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ORIGINAL ARTICLE

Decay of similarity of gamasid mite assemblages parasitic on Palaearctic small mammals: geographic distance, host-species composition or environment

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ABSTRACT

Aim The similarity between parasite assemblages should decrease with increasing geographic distance between them, increasing dissimilarity in environmental conditions, and/or increasing dissimilarity of the local host fauna, depending on the dispersal abilities of the parasites and the intimacy of their associations with the host. We tested for a decay in the similarity of gamasid mite assemblages parasitic on small mammals with increasing geographic, 'environmental' and 'host faunal' (= 'host') distances.

Location We used data on assemblages of haematophagous gamasid mites (superfamily Dermanyssoidea) parasitic on small mammals (Insectivora, Lagomorpha and Rodentia) from 26 different regions of the northern Palaearctic.

Methods Similarity in mite assemblages was investigated at the compound community level across all regions, and at the component community level, across populations of the same host species for each of 11 common host species. Similarity between pairs of mite communities was estimated using both the Jaccard and the Sorensen indices. Environmental distance was estimated as the dissimilarity between locations in a composite measure of climatic variables, and host faunal distance was simply taken as the reciprocal of indices of similarity between the composition of host faunas in different locations. Generalized Linear Models (GLM) and Akaike's Information Criterion were used to select the best model of decay in similarity as a function of geographic, 'environmental' and 'host faunal' distances.

Results Overall, despite slight differences among host species, the similarity in mite assemblages decreased with both increasing 'environmental' distance and increasing 'host faunal' distance, but was generally unaffected by geographic distance between regions. The similarity of component communities of gamasid mites among host populations was determined mainly by similarity in the physical environment, whereas that of compound communities varied mainly with host-species composition.

Main conclusions Our results indicate that the general decay in community similarity with increasing geographic distances does not apply to assemblages of gamasid mites; it is possible that they can overcome great distances by means of passive dispersal (either by phoresy or wind-borne), or more likely they occur wherever their hosts are found as a result of tight cospeciation in the past. Mite assemblages on small mammalian hosts seem to be affected mainly by local environmental conditions, and, to a much lesser extent, by the species composition of local host communities.

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Climate, community similarity, Dermanyssoidea, dispersal, haematophagous ectoparasites, host specificity, northern Palaearctic, small mammals.

INTRODUCTION

The distance decay of similarity in species composition among ecological communities consists of a decrease in the proportion of species shared by two communities with increasing distance between them (see Nekola & White, 1999 and references therein). This phenomenon is thought to be one of the most pervasive macroecological patterns (Nekola & White, 1999; Poulin, 2003; Bell *et al.*, 2006). Indeed, distance decay of similarity has been reported for a variety of both plant and animal taxa in a number of geographic regions and at a variety of scales (Nekola & White, 1999; Poulin, 2003; Burgham, 2004; Krasnov *et al.*, 2005; McDonald *et al.*, 2005; Palmer, 2005; Qian *et al.*, 2005; Nakaoka *et al.*, 2006; Thompson & Townsend, 2006). The ubiquity of the distance decay of similarity suggests the existence of similar mechanisms producing this pattern in different taxa.

The reasons for the distance decay of similarity can be both ecological (proximate) and evolutionary (ultimate), although it is sometimes difficult do disentangle these two types of factors. In addition, these processes are not mutually exclusive. On a proximate level, the decay of similarity among ecological communities with distance can be the result of a decrease in the environmental similarity of the locations studied and of the differential species responses to environmental variation (Tuomisto *et al.*, 2003). Ultimately, similarity can decrease with geographic distance as a result of (1) the higher probability that geographic barriers occur over greater distances, and (2) the limited dispersal abilities of organisms, even in homogenous environments. Indeed, Hubbell's (2001) neutral theory of biodiversity and biogeography predicts that the similarity of ecological communities among locations decreases with increasing geographic distance because of the spatially limited dispersal of organisms (see also Bell, 2001).

Recently, an increasing number of studies have reported a distance decay of similarity not only for free-living organisms but also for parasites (Poulin, 2003; Fellis & Esch, 2005; Krasnov *et al.*, 2005; Oliva & Gonzalez, 2005). Communities of parasites are ideal for such studies because species in parasite assemblages are often thoroughly enumerated (Poulin, 2003), and because, for many host species, different populations across large geographic areas have been surveyed for parasites. Most studies of the distance decay of similarity in parasite assemblages have been carried out on helminth parasites, however, and, to the best of our knowledge, only a single study has dealt with arthropod ectoparasites (Krasnov *et al.*, 2005). Consequently, the generality of the distance decay of similarity in parasite communities remains to be tested. Another reason why it is important to compare parasite communities between different geographic locations is that, in contrast to free-living species, environmental similarity for parasites involves not only the physical environment but also the environment resulting from the species composition of the host community. Therefore, if the decay of similarity among parasite assemblages with increasing geographic distance is caused by proximate reasons, this decay can be caused either by dissimilarity in the physical environment (e.g. climate), or by dissimilarity in host species composition, or by both. An additional cause of the geographic decay of similarity might be intraspecific geographic variation in host responses to parasite attacks (Ardia, 2005).

In our previous study attempting to disentangle the effects of geographic distance and host-community dissimilarity on the similarity among flea assemblages (Siphonaptera) of 10 host species, we found that similarity in flea assemblages among different populations of the same host decreased with increases in either geographic distance or host-community dissimilarity (or both) between these populations (Krasnov *et al.*, 2005). In six of 10 host species studied, host-community dissimilarity had a strong effect on the similarity of flea assemblages on a particular host species. The reason for this could be the relatively high dispersal and host-switching abilities of fleas (e.g. Darskaya & Besedina, 1961; Krasnov & Khokhlova, 2001) and the relatively long time that fleas spend off-host. Consequently, similarity among assemblages of ectoparasites with (a) lower mobility and (b) more intimate relationships with the host should be affected more strongly by geographic distance and variation in environmental conditions than by variation in host-community composition. In particular, this is because the high dispersal ability of mobile species will result in a higher degree of homogeneity among their communities (Nakaoka *et al.*, 2006).

To test this hypothesis, we examined the spatial variation in similarity among assemblages of haematophagous gamasid mites belonging to the superfamily Dermanyssoidea parasitic on small mammalian hosts across the Palaearctic. We asked how variable (if at all) the composition of mite assemblages is among different populations of the same host. We answered this question by comparing the similarity in mite assemblages among conspecific host populations that occur in different geographic locations under different environmental conditions, and that belong to host faunas with different species composition. We predicted that the similarity of mite assemblages will strongly decrease with an increase in either geographic distance and/or dissimilarity in physical environment, and less strongly (if at all) with increasing dissimilarity in host-species composition.

All previous studies of the geographic decay of similarity in parasite communities have focused on component communities (the assemblage of parasites in a host population), whereas

Table 1 Data on small mammals and mites from 26 regions used in the analyses. Numbers in parentheses represent the total numbers of sampled individuals.

Region	Number of species Hosts	Mites	Source
North Asian Far East	20 (1492)	19 (2645)	Yudin *et al.* (1976)
Altai Steppe	13 (197)	15 (325)	Davydova & Belova (1972)
Russian Far East	19 (25,925)	31 (36,044)	Volkov & Chernykh (1977)
Krasnodar region	20 (26,200)	28 (32,587)	Shevchenko *et al.* (1975)
Kuznetsk Alatau (Siberia)	10 (1241)	13 (406)	Igolkin *et al.* (1976)
Moscow region	11 (14,3204)	21 (12,5639)	Lopatina *et al.* (1998)
Novosibirsk region	26 (6470)	19 (13,741)	A. Dobrotvorsky (unpublished data)*
Omsk region (forest-steppe zone)	22 (7681)	24 (24,583)	N. Korallo (unpublished data)
Omsk region (steppe zone)	10 (75)	12 (959)	N. Korallo (unpublished data)
Omsk region (forest zone)	17 (1981)	16 (1299)	N. Korallo (unpublished data)
Tomsk region	15 (865)	17 (3583)	Davydova & Belova (1972)
Romania	16 (317)	23 (1552)	Lange & Hamar (1961)
Pskov region	10 (717)	8 (752)	Stanjukovich (1987)
Selenga River (Central Siberia)	14 (1982)	10 (4124)	Pauller *et al.* (1966)
Eastern Baikalo-Amur Magistral (BAM) (eastern Siberia)	15 (1490)	14 (6022)	Volkov *et al.* (1978)
Kamchatka peninsula	6 (265)	6 (153)	Vasiliev *et al.* (1978)
Buryatia	18 (4736)	30 (13,366)	Stupina (1979)
Western Predverkhoyanje (Yakutia)	12 (1588)	17 (5712)	Plesnivtseva (1982)
Eastern Kazakhstan	8 (57)	10 (2510)	Piontkovskaya & Ivanov (1960)
Slovakia	15 (1782)	18 (6368)	Ambros *et al.* (2001)
Western Taimyr peninsula	9 (582)	11 (8318)	Davydova *et al.* (1980)
Pur river (Northern Siberia)	6 (471)	13 (4851)	Davydova & Belova (1972)
Lower Ob' floodplain	6 (283)	14 (1838)	Davydova & Belova (1972)
Central Yakutia	6 (521)	10 (1449)	Elshanskaya & Popov (1974)
Eastern Taimyr peninsula	8 (2135)	9 (6154)	Bogdanov (1979)
Balkhash lake (Kazakhstan)	8 (12,532)	7 (3388)	Morozova *et al.* (1963)

*Data collected by the late A. Dobrotvorsky in 1982–87 were transferred to the Laboratory of Arthropod-Borne Viral Infections, Omsk Research Institute of Natural Foci Infections under the responsibility of N. P. Korallo.

geographic comparisons of similarity in compound communities of parasites (the assemblage of parasites in a host community) have not to our knowledge been carried out. Therefore, in addition to comparing the similarity in mite assemblages among conspecific host populations, we also compared the similarity in the entire mite assemblages on small mammalian hosts among different geographic regions.

There is substantial interspecific variation in the ecology and feeding modes of gamasids, as they include soil-dwelling and nidicolous predators, facultative and obligatory vertebrate ectoparasites and endoparasites (see Radovsky, 1985 for a review). Here, however, we focus exclusively on haematophagous mites collected from the bodies of their hosts. These mites use their host both as a food source and as a dispersal vehicle, and, thus, the association between these mite species and their hosts is assumed to be very intimate (Radovsky, 1985).

MATERIALS AND METHODS

Data on mites collected from the bodies of their hosts were obtained from published surveys and unpublished data that reported mite distribution and abundance on small mammals (Insectivora, Lagomorpha and Rodentia) in 26 regions of the northern Palaearctic (Table 1). These sources reported data on the number of mite species found on each of several small mammal species in a particular location. Only mite species that had been collected from a host body and had been reported to be haematophagous (obligate and facultative) were considered in this study. The lists of mammal and mite species in each region can be obtained from M.V. or B.K. on request. In total, we used data on 244,398 individuals of 78 mammal species from which 308,368 individual mites of 70 species were recovered.

To examine how the species composition of component and compound mite communities on a host species varies with geographic, 'host' or 'environmental' distance among host populations and communities, we selected 11 host species that occurred in at least four regions. These were *Sorex araneus* L., *Apodemus agrarius* Pall., *Arvicola terrestris* L., *Clethrionomys glareolus* Schzeb., *Clethrionomys rutilus* Pall., *Clethrionomys rufocanus* Sundevall, *Microtus arvalis* Pall., *Microtus gregalis* Pall., *Microtus oeconomus* Pall., *Ondatra zibethicus* L., and *Sicista betulina* Pall. For all possible pairs of localities, we computed (1) the pairwise similarity in mite species composition between assemblages, for each of the 11 host species and for the entire host community; (2) the similarity in host-species composition; and (3) the geographical and environmental distances between localities. To evaluate the similarity in mite species composition we used both the Jaccard index and the more quantitative Sorensen similarity index. The Jaccard index is based on presence/absence data. It represents the number of mite species shared by two host populations divided by the total number of mite species found in both populations. It ranges from zero (no species in common between two host populations) to one (the two host populations have exactly the same mite species). There are two versions of the Sorensen index. One is qualitative and similar to the Jaccard index, whereas the other is quantitative and is based on the relative abundance of different species in the assemblages: this is the most widely used measure of similarity (Magurran, 1988). In this study, the quantitative version of the Sorensen index was used. Similarity indices were computed using the EstimateS 7.5 software (Colwell, 2005).

The geographic distance between pairs of host populations was calculated as the linear distance between the centres of the respective regions (described in the relevant sources), obtained from a map using the ArcView 9.1 software. The 'host' distance between pairs of regions was calculated as the reciprocal of the Jaccard similarity index between the small mammal (Insectivora, Lagomorpha and Rodentia) faunas of these regions as well as the Sorensen similarity in host-species composition between regional surveys. Faunal lists for each region were compiled based on the following sources: Flint *et al.* (1970), Gromov & Baranova (1981), Dolgov (1985), Panteleev *et al.* (1990), and Malkova *et al.* (2003).

To calculate the 'environmental' distance between regions, we computed climatic variables (annual, winter and summer precipitation, mean surface air temperature in January, mean surface air temperature in July, and mean annual surface air temperature) and elevation parameters for each region using the Global Ecosystems data base (Kineman *et al.*, 2000). These variables were 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). We then substituted them with the scores of three principal components calculated from these seven variables after log-transformation. The resulting three factors explained 91.5% of the variance; their eigenvalues were 3.58, 1.59 and 1.23, and the factor loadings were 51.1%, 22.8% and 17.6%. We constructed the Euclidian distance matrix of environmental dissimilarity between each pair of regions using cluster analysis (UPGMA algorithm), expressing the distance between each pair of regions as a proportion of the maximal pairwise distance found.

All similarity and distance measures were log + 1-transformed prior to analyses. We analysed the effect of geographic, 'host' and 'environmental' distances on the Jaccard or Sorensen similarity indices of (a) compound and (b) component (separately for each of the 11 above-mentioned species) mite communities among regions using Generalized Linear Models (GLM) with a normal distribution and log-link function, and searched for the best model using Akaike's Information Criterion. We then further investigated the best models using multiple regression to evaluate how well geographic, 'host' or/and 'environmental' distances predict similarity in mite assemblages. Following Poulin (2003) and Krasnov *et al.* (2005), the significance of each of the best regression models found in each analysis was tested using a randomization approach (Manly, 1997) implemented with the RT 2.1 software (Western EcoSystems Technology, Inc., Cheyenne, WY, USA) because the pairwise similarity values and distances were not truly independent in a statistical sense. All regression probabilities were based on 10,000 permutations.

We avoided an inflated Type I error by performing sequential Bonferroni corrections of the significance level. Significance is only recorded at the adjusted level. The Bonferroni adjustment of alpha-level has been increasingly criticized by statisticians and ecologists in recent years because it often leads to the incorrect acceptance of the false null hypothesis (Rothman, 1990; Garcia, 2004; Nakagawa, 2004). However, analyses of our data with and without the Bonferroni adjustment produced similar results, so only the former are reported here.

RESULTS

A summary of the search for the best models explaining the variance in the similarity of mite assemblages using GLM is presented in Table 2. No relationship between either measure of similarity of mite assemblages and either distance measure was found in four of 11 host species (*S. araneus*, *M. arvalis*, *O. zibethicus*, and *S. betulina*). In the remaining host species, variance in the similarity of mite assemblages was explained best by 'environmental' distance, except for *C. glareolus*, in which the best predictor appeared to be geographic distance. The model that best explained the variance in the similarity of the compound communities of gamasids comprised both 'host' and 'environmental' distances for qualitative (Jaccard) and 'host' distance only for quantitative (Sorensen) similarity. In five of the six host species, both the qualitative similarity and the quantitative similarity of mite assemblages were explained best by the same distance factor. In *A. agrarius*, the variance in Jaccard similarity of mite assemblages was explained best by 'environmental' distance, whereas that in Sorensen similarity was best explained by 'host' distance.

In all cases where variance in the similarity of mite assemblages was explained well by a distance measure, this similarity significantly decreased with increasing distance (Table 3). Illustrative examples for 'environmental' distance (with *M. oeconomus*), geographic distance (with *C. glareolus*) and 'host' distance (with *A. agrarius*) are presented in Figs 1–3.

DISCUSSION

Our initial predictions were only partly supported. The results of this study demonstrated that, in general: (1) the rule of decaying similarity with geographic distance does not apply to

Table 2 The best models explaining the variance in similarity of species composition of gamasid mite assemblages on 11 small mammalian species and on the entire small-mammal community.

Host species or community	Index of similarity	Model	*N*	AIC	LR χ^2	*P*
S. araneus	Jaccard	GD	21	−74.88	1.72	0.19
	Sorensen	GD	21	−79.88	1.96	0.16
A. agrarius	Jaccard	ED	15	−62.88	10.55	< 0.0001
	Sorensen	SHD	15	−63.39	11.92	< 0.0001
A. terrestris	Jaccard	ED	36	−128.56	23.75	< 0.0001
	Sorensen	ED	36	−123.26	21.88	< 0.0001
C. glareolus	Jaccard	GD	36	−116.07	9.33	0.002
	Sorensen	GD	36	−118.79	11.36	< 0.001
C. rutilus	Jaccard	ED	120	−427.72	28.62	< 0.0001
	Sorensen	ED	120	−426.96	31.08	< 0.0001
C. rufocanus	Jaccard	ED	55	−207.53	11.74	< 0.0001
	Sorensen	ED	55	−210.81	19.92	< 0.0001
M. arvalis	Jaccard	GD	36	−129.32	0.69	0.40
	Sorensen	GD	36	−118.96	1.22	0.27
M. gregalis	Jaccard	ED	15	−67.68	12.82	< 0.001
	Sorensen	ED	15	−67.80	10.54	< 0.005
M. oeconomus	Jaccard	ED	105	−410.85	30.75	< 0.0001
	Sorensen	ED	105	−421.68	30.40	< 0.0001
O. zibethicus	Jaccard	JHD + ED + GD	22	−68.75	9.06	0.03
	Sorensen	SHD + ED	22	−74.91	6.15	0.05
S. betulina	Jaccard	JHD + ED	6	−18.76	6.01	0.05
	Sorensen	SHD + ED	6	−24.41	10.75	0.01
Entire community	Jaccard	JHD + ED	325	−1152.84	141.78	< 0.0001
	Sorensen	SHD	325	−1098.79	166.17	< 0.0001

The modelling was carried out using a Generalized Linear Model with the application of Akaike's Information Criterion (AIC) for the best model selection. JHD and SHD: 'host' distance (reciprocal Jaccard or Sorensen, respectively, similarity in small-mammal species composition), ED: 'environmental' distance (Euclidian distance between each pair of regions extracted from cluster analysis of three principal components of seven environmental variables; see text for explanations), GD: geographic distance, *N*: number of pairwise indices, LR: likelihood ratio.

Table 3 Summary of multiple regressions of similarity (SM) of gamasid mite assemblages between pairs of populations of seven small mammalian species, and between pairs of locations for the entire small-mammal community, against one or more distance measures according to the best model selected using Akaike's Information Criterion. See Table 2 for the abbreviations of distance measures. The significance of each regression model was tested using a randomization approach (Manly, 1997) (see text for explanation).

Host species or community	Index of similarity	Equation	r^2	*F*	*P*
A. agrarius	Jaccard	SM = 0.19 − 0.41ED	0.52	14.0	< 0.001
	Sorensen	SM = 0.27 − 0.54SHD	0.57	16.9	< 0.001
A. terrestris	Jaccard	SM = 0.21 − 0.59ED	0.50	33.7	< 0.0001
	Sorensen	SM = 0.25 − 0.60ED	0.48	30.8	< 0.0001
C. glareolus	Jaccard	SM = 0.31 − 0.06GD	0.25	11.3	< 0.001
	Sorensen	SM = 0.37 − 0.07GD	0.29	13.9	< 0.001
C. rutilus	Jaccard	SM = 0.18 − 0.40ED	0.22	33.8	< 0.0001
	Sorensen	SM = 0.23 − 0.43ED	0.24	37.1	< 0.0001
C. rufocanus	Jaccard	SM = 0.18 − 0.33ED	0.20	13.5	< 0.0005
	Sorensen	SM = 0.23 − 0.36ED	0.24	17.0	< 0.0001
M. gregalis	Jaccard	SM = 0.12 − 0.99ED	0.59	8.8	< 0.005
	Sorensen	SM = 0.17 − 0.85ED	0.52	6.4	< 0.01
M. oeconomus	Jaccard	SM = 0.19 − 0.42ED	0.26	35.9	< 0.0001
	Sorensen	SM = 0.23 − 0.40ED	0.26	35.6	< 0.0001
Entire community	Jaccard	SM = 0.21 − 0.50JHD − 0.03ED	0.39	105.4	< 0.0001
	Sorensen	SM = 0.27 − 0.64SHD	0.44	250.4	< 0.0001

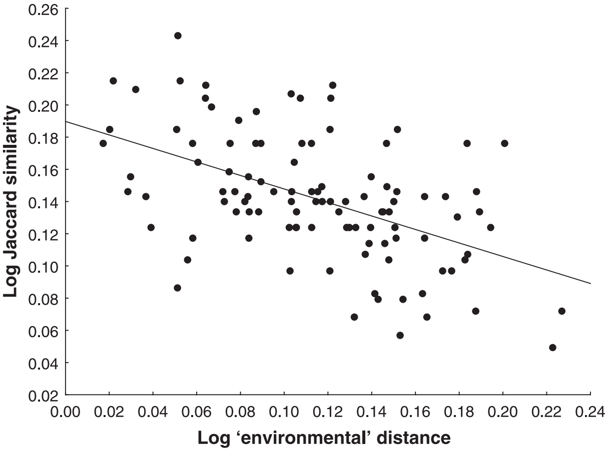

Figure 1 Relationship between similarity in mite species composition in *Microtus oeconomus* calculated using the Jaccard index and 'environmental' distance, between all 105 possible pairs of host populations ($n = 105$, $r^2 = 0.26$, $F = 35.9$, $P < 0.001$). 'Environmental' distance was evaluated using the scores of three principal components calculated from seven climatic and elevation variables (see Materials and methods for further explanations).

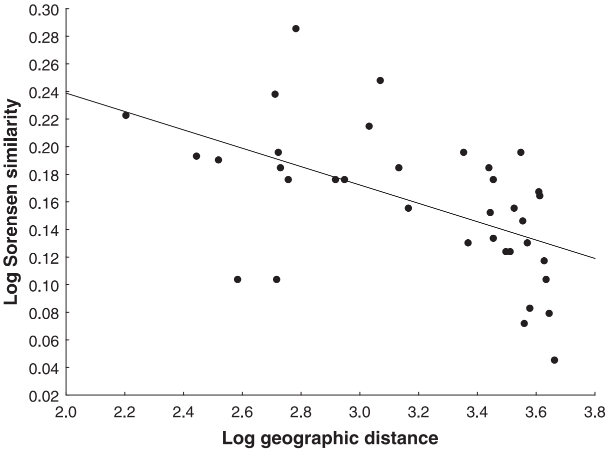

Figure 2 Relationship between similarity in mite species composition in *Clethrionomys glareolus* calculated using the Sorensen index and geographic distance, between all 36 possible pairs of host populations ($n = 36$, $r^2 = 0.29$, $F = 13.9$, $P < 0.001$). Geographic distance was calculated as the linear distance between the centres of each region (see Materials and methods for further explanations).

gamasid mite communities; (2) the similarity of component communities of gamasid mites among host populations is determined mainly by similarity in the physical environment, whereas that of compound communities varies mainly with host-species composition; and (3) for several host species, no measure of 'extrinsic' (geographic, 'host' and 'environmental') similarity used in this study correlated with the similarity of mite assemblages between host populations.

The most surprising result of this study is that, despite the limited active dispersal abilities of gamasid mites, the similarity of component communities did not depend on geographic distance. This suggests that the phenomenon of distance decay of similarity is not as universal as previously assumed (Nekola & White, 1999; Poulin, 2003; Krasnov *et al.*, 2005). There could be several reasons for this lack of an effect of geographic distance. First, the data can be confounded by taxonomic errors; for instance, several distinct species of mites from different areas have been lumped together under the same name. Molecular and genetic tools are now commonly revealing cryptic species in numerous parasite taxa (Hung *et al.*, 1999; Jousson *et al.*, 2000; Blouin, 2002). For example, the phytosiid mite species *Typhlodromus exhilaratus* and *Typhlodromus phialatus* have been considered synonyms by some authors (e.g. Chant & Yoshida-Shaul, 1987); however, a recent molecular analysis proved that *T. exhilaratus* and *T. phialatus* are distinct valid species (Tixier *et al.*, 2006). Based on reproductive incompatibility, another phytosiid, *Typhodromalus limonicus* s.l., was recently reclassified as two species, namely *T. limonicus* s.s. and *Typhlodromalus manihoti* (de Moraes *et al.*, 1994). Molecular studies have also resulted in the identification of other distinct but cryptic mite species (e.g. Edwards *et al.*, 1998). Such taxonomic errors are possible in our data set, given that the surveys were conducted at different times and in most cases by different people. These errors would mask any underlying effect of geographic distance. They should also, however, mask the effect of 'environmental' distance, and, since the latter effect emerges quite strongly, the influence of taxonomic artefacts is unlikely. In addition, in meta-analyses such as the one performed in this study, the identification of mite species by the original authors has to be accepted because there is no way of having all the specimens examined by a single person (Poulin, 2003). Second, spatial scale can also affect the results, because over small

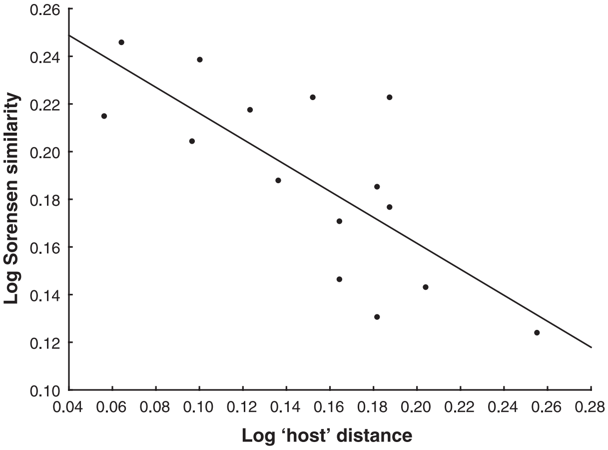

Figure 3 Relationship between similarity in mite species composition in *Apodemus agrarius* calculated using the Sorensen index and host distance, between all 15 possible pairs of 'host' populations ($n = 15$, $r^2 = 0.57$, $F = 16.9$, $P < 0.01$). 'Host' distance was calculated as the reciprocal Sorensen similarity in host-species composition between regional surveys (see Materials and methods for further explanations).

distances we would not expect an effect of distance (Nakaoka *et al.*, 2006; but see Palmer, 2005). However, our previous study of fleas, which demonstrated a clear distance decay of similarity, was carried out on roughly similar geographical scales to those in this study (Krasnov *et al.*, 2005). Consequently, differences in scale can also be ruled out as an explanation for the discrepancy between the results of this study and the earlier results for flea assemblages. Third, mite assemblages may be saturated with species and, if so, a limit on the number of locally coexisting mites could lead to greater homogeneity in species composition on any spatial scale (Poulin, 2003). However, this again would disagree with our previous results on fleas (Krasnov *et al.*, 2006), whose component communities were shown to be saturated, which did not preclude the existence of distance decay in similarity among their communities. Fourth, the simplest explanation for the similarity of mite communities at different locations could be the coevolution of the mites with the mammal species [see, for example, Bochkov & OConnor (2005) for atopomelid mites]. If a mite coevolved tightly with its host, it would spread around the Palaearctic together with the host. However, environmental conditions not suitable for sustained reproduction of the mite, causing local extinction, or massive host-switching by numerous species would disrupt this pattern (see Paterson & Banks, 2001). Host-switching of gamasid mites is probable if different host species share or use the same burrow, whereas host-switching resulting from intimate contact of two different host species outside the burrow is unlikely because the mobility of gamasid mites is limited. Finally, despite the limited abilities of gamasid mites to disperse actively, their passive dispersal (e.g. phoresy on various mammals and birds) should help them to overcome long distances (e.g. Tagiltsev, 1967, 1975). For example, haematophagous gamasids characteristic of rodents have been repeatedly found on larger host species (various mustelids and even brown bear) in Siberia (Davydova & Nikolsky, 1986; Senotrusova, 1987), and dispersal via accidental hosts has been recorded even in highly host-specific gamasids such as *Laelaps multispinosus* (Pauller *et al.*, 1966; Davydova & Belova, 1972) and *Laelaps muris* (Plesnivtseva & Zhovty, 1981). The possibility of aerial dispersal similar to that reported for other mite taxa, including gamasids (Brandenburg & Kennedy, 1982; Jung & Croft, 2001), also cannot be discarded *a priori*, although this has never been reported for ectoparasitic mite species and is highly unlikely. If mites are, indeed, spread by their hosts or by wind over long distances, but can establish only in areas where environmental conditions are suitable, distance will not present a barrier to their dispersal, thus explaining the absence of distance decay of similarity found in this study.

The relatively low degree of host specificity of many of the mite species considered in this study explains, at least partly, why the similarity of component communities of these parasites was not affected by dissimilarity in species composition of their host 'milieu'. Indeed, *Androlaelaps glasgowi* (= *A. fahrenholzi*), *Haemogamasus ambulans* and *Hirstionyssus isabellinus* dominated among mite species in the surveyed regions. These species have been recorded on a large number of hosts, sometimes phylogenetically distant ones (Radovsky, 1985; Senotrusova, 1987). For example, in Kazakhstan, *A. glasgowi* has been found on more than 35 species of mammals belonging to 3 orders, as well as on birds and in their nests (Senotrusova, 1987). Furthermore, this mite is probably the most common dermanyssoid found on small mammals and is cosmopolitan in its distribution. It is a fairly active species that probably supplements its diet with other arthropods, and is often seen in soil and litter samples (e.g. Zemskaya, 1973). This mite will probably populate any small-mammal nest that provides not only a continual source of arthropods but also a dependable source for a blood meal. *Androlaelaps glasgowi* is probably the least host-specific of any mite from our data set and it could possibly create some noise in the analysis. It should be noted, however, that low host-specificity does not necessarily imply relative ease of host-switching at ecological (but not evolutionary) time-scales. Another, not necessarily alternative, explanation for the lack of a relationship between the similarity of host communities and that of component communities of mites could stem from the asymmetry of interactions among mites and mammals, similar to that found for metazoan parasite–fish host and flea–mammalian host associations (Vazquez *et al.*, 2005). In particular, in these associations, host-specialist parasites tend to parasitize highly abundant host species, whereas less abundant host species tend to be parasitized by generalist parasites. Given that the host species considered in our study are highly abundant (as can be determined from the original sources), they are expected to be exploited by host-specific mites, which are probably not affected by co-occurring host species other than the target one. However, this explanation remains to be tested.

In contrast to the case for component communities, host-species composition had a strong effect on the similarity of compound communities of mites among regions, suggesting that the compositions of compound and component communities of these arthropods are governed by different rules. Presumably, the limited host-switching ability of individual mites could be a reason why the composition of the mite assemblage from the entire pool of host species depends on the species composition of the latter, whereas this seems not to be the case for the mite assemblage on a particular host in a particular location.

Our prediction of a strong relationship between the similarity of mite assemblages and the similarity of environmental conditions appeared to be well supported. The cause for this is probably the high sensitivity of gamasids to climatic factors, such as temperature and moisture (Zemskaya, 1973; Krantz, 1978). Nevertheless, this prediction was supported for only seven of 11 host species. There could be a number of reasons why no correlates of similarity of mite assemblages were found in the remaining four host species. In our data set, *S. betulina* was examined for mites in four localities only, providing only six data points for the analyses, a number too low to detect significant correlations. However, prior to the implementation of the Bonferroni adjustment of the significance level, the similarity of mite assemblages on this host tended to be negatively correlated with 'host' and 'environmental' distances, but not with geographic distance (Table 2). Taxonomic uncertainties may actually apply in the case of both *S. araneus* and *M. arvalis*. Each of these host species, as identified in the original sources, seems to represent more than one species or, at least, more than one chromosome race (see Meyer *et al.*, 1996 for *M. arvalis* and Basset *et al.*, 2006 for *S. araneus*, and references therein). Finally, *O. zibethicus* was introduced only recently into the Palaearctic, and therefore its parasite assemblages (including mites) may not yet be fully established, although some of the specific muskrat mites (e.g. *Laelaps multispinosus*) have a Nearctic origin (Zemskaya, 1973).

In conclusion, our results suggest that the mite assemblages on small mammalian hosts are affected mainly by local environmental conditions, and, to a much lesser extent, by the species composition of local host communities, whereas the distance decay of similarity appears not to be a general rule for these parasites.

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REFERENCES

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

Ardia, D.R. (2005) Tree swallows trade off immune function and reproductive effort differently across their range. *Ecology*, **86,** 2040–2046.

Basset, P., Yannic, G., Brünner, H. & Hausser, J. (2006) Restricted gene flow at specific parts of the shrew genome in chromosomal hybrid zones. *Evolution*, **60,** 1718–1730.

Bell, G. (2001) Neutral macroecology. *Science*, **293,** 2413–2418.

Bell, G., Lechowicz, M.J. & Waterway, M.J. (2006) The comparative evidence relating to functional and neutral interpretations of biological communities. *Ecology*, **87,** 1378–1386.

Blouin, M.S. (2002) Molecular prospecting for cryptic species of nematodes: Mitochondrial DNA versus internal transcribed spacer. *International Journal for Parasitology*, **32,** 527–531.

Bochkov, A.V. & 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).

Brandenburg, R.L. & Kennedy, G.G. (1982) Intercrop relationships and spider mite dispersal in a corn/peanut agro-ecosystem. *Entomologia Experimantalis et Applicata*, **32,** 269–276.

Burgham, R.J. (2004) Alpha and beta diversity of lianas in Yasuni, Ecuador. *Forest Ecology and Management*, **190,** 43–55.

Chant, D.A. & Yoshida-Shaul, E. (1987) A world review of the pyri species group in the genus Typhlodromus Scheuten (Acari: Phytoseiidae). *Canadian Journal of Zoology*, **65,** 1770–1804.

Colwell, R.K. (2005) *EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application*, http://viceroy.eeb.uconn.edu/EstimateS.

Darskaya, N.F. & Besedina, K.P. (1961) On the possibility of flea feeding on reptiles. *Proceedings of the Scientific Anti-Plague Institute of Caucasus and Trans-Caucasus*, **5,** 33–39 (in Russian).

Davydova, M.S. & Belova, O.S. (1972) Fauna of gamasid mites of the floodplain of the Ob' River. *Biological resources of Ob' valley* (ed. by A.A. Maksimov), pp. 306–324. Nauka, Novosibirsk (in Russian).

Davydova, M.S. & Nikolsky, V.V. (1986) *Gamasid mites of Western Siberia*. Nauka, Novosibirsk (in Russian).

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

Dolgov, V.A. (1985) *Sorex shrews of the Old World*. Moscow University Press, Moscow (in Russian).

Edwards, O.R., Melo, E.L., Smith, L. & Hoy, M.A. (1998) Discrimination of three Typhlodromalus species (Acari: Phytoseiidae) using random amplified polymorphic DNA markers. *Experimental and Applied Acarology*, **22,** 101–109.

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

Fellis, K.J. & Esch, G.W. (2005) Variation in life cycle affects the distance decay of similarity among bluegill sunfish parasite communities. *Journal of Parasitology*, **91,** 1484–1486.

Flint, V.E., Chugunov, Y.D. & Smirin, V.M. (1970) *Mammals of the USSR*. Mysl, Moscow (in Russian).

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

Gromov, I.M. & Baranova, G.I. (1981) *Check-list of mammals of the USSR*. Nauka, Leningrad (in Russian).

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.

Hung, G.C., Chilton, N.B., Beveridge, I., Zhu, X.Q., Lichtenfels, J.R. & Gasser, R.B. (1999). Molecular evidence for cryptic species within *Cylicostephanus minutus* (Nematoda: Strongylidae). *International Journal for Parasitology*, **29,** 285–291.

Igolkin, N.I., Zhivotyagina, N.A. & Zamesov, N.V. (1976) Ectoparasites of small mammals of the mountain taiga of the Kuznetsk Alatau and adjacent regions of the Tisul forest-steppe. *Problems of Biology and Agronomy* (ed. by G.N. Blinkov), pp. 78–88. Tomsk State University, Tomsk (in Russian).

Jousson, O., Bartoli, P. & Pawlowski, J. (2000) Cryptic speciation among intestinal parasites (Trematoda: Digenea) infecting sympatric host fishes (Sparidae). *Journal of Evolutionary Biology*, **13,** 778–785.

Jung, C. & Croft, B.A. (2001) Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): estimating falling speed and dispersal distance of adult females. *Oikos*, **94,** 182–190.

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. & 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.

Krantz, G.W. (1978) *A manual of acarology*, 2nd edn. Oregon State University Book Stores, Corvallis.

Krasnov, B.R. & Khokhlova, I.S. (2001) The effect of behavioural interactions on the exchange of flea (Siphonaptera) between two rodent species. *Journal of Vector Ecology*, **26,** 181–190.

Krasnov, B.R., Shenbrot, G.I., Mouillot, D., Khokhlova, I.S. & 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., Stanko, M., Khokhlova, I.S., Miklisova, D., Morand, S., Shenbrot, G.I. & Poulin, R. (2006) Relationships between local and regional species richness in flea communities of small mammalian hosts: saturation and spatial scale. *Parasitology Research*, **98,** 403–413.

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

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

Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.

Malkova, M.G., Sidorov, G.N., Bogdanov, I.I., Krjuchkov, V.S. & Stankovsky, A.P. (2003). *Mammals of the Omsk Region: key and handbook*. Izdatel-Polygraphist, Omsk (in Russian).

Manly, B.F.J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*, 2nd edn. Chapman & Hall, London.

McDonald, R., McKnight, M., Weiss, D., Selig, E., O'Connor, M., Violin, C. & Moody, A. (2005) Species compositional similarity and ecoregions: do ecoregion boundaries represent zones of high species turnover? *Biological Conservation,* **126,** 24–40.

Meyer, M.N., Golenistchev, F.I., Radzhabli, S.I. & Sablina, O.L. (1996) Voles (subgenus *Microtus* Schrank) of Russia and adjacent territories. *Proceedings of the Zoological Institute of Russian Academy of Sciences*, **232,** 3–320 (in Russian).

de Moraes, G.J., Mesa, N.C., Braun, A. & Melo, E.L. (1994) Definition of the Amblyseius limonicus species group (Acari: Phytoseiidae), with descriptions of two new species and new records. *International Journal of Acarology*, **20,** 209–217.

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

Nakagawa, S. (2004) A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology*, **15,** 1044–1045.

Nakaoka, M., Ito, N., Yamamoto, T., Okuda, T. & Noda, T. (2006) Similarity of rocky intertidal assemblages along the Pacific coast of Japan: effects of spatial scales and geographic distance. *Ecological Research*, **21,** 425–435.

Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26,** 867–878.

Oliva, M.E. & Gonzalez, M.T. (2005) The decay of similarity over geographical distance in parasite communities of marine fishes. *Journal of Biogeography*, **32,** 1327–1332.

Palmer, M.W. (2005) Distance decay in an old-growth neotropical forest. *Journal of Vegetation Science*, **16,** 161–166.

Panteleev, P.A., Terekhina, A.N. & Varshavsky, A.A. (1990) *Ecologico-geographic variation in rodents*. Nauka, Moscow (in Russian).

Paterson, A.M. & Banks, J. (2001) Analytical approaches to measuring cospeciation of host and parasites: Through a glass, darkly. *International Journal for Parasitology*, **31,** 1012–1022.

Pauller, O.F., Elshanskaya, N.I. & 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).

Piontkovskaya, S.P. & 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*. PhD thesis, Novosibirsk State University, Novosibirsk (in Russian).

Plesnivtseva, G.G. & Zhovty, I.F. (1981) New data on ectoparasites of mammals in Yakutia. Fauna and ecology of arthropods of Siberia. *Proceedings of the V meeting of Siberian entomologists* (ed. by A.I. Tcherepanov), pp. 261–263. Nauka, Novosibirsk (in Russian).

Poulin, R. (2003) The decay of similarity with geographical distance in parasite communities of vertebrate hosts. *Journal of Biogeography*, **30,** 1609–1615.

Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, **8,** 15–22.

Radovsky, F.J. (1985) Evolution of mammalian mesostigmatid mites. *Coevolution of parasitic arthropods and mammals* (ed. by K.C. Kim), pp. 441–504. John Wiley, New York.

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

Senotrusova, V.N. (1987) *Gamasid mites – parasites of wild animals in Kazakhstan*. Nauka, Kazakh SSR Branch, Alma-Ata (in Russian).

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

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. *Zooparasitology of the Baikal lake valley* (ed. by N.M. Pronin), pp. 134–151. Ulan-Ude, (in Russian).

Tagiltsev, A.A. (1967) Ecology of gamasoid mites in the nests of the forest dormouse (*Dryomys nitedula* Pall.). *Parazitologiya*, **1,** 507–511 (in Russian).

Tagiltsev, A.A. (1975) Ecological aspects of the gamasid mite studies in natural foci of some arboviral diseases. DSc thesis, Academy of Sciences of Kyrgyz SSR, Frunze, USSR (in Russian).

Thompson, R. & Townsend, C. (2006) A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, **75,** 476–484.

Tixier, M.S., Kreiter, S., Barbar, Z., Ragusa, S. & Cheval, B. (2006) Status of two cryptic species, *Typhlodromus exhilaratus* Ragusa and *Typhlodromus phialatus* Athias-Henriot (Acari: Phytoseiidae): consequences for taxonomy. *Zoologica Scripta*, **35,** 115–122.

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, **299,** 241–244.

Vasiliev, G.I., Antsiferov, M.I., Veropanov, Y.V., Vinokur, B.S. & 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).

Vazquez, D.P., Poulin, R., Krasnov, B.R. & Shenbrot, G.I. (2005) Species abundance patterns and the distribution of specialization in host–parasite interaction networks. *Journal of Animal Ecology*, **74,** 946–955.

Volkov, V.I. & Chernykh, P.A. (1977) Gamasina mites of the Priamurye region. *Haematophagous arthropods and their control in the new developed territories in Far East* (ed. by V.I. Volkov), pp. 42–68. Nauka, Leningrad (in Russian).

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

Yudin, B.S., Krivosheev, V.G. & Belyaev V.G. (1976) *Small mammals of the northern Far East*. Nauka, Novosibirsk (in Russian).

Zemskaya, A.A. (1973) *Parasitic gamasid mites and their medical significance*. Meditsina, Moscow (in Russian).

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