omsk Research Institute of Natural Foci Infections, Mira str. 7, 644080 Omsk, Russia*
[4] *Department of Ecology and Environment Conservation, Omsk State Pedagogical University, Tukhachevskogo emb. 14, 644099 Omsk, Russia*
[5] *UMR CNRS-UMII 5119 Ecosystemes Lagunaires, University of Montpellier II, CC093, FR-34095 Montpellier Cedex 5, France*
[6] *Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand*

(*Received 13 June 2007; revised 6 August 2007; accepted 6 August 2007; first published online 2 October 2007*)

SUMMARY

The abundance and diversity of parasites vary among different populations of host species. In some host-parasite associations, much of the variation seems to depend on the identity of the host species, whereas in other cases it is better explained by local environmental conditions. The few parasite taxa investigated to date make it difficult to discern any general pattern governing large-scale variation in abundance or diversity. Here, we test whether the abundance and diversity of gamasid mites parasitic on small mammals across different regions of the Palaearctic are determined mainly by host identity or by parameters of the abiotic environment. Using data from 42 host species from 26 distinct regions, we found that mite abundances on different populations of the same host species were more similar to each other than expected by chance, and varied significantly among host species, with half of the variance among samples explained by differences between host species. A similar but less pronounced pattern was observed for mite diversity, measured both as species richness and as the taxonomic distinctness of mite species within an assemblage. Strong environmental effects were also observed, with local temperature and precipitation correlating with mite abundance and species richness, respectively, across populations of the same host species, for many of the host species examined. These results are compared to those obtained for other groups of parasites, notably fleas, and discussed in light of attempts to find general rules governing the geographical variation in the abundance and diversity of parasite assemblages.

Key words: abundance, gamasid mites, repeatability, small mammals, species richness.

INTRODUCTION

Any scientific study, including those on parasite ecology, reveals some patterns or processes. However, a question always remains: how general are these patterns and processes and to what extent do they apply to taxa, settings, or times other than those that were the subject of study? The findings of a particular study should invariably be validated by studies in other geographical locations or on other taxa, if we are to uncover any general law (Poulin, 2007). The identification of such patterns would suggest that apparently diverse and idiosyncratic assemblages may have common and self-organizing principles. Ultimately, the goal of such a comparative approach should be to identify these processes underpinning any observed universal pattern.

For example, studies of variation in parasite abundance and/or species richness across different populations of the same host species have demonstrated that these parameters, on the one hand, represent genuine host species traits. This was found, for example, for nematodes (abundance) (Arneberg *et al*. 1997) and fleas (abundance and species richness) (Krasnov *et al*. 2005, 2006) in mammalian hosts and endoparasites of teleost fish (abundance) (Poulin, 2006), but not for intestinal helminths of mammals (species richness) (Poulin and Mouillot, 2004). On the other hand, these parameters might be also

* Corresponding author: Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 84490 Midreshet Ben-Gurion, Israel. Tel: +972 8 6596841. Fax: +972 8 6596772. E-mail: krasnov@bgu.ac.il

doi:10.1017/S003118200700368X Printed in the United Kingdom

substantially affected by environmental parameters and be considered as characteristic of a geographical locality (Krasnov *et al*. 2006). Furthermore, when taxonomic composition of parasite assemblages rather than mere number of species was taken into account, it appeared that this parameter was repeatable in helminth endoparasites of mammals (Poulin and Mouillot, 2004) but was as variable across, as within, host species in fleas (Krasnov *et al*. 2005). Thus, at first glance, one may conclude that the repeatability of parasite abundance within host species emerges as a general rule while species richness and taxonomic diversity do not, although whether it applies universally within localities across host species remains to be further validated.

When the percentage of variation among samples accounted for by differences among host species is considered, it appears that the relative strength of the effect of host identity on parasite species richness varies greatly among parasite and host taxa. For example, the difference between mammalian hosts as opposed to that among populations within a host explained 32·8% of the variation for flea assemblages on mammals (Krasnov *et al*. 2005), 32% for larval trematodes in snails (Poulin and Mouritsen, 2003), but only 14·5% for intestinal helminths in mammals (Poulin and Mouillot, 2004). On the other hand, the proportion of the variance in parasite abundance or prevalence that occurred among host species, as opposed to within, was 24·1% for mammalian hosts and fleas (for abundance), whereas this value attained 23% for larval trematodes in snail hosts (for prevalence) (Poulin and Mouritsen, 2003) and only 13% for various metazoan parasites in fish hosts (for abundance) (Poulin, 2006). This suggests that the effect of host identity on infestation parameters of different parasite taxa depends on some peculiarities of the relationships in a particular host-parasite association. For example, assemblages of fleas were found to be affected little by morphological and physiological features of a host species, but much more strongly by the parameters of the host environment (Krasnov *et al*. 2004). As mentioned above, in this parasite-host association, the proportion of the variation in parasite abundance and species richness among host samples associated with differences between host species was not particularly high (Krasnov *et al*. 2005, 2006).

Another taxon of haematophagous arthropods, gamasid mites, display quite different patterns in their relationships with host features (Korallo *et al*. 2007). When the diversity of these parasites was considered among roughly the same set of host species in roughly the same geographical area as with fleas, it appeared to be strongly affected by species-specific host features and much less by parameters of the host environment. Consequently, mite assemblages are expected to depend more strongly on host identity than was the case for fleas.

Gamasids are characterized by extremely high interspecific variation in their ecology and feeding modes. They include soil-dwelling and nidicolous predators, and both facultative and obligate vertebrate ecto- and endoparasites (see Radovsky, 1985 for review). However, here we focused on haematophagous species 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).

The aim of this study was to test whether the abundance and diversity of gamasid mites parasitic on small mammals from 26 different geographical regions of the Palaearctic are determined mainly by host identity rather than by parameters of the abiotic environment. The focus of our analyses is on the contemporary patterns that can be observed, rather than on their underlying co-phylogenetic historical origins. We evaluated the repeatability of estimates of mite abundance and diversity across populations of the same host species, to determine if the abundance and diversity are repeatable within host species; i.e. if the values of abundance and diversity are more similar among populations of the same host species or regions than among different host species or regions, respectively. In addition, we searched for correlations between the abiotic characteristics of a region and mite abundance and diversity, separately for several host species.

MATERIALS AND METHODS

Data set

Data on gamasid mites collected from the bodies of small mammals (Soricomorpha, Lagomorpha and Rodentia) in 26 different regions of the Palaearctic were obtained from published surveys and unpublished data that reported the number of mites of a particular species found on each given small mammal species in a particular location (Table 1). We used data on host species that (a) occurred and were found infested with gamasid mites in at least 2 regions and (b) were represented in a regional survey by at least 3 individuals. This amounted to 42 host species (31 rodents, 10 soricomorphs and 1 lagomorph) occurring in 26 regions and comprising 237 host-region associations.

Abundance and diversity estimates

For each host species in each region we calculated abundance of all mite species as well as 2 measures of the diversity of mite assemblages, namely species richness and taxonomic distinctness (Δ^+). Abundance of mites was calculated as mean number of mites per individual host. Other measures of infection level, such as prevalence and intensity of

Table 1. Data on small mammals from 26 regions used in the analyses

(Numbers in parentheses represent the total numbers of sampled individuals.)

Region	Number of species (individuals)	Source
North Asian Far East	11 (1228)	Yudin *et al*. (1976)
Altai Steppe	6 (146)	Davydova and Belova (1972)
Russian Far East	16 (24 683)	Volkov and Chernykh (1977)
Krasnodar region	14 (25 703)	Shevchenko *et al*. (1975)
Kuznetsk Alatau (Siberia)	9 (1238)	Igolkin *et al*. (1976)
Moscow region	11 (143 204)	Lopatina *et al*. (1998)
Novosibirsk region	23 (6452)	Dobrotvorsky, unpublished data
Omsk region (forest-steppe zone)	22 (7681)	Korallo, unpublished data
Omsk region (steppe zone)	4 (56)	Korallo, unpublished data
Omsk region (forest zone)	13 (1,953)	Korallo, unpublished data
Tomsk region	9 (533)	Davydova and Belova (1972)
Romania	13 (260)	Lange and Hamar (1961)
Pskov region	4 (693)	Stanjukovich (1987)
Selenga River (Central Siberia)	8 (1793)	Pauller *et al*. (1966)
Eastern Baikalo-Amur Magistral (BAM) (Eastern Siberia)	13 (1453)	Volkov *et al*. (1978)
Kamchatka Peninsula	5 (255)	Vasiliev *et al*. (1978)
Buryatia	11 (4,105)	Stupina (1979)
Western Predverkhoyanje (Yakutia)	10 (1,576)	Plesnivtseva (1982)
Eastern Kazakhstan	3 (22)	Piontkovskaya and Ivanov (1960)
Slovakia	7 (1635)	Ambros *et al*. (2001)
Western Taimyr Peninsula	8 (581)	Davydova *et al*. (1980)
Pur River (Northern Siberia)	4 (323)	Davydova and Belova (1972)
Lower Ob' floodplain	4 (103)	Davydova and Belova (1972)
Central Yakutia	4 (493)	Elshanskaya and Popov (1972)
Eastern Taimyr peninsula	3 (1,780)	Bogdanov (1979)
Balkhash lake (Kazakhstan)	1 (12)	Morozova *et al*. (1963)

infestation, were not available for most of the regions considered. Mite abundance correlated weakly, albeit significantly, with host sampling effort (number of host individuals examined) ($r^2 = 0{\cdot}02$, $F_{1,234} = 5{\cdot}6$, $P < 0{\cdot}05$; after log transformation). Consequently, to control for the confounding effort of unequal sampling, the original values of mite abundance were substituted with their residual deviations from the regression on sampling effort in log-log space.

The two measures of mite species diversity we used were (a) the number of mite species found on a host species, or species richness and (b) average taxonomic distinctness (Δ^+) of the mite species present. Estimates of parasite species richness may be biased if some hosts are examined more intensively than others (Morand and Poulin, 1998). Indeed, mite species richness appeared to be strongly affected by sampling effort ($r^2 = 0{\cdot}44$, $F_{1,234} = 186{\cdot}3$, $P < 0{\cdot}001$). Consequently, each value of mite species richness was then substituted by its residual deviation from a regression on the number of hosts examined in log-log space. This provided a measure of mite species richness that is independent of sampling effort.

When these mite 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 mite species, computed across all possible pairs of mite species (Clarke and Warwick, 1998, 1999; Warwick and Clarke, 2001; Poulin and Mouillot, 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^+. Using the taxonomic classification of Bregetova (1956), Radovsky (1985), and Halliday (1998), all mite species were fitted into a taxonomic structure with 4 hierarchical levels above species, i. e. genus, subfamily, family and superfamily (Dermanyssoidea). 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 subgenus or species group). However, since 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 number of mite species exploiting a host species was significantly positively correlated (albeit weakly) with Δ^+ ($r^2 = 0{\cdot}37$, $F_{1,234} = 140{\cdot}8$, $P < 0{\cdot}001$), indicating that this measure was influenced by the number of species in an assemblage. Therefore, in subsequent analyses Δ^+ was corrected for mite species richness in an assemblage by substituting the original values with their residual deviations from the regression on mite species richness in log-(log + 1) space.

Table 2. Linear correlation (r) between each of the principal components (factors F1, F2 and F3) and each of 7 environmental variables calculated for each of 26 geographical regions

	Principal component		
Environmental variable	F1	F2	F3
Mean elevation	0·34	0·76	−0·32
Annual precipitation	0·18	0·50	0·84
Winter precipitation	−0·03	0·92	0·26
Summer precipitation	0·19	−0·17	0·91
Mean surface air temperature of January	0·88	0·12	0·45
Mean surface air temperature of July	0·93	0·14	−0·02
Mean annual surface air temperature	0·74	0·03	0·62

Environmental factors

For each region, we computed climatic variables (annual, winter and summer precipitation, mean surface air temperature of January, mean surface air temperature of July, and mean annual surface air temperature) and elevation parameters using the Global Ecosystems database (Kineman *et al*. 2000). These variables where calculated for a buffer of 100×100 km around the centre of each region (because it was not possible to pinpoint the precise sampling area for some of the regions). Because some of these variables strongly correlated with each other, we substituted them with the scores of principal components calculated from these 7 variables. The resulting 3 factors explained 91·5% of the variance, and their eigenvalues were 3·58, 1·59 and 1·23. The first factor (F1) represented an increase in air temperature, whereas the second (F2) and third (F3) factors represented an increase in (a) mean elevation and winter precipitation and (b) annual and summer precipitation, respectively (Table 2).

Data analysis

To determine whether abundance and species diversity of mite assemblages, expressed either as mite species richness or average taxonomic distinctness among mites (Δ^+), are geographically invariant, i.e. a parameter that varies less among populations of the same host species than among host species, we performed a repeatability analysis (see Arneberg *et al*. 1997; Poulin and Mouritsen, 2003; Poulin and Mouillot, 2004; Krasnov *et al*. 2005, 2006). Using host species which occurred in at least 2 regions, we analysed the variation in the mite abundance, number of mite species and taxonomic distinctness among mites (Δ^+) in 3 separate one-way ANOVAs in which host species was the independent factor. A significant effect of host species would indicate that the measures are repeatable within host species, i.e. that they are more similar to each other than to values from other host species. We estimated the proportion of the total variance originating from differences among host species, as opposed to within species, following Sokal and Rohlf (1995). To assess whether mite abundance and diversity are determined also by a complex of environmental conditions, we performed the repeatability analyses using regions where at least 2 of 42 hosts occurred (as a proxy for geographical differences in a set of environmental conditions) instead of host species as the single factor (25 regions). A significant effect of region would indicate that the mite abundances and/or diversities are repeatable within region, i.e. that they are more similar among populations of different host species within the same region than among regions.

We analysed the effect of environmental parameters (expressed as 3 composite variables extracted from original environmental measures using principal component analysis, see above) on variation in abundance and diversity of mite assemblages across regions, within each of 18 host species which occurred in at least 6 regions using Generalized Linear Models (GLM) with a normal distribution and power-link function, and searched for the best model using the Akaike's Information Criterion. Then, we tested the significance of the parameter estimates in each best model using the Wald statistic.

We did not apply the Bonferroni adjustment of alpha-level as this approach has been increasingly criticized by statisticians and ecologists in recent years, because it often leads to the incorrect acceptance of the false null hypothesis when multiple comparisons are in fact independent of one another (Rothman, 1990; Perneger, 1998, 1999; Moran, 2003; Garcia, 2004) as is the case in our study.

RESULTS

Each of the 42 host species in the data set was recorded from between 2 and 17 regions. The repeatability analysis for these host species demonstrated that mean mite abundance per host individual was repeatable within host species. Abundances of mites on the same host species were more similar to each other than expected by chance, and varied significantly among hosts ($F_{41,194} = 6{\cdot}6$, $P < 0{\cdot}0001$), with 50·3% of the variation among samples explained by differences between host species (Fig. 1A). At the same time, abundances of mites were also repeatable among host species within a region ($F_{24,210} = 2{\cdot}7$, $P < 0{\cdot}0001$), although only 16·3% of the variation among samples was accounted for by differences between regions (Fig. 1B).

Host- and region-related patterns of variation in mite species diversity differed from those for

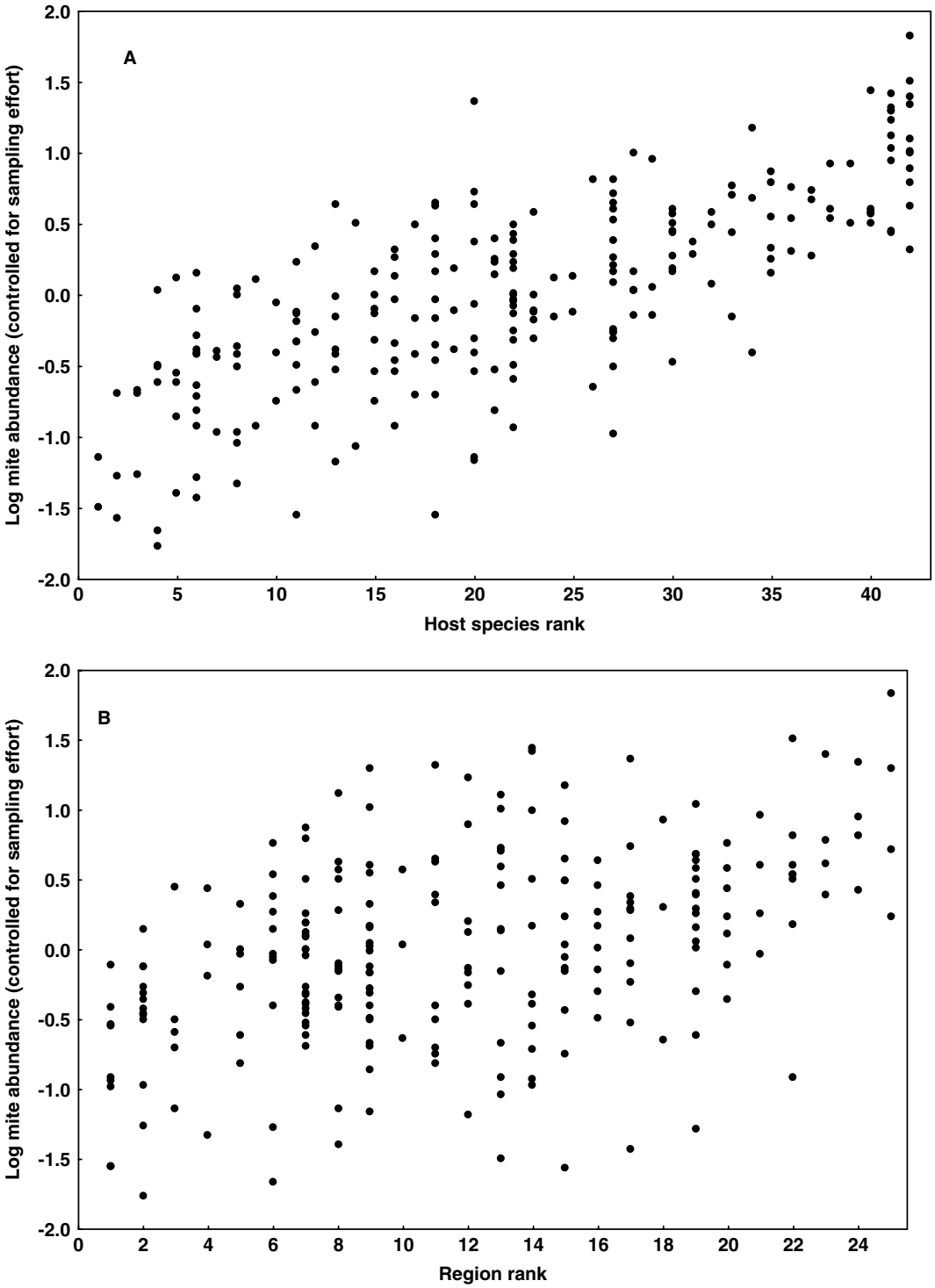

Fig. 1. Rank plot of mite abundance across 42 hosts (A) and 25 regions (B). The 42 host species recorded in at least 2 regions (A) and 25 regions where at least 2 host species occurred (B) are ranked according to mean log-transformed mite abundance values corrected for host sampling effort, with rank 1 given to the host or region with the lowest mean mite abundance; all sample estimates are plotted for each host species or region. If variation is small within compared to between host species or region, we expect the points of the plot to stretch from the lower left to the upper right corner, with few or no points in either the upper left or lower right corner.

abundance. Although mite species richness was repeatable both within host species among regions and among host species within a region ($F_{41,194}=2{\cdot}6$ and $F_{24,210}=4{\cdot}7$, respectively; $P<0{\cdot}01$ for both; Fig. 2), the percentage of the variation among samples explained by differences between host species was slightly lower than that accounted for by differences between regions (22·4% versus 29·5%, respectively). In contrast, taxonomic distinctness of mite assemblages was only weakly, but significantly, repeatable

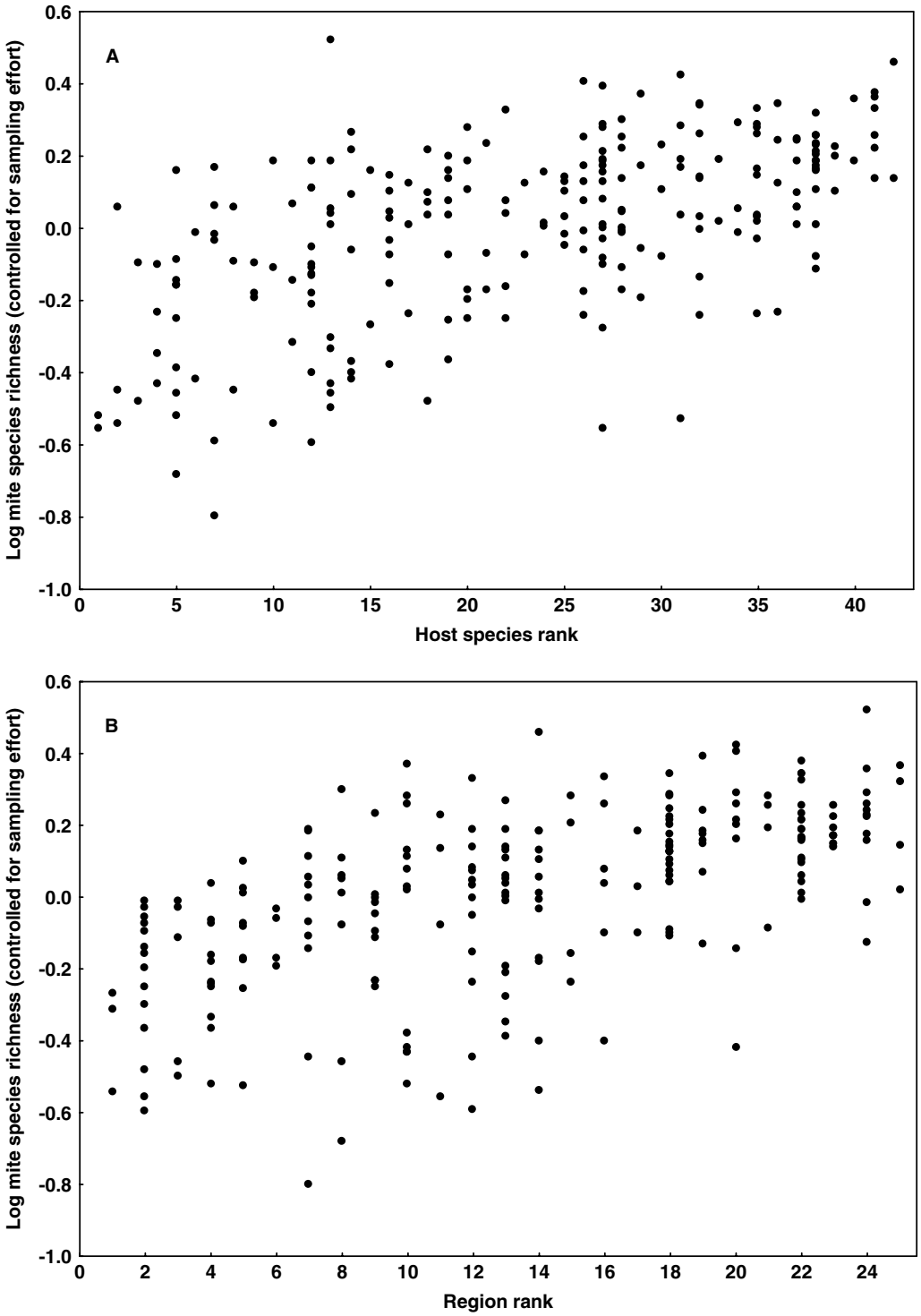

Fig. 2. Rank plot of mite species richness across 42 hosts (A) and 25 regions (B). See Fig. 1 for explanations.

within host species ($F_{41,194}=1{\cdot}7$, $P<0{\cdot}05$) with only 10·3% of the variation among samples accounted by differences between hosts, but it was not repeatable among host species within a region ($F_{24,210}=1{\cdot}3$, $P>0{\cdot}1$) (Fig. 3).

In 15 of 18 host species (except for *Apodemus agrarius*, *Micromys minutus* and *Mus musculus*), at least 1 of the parameters characterizing mite assemblages was correlated (positively or negatively) with at least 1 environmental factor. Of them, mite abundance was affected by the environment in 13 hosts, whereas mite species richness and taxonomic diversity were affected by the environment in 7 hosts each (although these two sets of host species were different) (Tables 3 and 4). In addition, as can be seen from Table 4, mite abundance was affected by air temperature (F1; alone or in interaction with other factors) in 11 hosts (positively in 6 cases and

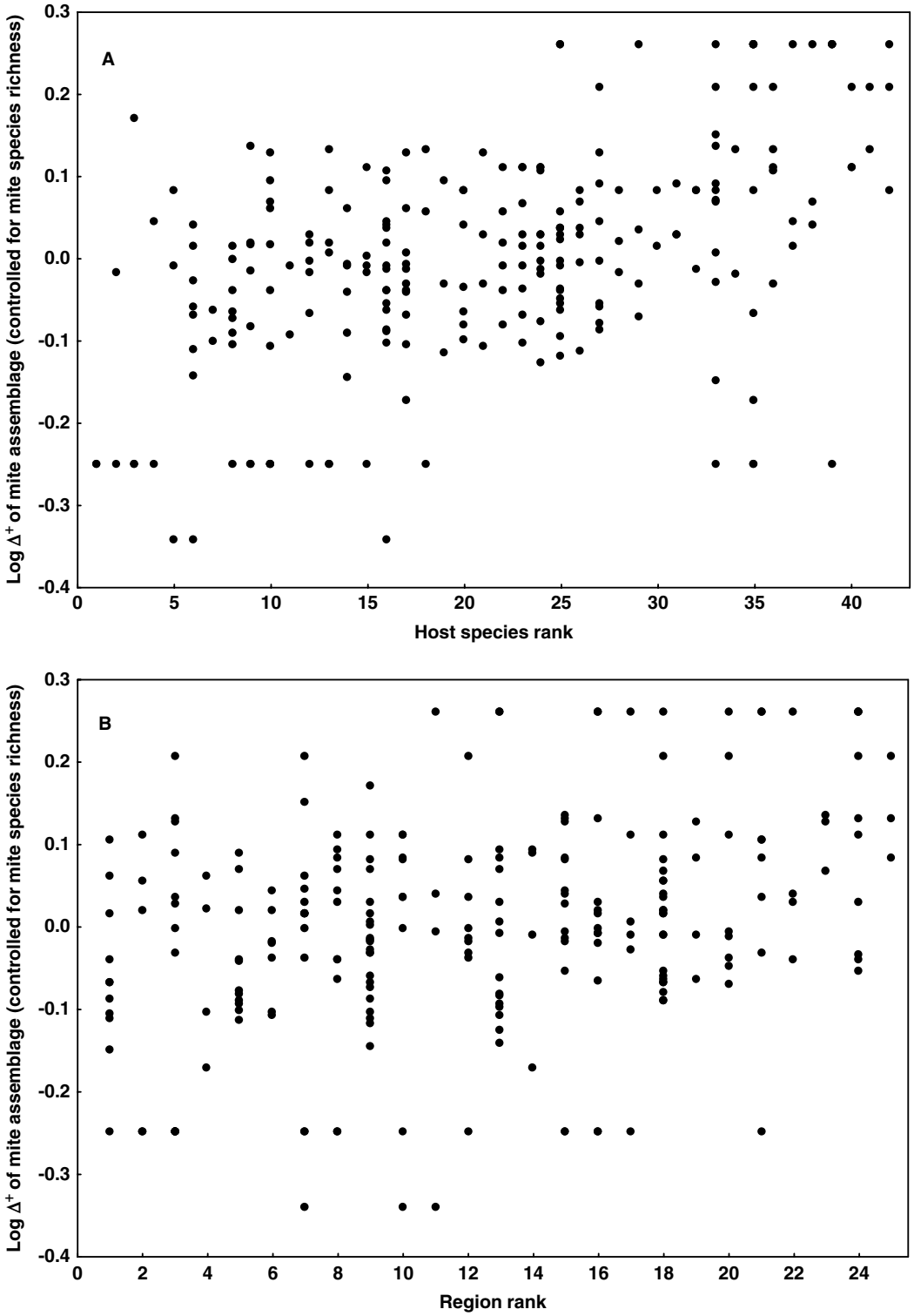

Fig. 3. Rank plot of mite taxonomic distinctness (Δ^+) across 42 hosts (A) and 25 regions (B). See Fig. 1 for explanations.

negatively in 5 cases), by elevation (F2; alone or in interaction with other factors) in 7 hosts (positively in 4 cases and negatively in 3 cases) and by precipitation (F3; alone or in interaction with other factors) in 7 hosts (positively in 2 cases and negatively in 5 cases) (see an illustrative example with *Arvicola amphibius* in Fig. 4). Similarly, mite species richness was affected by factor F1 in 4 hosts (positively in all cases), by factor F2 in 3 hosts (positively in 2 cases and negatively in 1 case) and by factor F3 in 6 hosts (positively in 2 cases and negatively in 4 cases) (see an illustrative example with *Microtus arvalis* in Fig. 5). Taxonomic distinctness of mite assemblages was affected by factor F1 in 4 hosts (positively in 1 case

Table 3. The significant ($P<0{\cdot}05$) best models explaining variance in abundance (A), species richness (SR) and taxonomic distinctness (Δ^+) of gamasid mite assemblages on 15 small mammalian species

(The modelling was carried out using a Generalized Linear Model with the application of Akaike's Information Criterion (AIC) for the best model selection. F1, F2 and F3 are composite variables extracted from 7 environmental variables calculated for each region (see text and Table 2 for explanations).)

Host species	Parameter of mite assemblage	Model	AIC	Likelihood ratio χ^2
Apodemus peninsulae	A	F2	2·21	6·51
Apodemus sylvaticus	A	F2	3·88	13·10
	SR	F1, F2, F3	16·27	22·33
Arvicola amphibius	A	F1	7·25	8·15
	Δ^+	F1, F2	27·16	9·49
Eutamias sibiricus	A	F1, F2	0·73	12·79
	SR	F1, F2, F3	−21·97	15·53
Microtus agrestis	A	F1, F3	7·17	17·21
	SR	F2, F3	8·13	16·79
	Δ^+	F1, F2, F3	22·46	19·28
Microtus arvalis	SR	F3	4·09	4·01
Microtus gregalis	A	F1, F2	0·23	7·48
Microtus oeconomus	A	F1, F2, F3	6·34	24·14
Myodes glareolus	A	F2, F3	6·75	13·29
	Δ^+	F3	28·70	10·71
Myodes rufocanus	A	F1, F3	18·90	7·74
	SR	F1	−11·94	4·33
Myodes rutilus	A	F1, F3	14·62	6·02
Ondatra zibethica	Δ^+	F3	4·74	6·01
Rattus norvegicus	A	F3	21·40	8·05
	SR	F3	2·80	6·64
Sorex araneus	A	F1, F2, F3	7·94	10·54
	Δ^+	F1	19·70	5·22
Sorex caecutiens	A	F1, F2, F3	0·73	12·79
	SR	F1, F3	−21·97	15·53
	Δ^+	F1, F3	−16·08	3·91

and negatively in 3 cases), by factor F2 in 2 hosts (positively in 1 case and negatively in 1 case) and by factor F3 in 4 hosts (positively in 1 case and negatively in 3 cases). In other words, abundance of mites was affected mainly by air temperature, whereas mite species richness was affected mainly by precipitation (see an illustrative example with *Ondatra zibethica* in Fig. 6).

DISCUSSION

The results of this study support our expectation that abundance and taxonomic diversity of gamasid mite assemblages depend more on host identity than on environmental parameters, although the species richness of mites appeared to be almost equally dependent on host identity and environmental factors. In other words, the abundance and taxonomic diversity of mites can be considered as genuine host species characters with some host species harbouring consistently higher numbers of mites representing more higher taxa than other host species. Furthermore, the species richness of the component communities of gamasid mites may instead represent a local characteristic, with some localities being characterized by higher mite species richness in all host species than other localities.

These results support the idea that part of the parasite community observed on a host is due to its identity, as a direct result of the co-phylogenetic history of hosts and their parasites, whereas another part is due to its specific geographical location (Kennedy and Bush, 1994). In the case of gamasid mites, the source of variation associated with host identity must derive from interspecific differences in host biology. For example, mite diversity has been shown to correlate with host body mass (Korallo *et al*. 2007). However, the direction of this correlation depends on which higher host taxon is considered. Larger rodents harboured less diverse mite assemblages, whereas the opposite was true for soricomorphs. Differences in basal metabolic rate can also play a role. In general, rodent hosts with higher basal metabolic rates harbour more diverse mite assemblages than hosts with lower BMR (Korallo *et al*. 2007). Both these features, body mass and basal

Table 4. Parameter estimates for the significant best models (see Table 3) explaining variance in abundance (A), species richness (SR) and taxonomic distinctness (Δ^+) of gamasid mite assemblages on 15 small mammalian species

(F1, F2 and F3 are composite variables extracted from 7 environmental variables calculated for each region (see text and Table 2 for explanations). All parameters are significant ($P<0{\cdot}05$).)

Host species	Parameter of mite assemblage	Model	Wald statistic for parameter estimates
A. peninsulae	A	0·20F2	10·4
A. sylvaticus	A	0·62F2	48·5
	SR	0·17F1 + 0·14F2 − 0·25F3	33·1/32·6/167·5
A. amphibius	A	−0·31F1	10·3
	Δ^+	−0·04F1 + 0·09F2	5·0/8·9
E. sibiricus	A	0·15F1 + 0·67F2	10·1/29·5
	SR	0·03F1 + 0·02F2 + 0·11F3	6·0/17·3/49·6
M. agrestis	A	0·33F1 + 0·32F3	5·1/20·0
	SR	−0·62F2 + 0·21F3	77·7/7·4
	Δ^+	−0·16F1 − 0·14F2 + 0·16F3	15·0/60·6/64·1
M. arvalis	SR	−0·18F3	6·6
M. gregalis	A	0·40F1 − 0·35F2	9·3/6·5
M. oeconomus	A	−0·20F1 − 0·66F2 − 0·25F3	4·8/27·2/12·1
M. glareolus	A	−0·74F2 + 0·40F3	16·8/9·9
	Δ^+	−0·09F3	20·6
M. rufocanus	A	0·24F1 − 0·45F3	4·8/8·3
	SR	0·14F1	4·6
M. rutilus	A	−0·25F1 − 0·20F3	5·0/4·4
O. zibethica	Δ^+	−0·13F3	8·7
R. norvegicus	A	−0·44F3	8·1
	SR	−0·19F3	8·2
S. araneus	A	0·75F1 − 0·60F2 − 0·51F3	4·6/9·4/14·3
	Δ^+	−0·16F1	4·1
S. caecutiens	A	1·28F1 + 0·23F2 − 1·63F3	44·1/12·2/55·7
	SR	0·92F1 − 0·89F3	95·0/68·7
	Δ^+	0·34F1 − 0·44F3	119·8/155·6

metabolic rate, are rather conservative within-species (Peters, 1983; Degen, 1997).

The likely source of geographical variation in mite assemblages is the local diversity of the host's biotic and abiotic environment. For example, a richer community of co-habitating hosts increases the probability of lateral transfer of parasites and, thus, affects richness and composition of a parasite assemblage (Caro *et al*. 1997; but see Korallo *et al*. 2007 for gamasid mites). The abiotic environment external to a host, such as air temperature and precipitation or substrate texture, can also affect parasite species composition (Galaktionov, 1996; Krasnov *et al*. 1998). Indeed, gamasid mites, both parasitic (e.g. Carrol *et al*. 1992) and free-living (e.g. Sjursen *et al*. 2005), are strongly affected by temperature with different species having different temperature preferences (e.g. Avdonin and Striganova, 2005). Another factor that may strongly affect mite abundance is relative humidity (e.g. Mašan and Stanko, 2005). Furthermore, humidity tolerance varies among mite species. For example, *Ophionyssus galloticolus* is more tolerant of low humidity than *Ophionyssus natricis* (Bannert *et al*. 2000).

Differential environmental preferences by different species may be a reason behind the inconsistent relationships between various aspects of mite assemblages and environmental variables across host species. Indeed, environmental factors were often correlated with one or more parameters of mite assemblages either positively or negatively, but no distinct prevailing trend could be distinguished. The repeatability of mite species richness and their taxonomic distinctness suggests that, in general, every host species harbours a mite assemblage of a certain composition independently of its geographical locality. If, for example, most mite species in a host-specific assemblage prefer relatively low temperature, then the abundance of mites would decrease with increasing air temperature, whereas the opposite would be true if most mite species in a host-specific assemblage preferred relatively high temperatures. However, no data supporting this explanation are available. This is because environmental preferences for the vast majority of mite species in our data set are unknown.

A comparison of the amount of variance among samples accounted for by differences among host

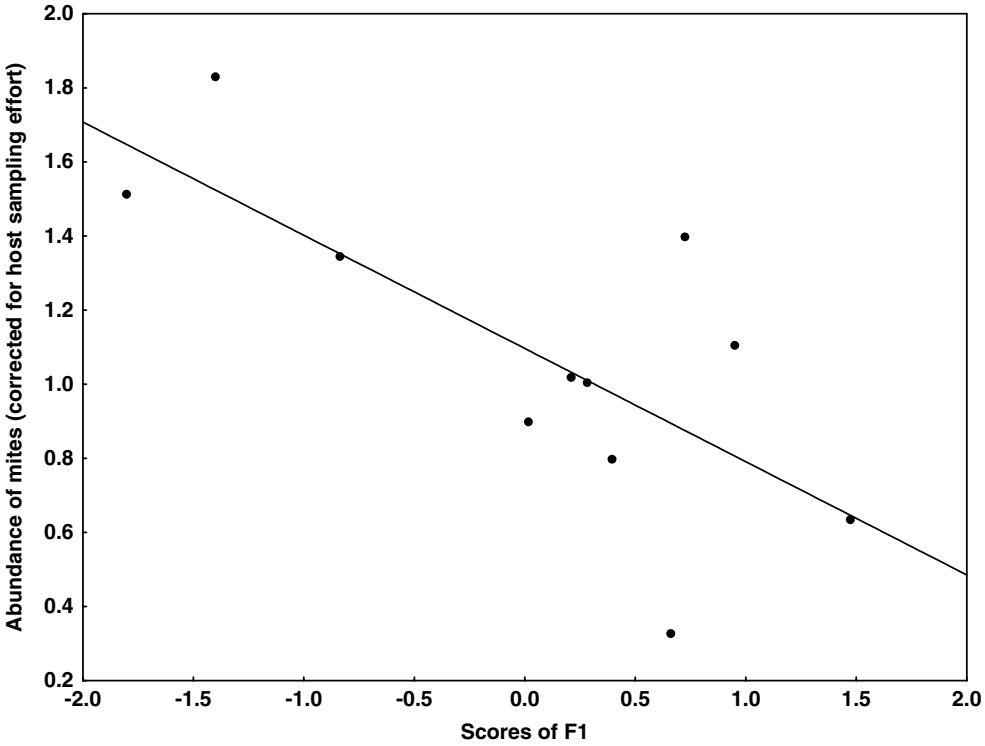

Fig. 4. Relationship between total mite abundance and scores of factor F1 across populations of *Arvicola amphibus*.

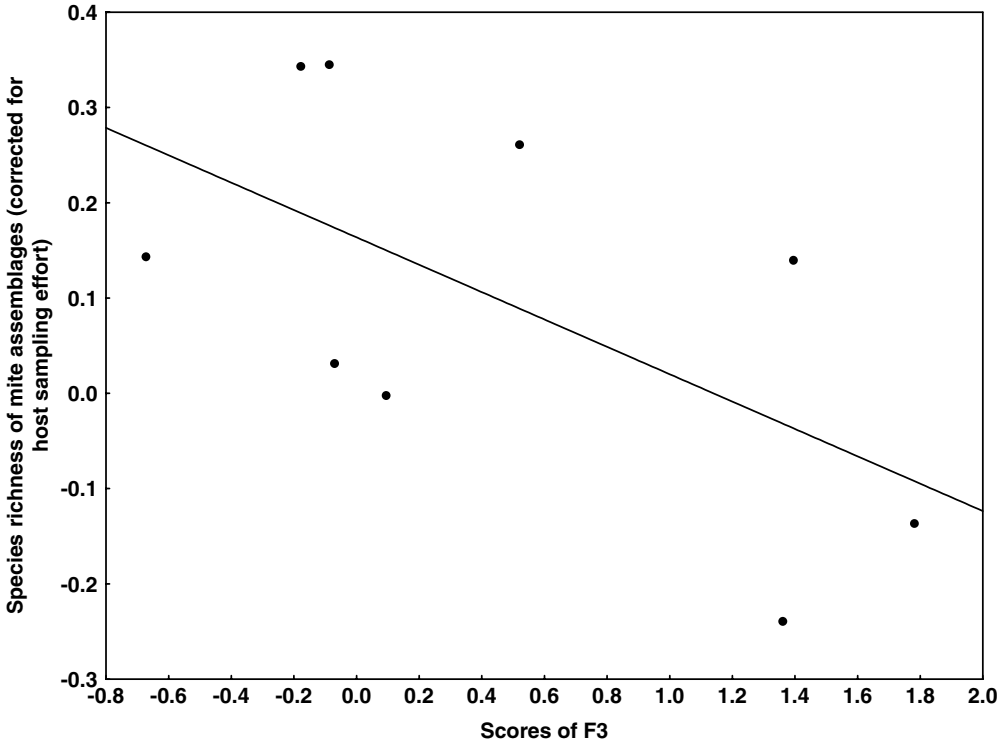

Fig. 5. Relationship between species richness of mite assemblages and scores of factor F3 across populations of *Microtus arvalis*.

species or regions as opposed to those within hosts and regions suggests that the abundance and taxonomic distinctness of mites is mainly determined by host identity, whereas their species richness depends almost equally on both host identity and geographical locality. A reason for repeatable mite species richness among populations within a host species may be associated with some host constraints on how

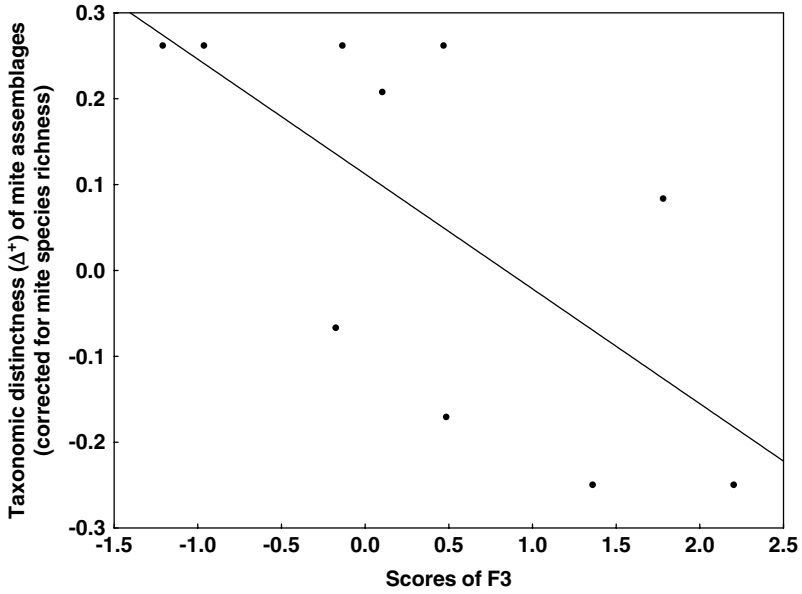

Fig. 6. Relationship between taxonomic distinctness of mite assemblages and scores of factor F3 across populations of *Ondatra zibethica*.

many mite species it can harbour. For example, there can be a limit to a host's ability to cope with multiple mite species, such that the host manages to maintain mite pressure (expressed as a number of parasite species) at a 'tolerable' level (Combes, 2001). The repeatability of mite species richness among host species within a region may be due to variability in the external environment that can lead to, for example, extinction of certain mite species in some regions due to unsuitable microclimatic conditions in host burrows.

Taxonomic distinctness of mite assemblages was found to be weakly, albeit significantly, repeatable within a host species, as reported for helminths (Poulin and Mouillot, 2004), but not for fleas (Krasnov *et al*. 2005). This means that whenever a new species is added to a host's mite community, this species is not a random addition from the regional pool of mite species but rather is closely related to the mite species that a host already harbours. As in closely-related free-living species that have similar life-history traits (Brooks and McLennan, 1991; Harvey and Pagel, 1991), closely-related mite species may also have similar environmental and host preferences. Therefore, the suitability of a host species for a new mite species may be indicated by the occurrence of this mite's close relatives in mite assemblages already on this host. This supports our previous findings of a high similarity in the composition of mite communities within a host species at different, sometimes geographically distant, locations (Vinarski *et al*. 2007). Another explanation for the repeatability of mite taxonomic distinctness may be related to co-evolution of mites with their hosts. In other words, this pattern can arise as a consequence of a co-evolutionary history dominated mainly by co-speciation. If a mite lineage co-evolved tightly with its host, then it would only spread around the Palaearctic together with the host. Although no study on the co-evolution of dermanyssoid mites and their mammalian hosts has been carried out, strong evidence for such a pattern of co-evolution was found in other parasitic mites (Bochkov and OConnor, 2005). In addition, the contrasting patterns of repeatability of taxonomic distinctness obtained for mite and flea assemblages suggest that the 'tightness' of association between a parasite and its host matters when within-host geographical variation of parasite assemblage structure is considered. Fleas spend a considerable time off host and are strongly affected by the off-host environment and, although they are obligate haematophages, their larvae are almost never parasitic (Marshall, 1981). The gamasids considered in this study are either obligate or facultative parasites. However, haematophagy is a characteristic feeding mode not only for the imago but also for nymphal stages of many dermanyssoid mites (Radovsky, 1969, 1985). Moreover, some mite species spend their entire life-cycle on the host body (Zemskaya, 1969). The dependence of both imago and pre-imaginal stages on the host can be, at least in part, responsible for the tighter association between mites and hosts than is the case for fleas and hosts and, thus, for the repeatability of taxonomic diversity of mite assemblages within a host species. Nevertheless, although this parameter has not been found to be repeatable within a geographical locality in general, it was affected by environmental factors among different populations of 6 host species (*Arvicola amphibius*, *Microtus agrestis*, *Myodes glareolus*, *Ondatra zibethica*, *Sorex araneus* and *Sorex caecutiens*). In

most cases, the taxonomic diversity of mites in these hosts decreased with an increase in winter precipitation and/or air temperature. Most of these hosts occupy habitats that are frequently flooded by melting snow which starts earlier in spring in areas with high air temperatures and which can cause the disappearance of those mite lineages that spend their life both on the host body and in host burrows in areas with high levels of snowfall.

Environmental factors clearly influenced mite assemblages: the abundance of mites was mainly affected by air temperature, whereas the diversity of mites was mainly affected by precipitation. These results call for some explanation. It is possible that the effect of air temperature on mites is mainly direct and manifested in the temperature-dependence of survival and developmental rates in mite individuals (Zemskaya, 1973), thus resulting in variation in abundance of any mite independently of its species identity. In contrast, the effect of precipitation on mite communities may be mediated by its effect on habitat heterogeneity, which would indirectly cause variation in the structure of mite communities.

To conclude, the results of this study allow us to understand better the lack of generality in some ecological rules governing parasite communities (Poulin, 2007). A particular type of relationship within each parasite-host association, such as the tightness of association between a parasite and its host's body versus the external environment, seems to be of primary importance for the manifestation of any ecological pattern.

We thank Carl Dick and an anonymous referee for their helpful comments on an earlier version of the manuscript. This study was partly supported by the Israel Science Foundation (Grant no. 249/04 to B.R.K). This is publication no. 577 of the Mitrani Department of Desert Ecology and no. 229 of the Ramon Science Center.

REFERENCES

Ambros, M., Diduch, A. and Stollmann, A. (2001). Poznámky k faune roztočov (Acarina: Mesostigmata) drobných cicavcov (Insectivora, Rodentia) Starohorských vrchov. *Folia Faunistica Slovaca* **6**, 33–45 (in Slovakian).

Arneberg, P., Skorping, A. and Read, A. F. (1997). Is population density a species character? Comparative analyses of the nematode parasites of mammals. *Oikos* **80**, 289–300.

Avdonin, V. V. and Striganova, B. R. (2005). Temperature as a factor of niche separation in free-living mesostigmatid mites (Mesostigmata: Arachida, Parasitiformes) of storm detritus. *Biology Bulletin* **31**, 488–494.

Bannert, B., Karaca, H. Y. and Wohltmann, A. (2000). Life cycle and parasitic interaction of the lizard-parasitizing mite *Ophionyssus galloticolus* (Acari: Gamasida: Macronyssidae), with remarks about the evolutionary consequences of parasitism in mites. *Experimental and Applied Acarology* **24**, 597–613.

Bochkov, A. V. and OConnor, B. M. (2005). Phylogeny and host associations of the fur-mite subgenus *Listrophoroides* (sensu stricto) Hirst (Acari: Atopomelidae) with an intriguing example of synhospitality on rats of the genus *Maxomys*. *Invertebrate Systematics* **19**, 437–498.

Bogdanov, I. I. (1979). Gamasoid mites of the Taimyr peninsula. *Parazitologiya* **13**, 474–482 (in Russian).

Bregetova, N. G. (1956). *Gamasoidea. Keys to the Fauna of the USSR, Issue 61*. Academy of Science of USSR, Leningrad (in Russian).

Brooks, D. R. and McLennan, D. A. (1991). *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. University of Chicago Press, Chicago.

Caro, A., Combes, C. and Euzet, L. (1997). What makes a fish a suitable host for Monogenea in the Mediterranean? *Journal of Helminthology* **71**, 203–210.

Carrol, J. E., Young, K. W. and Bruce, W. A. (1992). Simple in-vitro feeding system for northern fowl mites (Acari: Macronyssidae). *Journal of Economic Entomology* **85**, 848–852.

Clarke, K. R. and Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* **35**, 523–531.

Clarke, K. R. and Warwick, R. M. (1999). The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Marine Ecology Progress Series* **184**, 21–29.

Combes, C. (2001) *Parasitism. The Ecology and Evolution of Intimate Interactions*. University of Chicago Press, Chicago.

Davydova, M. S. and Belova, O. S. (1972). Fauna of gamasid mites of the floodplain of the Ob' River. In *Biological Resources of the Ob' River Valley* (ed. Maksimov, A. A.), pp. 306–324. Nauka, Novosibirsk, USSR (in Russian).

Davydova, M. S., Nikolsky, V. V., Yudin, B. S., Dudareva, G. V. and Belova, O. S. (1980). Gamasid mites of the tundra of the Central Siberia. In *Parasitic Insects and Mites of Siberia* (ed. Davydova, M. S.), pp. 141–148. Nauka, Novosibirsk, USSR (in Russian).

Degen, A. A. (1997). *Ecophysiology of Small Desert Mammals*. SpringerVerlag, Berlin-Heidelberg-New York.

Elshanskaya, N. I. and Popov, M. N. (1974). Zoologico-parasitological characteristics of the river Kenkeme valley (Central Yakutia). In *Theriology, Volume 1* (ed. Kolosova, L. D. and Lukyanova, I. V.), pp. 368–372. Nauka, Novosibirsk, USSR (in Russian).

Galaktionov, K. V. (1996). Life cycles and distribution of seabird helminths in Arctic and subArctic regions. *Bulletin of the Scandinavian Society for Parasitology* **6**, 31–49.

Garcia, L. V. (2004). Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**, 657–663.

Halliday, R. B. (1998). *Mites of Australia: a Checklist and Bibliography*. CSIRO Publishing, Melbourne.

Harvey, P. H. and Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.

Igolkin, N. I., Zhivotyagina, N. A. and Zamesov, N. V. (1976). Ectoparasites of small mammals of the mountain taiga of the Kuznetsk Alatau and adjacent regions of the

Tisul forest-steppe. In *Problems of Biology and Agronomy* (ed. Blinkov, G. N.), pp. 78–88. Tomsk State University, Tomsk, USSR (in Russian).

Kennedy, C. R. and Bush, A. O. (1994). The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* **109**, 187–196.

Kineman, J. J., Hastings, D. A., Ohrenschall, M. A., Colby, J., Schoolcraft, D. C., Klaus, J., Knight, J., Krager, L., Hayes, P., Oloughlin, K., Dunbar, P., Ikleman, J., Anderson, C., Burland, J., Dietz, J., Fisher, H., Hannaughan, A., Kelly, M., Boyle, S., Callaghan, M., Delamana, S., Di, L., Gomolski, K., Green, D., Hochberg, S., Holquist, W., Johnson, G., Lewis, L., Locher, A., Mealey, A., Middleton, L., Mellon, D., Nigro, L., Panskowitz, J., Racey, S., Roake, B., Ross, J., Row, L., Schacter, J. and Weschler, P. (eds.) (2000). *Global Ecosystems Database. Version II: Database, User's Guide, and Dataset Documentation*. US Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center. http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/go.htm

Korallo, N. P., Vinarski, M. V., Krasnov, B. R., Shenbrot, G. I., Mouillot, D. and Poulin, R. (2007). Are there general rules governing parasite diversity? Small mammalian hosts and gamasid mite assemblages. *Diversity and Distributions* **13**, 353–360.

Krasnov, B. R., Shenbrot, G. I., Medvedev, S. G., Khokhlova, I. S. and Vatschenok, V. S. (1998). Habitat-dependence of a parasite-host relationship: flea assemblages in two gerbil species of the Negev Desert. *Journal of Medical Entomology* **35**, 303–313.

Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S. and Degen, A. A. (2004). Flea species richness and parameters of host body, host geography and host ''milieu''. *Journal of Animal Ecology* **73**, 1121–1128.

Krasnov, B. R., Shenbrot, G. I., Mouillot, D., Khokhlova, I. S. and Poulin, R. (2005). Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographic distance or faunal similarity? *Journal of Biogeography* **32**, 633–644.

Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S. and Poulin, R. (2006). Is abundance a species attribute of haematophagous ectoparasites? *Oecologia* **150**, 132–140.

Lange, A. B. and Hamar, M. (1961). Gamasoid mites of rodents and insectivores of the People's Republic of Romania. *Scientific Reports of Higher Education, Biological Sciences* **1**, 21–28 (in Russian).

Lopatina, Y. V., Petrova, A. D. and Timoshkov, V. V. (1998). Gamasina mites of small mammals from parks and ruderal areas of Moscow. *Parazitologiya* **32**, 118–128 (in Russian).

Marshall, A. G. (1981). *The Ecology of Ectoparasite Insects*. Academic Press, London

Mašan, P. and Stanko, M. (2005). Mesostigmatic mites (Acari) and fleas (Siphonaptera) associated with nests of mound-building mouse, *Mus spicilegus* Petényi, 1882 (Mammalia, Rodentia). *Acta Parasitologica* **50**, 228–234.

Moran, M. D. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**, 403–405.

Morand, S. and Poulin, R. (1998). Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* **12**, 717–727.

Morozova, I. V., Bibikova, V. A. and Kalutenova, Z. P. (1963). On fauna of gamasid mites of the Sary-Ishikotrau Sands. *Zoologicheskyi Zhurnal* **42**, 1872–1876 (in Russian).

Pauller, O. F., Elshanskaya, N. I. and Shvetsova, I. V. (1966). Ecological-faunistical review of ectoparasites of small mammals and birds in the tularemia focus in the delta of the Selenga River. *Proceedings of the Irkutsk State Research Anti-Plague Institute of Siberia and Far East* **26**, 322–332 (in Russian).

Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. *British Medical Journal* **316**, 1236–1238.

Perneger, T. V. (1999). Adjusting for multiple testing in studies is less important than other concerns. *British Medical Journal* **318**, 1288.

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Piontkovskaya, S. P. and Ivanov, A. V. (1960). Mites and fleas of some rodents, insectivores and birds in the natural foci of the mite rickettsiosis in Eastern Kazakhstan. *Zoologicheskyi Zhurnal* **39**, 200–206 (in Russian).

Plesnivtseva, G. G. (1982). Ectoparasites of Mammals of the Western Predverkhoyanje. Ph.D. thesis, Novosibirsk State University, USSR (in Russian).

Poulin, R. (2006). Variation in infection parameters among populations within parasite species: intrinsic properties versus local factors. *International Journal for Parasitology* **36**, 877–885.

Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology* **134**, 763–776.

Poulin, R. and Mouillot, D. (2004). The evolution of taxonomic diversity in helminth assemblages of mammalian hosts. *Evolutionary Ecology* **18**, 231–247.

Poulin, R. and Mouritsen, K. N. (2003). Large-scale determinants of trematode infections in intertidal gastropods. *Marine Ecology Progress Series* **254**, 187–198.

Radovsky, F. J. (1969). Adaptive radiation in the parasitic Mesostigmata. *Acarologia* (*Paris*) **11**, 450–483.

Radovsky, F. J. (1985). Evolution of mammalian mesostigmatid mites. In *Coevolution of Parasitic Arthropods and Mammals* (ed. Kim, K. C.), pp. 441–504. John Wiley, New York.

Rothman, K. J. (1990). No adjustments are needed for multiple comparisons. *Epidemiology* **1**, 43–46.

Shevchenko, Z. G., Strihanova, E. V., Petrova, R. A., Timofeev, M. N. and Meleshko, N. S. (1975). Materials of the study of Gamasina mites of the Krasnodar region. *Problems of Particularly Dangerous Infections* **3–4 (43–44)**, 103–111 (in Russian).

Sjursen, H., Michelsen, A. and Jonasson, S. (2005). Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems. *Applied Soil Ecology* **30**, 148–161.

Sokal, R. R. and Rohlf, F. J. (1995). *Biometry, 3rd Edn.* W. H. Freeman and Co., New York.

Stanjukovich, M. K. (1987). Ectoparasites of small mammals from the south of the Pskov region. *Parazitologiya* **21**, 109–114 (in Russian).

Stupina, A. G. (1979). Ectoparasites of small mammals of Northern and Central Buryatia. In *Zooparasitology of the Baikal Lake Valley* (ed. Pronin, N. M.), pp. 134–151. Ulan-Ude, USSR (in Russian).

Vasiliev, G. I., Antsiferov, M. I., Veropanov, Y. V., Vinokur, B. S. and Kireeva, S. T. (1978). Ectoparasites of small mammals, their nests and bird nests in the floodplain of the Kamchatka river. *Parazitologiya* **12**, 539–542 (in Russian).

Vinarski, M. V., Korallo, N. P., Krasnov, B. R., Shenbrot, G. I. and Poulin, R. (2007). Decay of similarity of gamasid mite assemblages parasitic on Paleoarctic small mammals: geographic distance, host species composition or environment? *Journal of Biogeography* (*in the Press*), *doi:* 10.1111/j.1365-2699.2007.01735.x.

Volkov, V. I. and Chernykh, P. A. (1977). Gamasina mites of the Priamurye region In *Haematophagous Arthropods and their Control in the Newly Developing Territories of the Far East* (ed. Volkov, V. I.), pp. 42–68. Leningrad, USSR (in Russian).

Volkov, V. I., Dolgikh, A. M., Katzko, V. I., Zarubina, V. N. and Prasolova, N. N. (1978). Ectoparasites of small mammals of the eastern part of the BAM. *Parazitologiya* **12**, 529–538 (in Russian).

Warwick, R. M. & Clarke, K. R. (2001). Practical measures of marine biodiversity based on relatedness of species. *Oceanography and Marine Biology* **39**, 207–231.

Yudin, B. S., Krivosheev, V. G. and Belyaev V. G. (1976). *Small Mammals of the Northern Far East*. Nauka, Novosibirsk, USSR (in Russian).

Zemskaya, A. A. (1969). Types of parasitism of gamasid mites. *Medical Parasitology and Parasitic Diseases* [*Meditsinskaya parazitologiya i parazitarnye bolezni*] **38**, 393–405 (in Russian).

Zemskaya, A. A. (1973). *Parasitic Gamasid Mites and their Medical Importance*. Meditsina, Moscow, USSR (in Russian).