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Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographical distance or faunal similarity?

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ABSTRACT

Aim Spatial variation in the diversity of fleas parasitic on small mammals was examined to answer three questions. (1) Is the diversity of flea assemblages repeatable among populations of the same host species? (2) Does similarity in the composition of flea assemblages among populations of the same host species decay with geographical distance, with decreasing similarity in the composition of local host faunas, or with both? (3) Does the diversity of flea assemblages correlate with climatic variables?

Location The study used previously published data on 69 species of small mammals and their fleas from 24 different regions of the Holarctic.

Methods The diversity of flea assemblages was measured as both species richness and the average taxonomic distinctness of their component species. Similarity between flea assemblages was measured using both the Jaccard and Morisita–Horn indices, whereas similarity in the composition of host faunas between regions (host 'faunal' distance) was quantified using the Jaccard index. Where appropriate, a correction was made for the potentially confounding influence of phylogeny using the independent contrasts method.

Results Flea species richness varied less within than among host species, and is thus a repeatable host species character; the same was not true of the taxonomic distinctness of flea assemblages. In almost all host species found in at least five regions, similarity in flea assemblages decreased with increases in either or both geographical and faunal distance. In most host species, the diversity of flea assemblages correlated with one or more climatic variable, in particular mean winter temperature.

Main conclusions Spatial variation in flea diversity among populations of the same mammal species is constrained by the fact that it appears to be a species character, but is also driven by local climatic conditions. The results highlight how ecological processes interact with co-evolutionary history to determine local parasite biodiversity.

Keywords

Faunal similarity, fleas, geographical distance, Holarctic mammals, parasite species richness, small mammals.

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INTRODUCTION

Patterns of spatial variation in biological diversity represent one of the central themes in modern biogeography and ecology (Rosenzweig, 1995; Gaston & Williams, 1996). Much of the knowledge about these patterns available to date is based strictly on studies of free-living organisms (Rosenzweig, 1995), whereas patterns of parasite diversity have until now attracted

much less attention. However, parasites form a large proportion of the diversity of life, and parasite communities represent convenient models for investigations of spatial diversity patterns (Poulin, 2003). Species richness of parasite communities is usually not extremely high and, thus, enumeration of all species is quite possible. Representative data on the parasite communities from different host species within the same geographical region and those from several populations of the same host across different geographical regions are available from the literature.

Indeed, the number of studies aiming to explain patterns of parasite species richness among host species has increased greatly during the last decade (see Poulin, 1998; Combes, 2001 and references therein). In fact, Combes (2001) listed as many as 16 different (not necessarily alternative) hypotheses related to correlates of parasite species richness among different host species. Although some of these hypotheses have never been tested, and testing of others has provided contradictory results (e.g. Price & Clancy, 1983; but see Guegan & Kennedy, 1993), it is now commonly accepted that parasite species are not distributed randomly among their hosts but rather parasite species richness results from multiple host-related factors (Caro *et al.*, 1997; Morand & Poulin, 1998; Morand & Harvey, 2000). However, most studies of parasite species richness have focused on a broad scale (e.g. among different host species), whereas patterns of diversity of parasite communities on a smaller scale (e.g. among different populations of the same host species) are much less studied (Carney & Dick, 2000; Poulin & Valtonen, 2002; Poulin, 2003; Calvete *et al.*, 2004). In addition, geographical variation in the diversity of parasite xenocommunities (*sensu* Combes, 2001) in the same host species has been studied mainly in endoparasites (e.g. Kisielewska, 1970; Kennedy & Bush, 1994). For example, Poulin (2003) found that the similarity in the composition of helminth communities in vertebrate hosts decreased with increasing geographical distance between host populations, although this was only true for some host species and not others. On the contrary, ectoparasite xenocommunities have attracted much less attention (e.g. Proctor & Jones, 2004). However, ectoparasites, particularly periodic ones such as fleas, must be strongly influenced by the characteristics of their off-host environment. Consequently, species diversity of ectoparasites should demonstrate strong geographical variation and covary with the parameters related to the host environment such as climate and the species composition of sympatric host species.

Fleas (Siphonaptera) are characteristic mammalian ectoparasites, most abundant and diverse on small and medium-sized species. In most fleas, all stages of the life cycle are spent off the host, except for the adults that feed intermittently on the host. Here, we examined spatial variation in species diversity and similarity of flea assemblages on small mammalian hosts. We used two measures of diversity of flea assemblages: flea species richness and the taxonomic distinctness of species within an assemblage. The latter measure is based on the average taxonomic distances between species in an assemblage (Clarke & Warwick, 1998, 1999, 2001 Warwick & Clarke, 2001), and provides a measure of the composition, and not the size, of an assemblage.

The aims of this study were threefold. First, we asked whether diversity of the flea assemblage on a host species, measured either as flea species richness or taxonomic distinctness, is a true host characteristic. In other words, we asked if the diversity of flea assemblages is repeatable within a host species, i.e. a feature that varies less among different populations of the same host species than among different host species. Repeatability of flea species richness within a host species would indicate that the accumulation of flea species in a host population reaches the same upper limit on all populations of the same host species. In contrast, repeatability of taxonomic distinctness would suggest similar patterns of host colonization and intra-host speciation across all conspecific populations in the course of the co-evolutionary history of fleas and mammals (Poulin & Mouillot, 2004).

Secondly, we asked how variable (if at all) the diversity and composition of flea assemblages are among different populations of the same host by comparison of the similarity in flea assemblages among conspecific host populations that occur in different geographical locations and belong to host faunas of different species composition. The proportion of species shared by two communities often decreases with increasing distance between them (distance decay of similarity; see Nekola & White, 1999; Poulin, 2003 and references therein). A decrease of similarity with increasing distance has been shown not only for free-living organisms but for helminth parasites also (Poulin, 2003). Consequently, we predicted that the similarity in flea assemblages between different populations of the same host would decrease with increasing distance between these populations as is the case with communities of both free-living organisms and helminths. The decrease of similarity in biological communities with distance can arise because of various mechanisms: one of them being a decrease in environmental similarity with increasing distances (Nekola & White, 1999). However, environmental similarity for parasites involves not only the physical environment but also an environment represented by the species composition of the host community (host 'faunal' environment). For example, host species in communities of similar composition but under different environmental conditions can support similar flea assemblages and vice versa. Consequently, we predicted the same pattern for 'faunal' dissimilarities as expected for geographical distances, namely that similarity in flea assemblages would decrease with increasing dissimilarity of host 'milieu'.

Finally, we determined the effect of the off-host climatic conditions on the diversity of flea assemblages of the same host species. The effect of climatic variables on the diversity and composition of flea assemblages can be related to the microclimatic and substrate (mediated via microclimate) preferences of the off-host stages of fleas (eggs, larvae and/or pupa) as well as of adult fleas (e.g. Krasnov *et al.*, 1998).

MATERIALS AND METHODS

Data set

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Insectivora, Lagomorpha and Rodentia) in 24 different regions of the Holarctic (Table 1). These sources provided data on the number of individuals of a particular flea species found on a number of individuals of a particular host species. We cross-checked the flea species lists with the catalogue of Lewis & Lewis (1990) to resolve cases of synonymy. Single findings of a flea species on a host species or in a region were considered accidental and were not included in the analyses. Synanthropic widespread mammalian species (*Mus musculus* L., *Rattus rattus* L. and *Rattus norvegicus* Berkenhout) were considered in the borders of their natural geographical ranges only.

We included in the analyses only those mammal species that were recorded in at least two regions. In total, we used data on 254 mammal samples, representing 366,737 individuals of 69 species from which 1,292,643 individual fleas of 246 species were recovered. The number of hosts examined in a survey is an important determinant of the number of the less common parasite species found and estimates of flea species richness might be inaccurate for smaller samples (see Walther *et al.*, 1995; Stanko *et al.*, 2002). Consequently, sampling effort was included as a potential confounding variable in the

repeatability analysis (see below), whereas only data from surveys that examined at least 10 individual hosts per population were included in the similarity analyses (60 species, see below).

Measures of flea abundance and species diversity

We used the mean number of flea individuals per individual host of a given species in a given region as a measure of flea abundance on a host in a region. The two measures of flea species diversity we used were: (a) the number of flea species found on a host species, or species richness, corrected for sampling effort (residuals of the linear regression against number of hosts examined); and (b) average taxonomic distinctness (Δ^+) and the variance in taxonomic distinctness (Λ^+) of the flea species present. When these flea 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 two flea species, computed across all possible pairs of flea species (Clarke & Warwick, 1998, 1999; Warwick & Clarke, 2001; Poulin & Mouillot, 2003a, 2004). The greater the taxonomic distinctness between flea species, the higher the number of steps needed, and the higher the value of the index Δ^+. Using the taxonomic classification of Hopkins & Rothschild (1953, 1956, 1962, 1966, 1971), Traub *et al.* (1983) and Medvedev (1998), all flea species included here were fitted into a taxonomic structure with eight hierarchical levels above species, i.e. subgenus (or

Table 1 Data on small mammals and fleas from 24 regions used in the analyses. Numbers in parentheses represent the total numbers of sampled individuals (data include mammal species in which no less than two populations were examined)

Region	Number of host species	Number of flea species	Source
Adzharia, southern Caucasus	9 (7487)	16 (1323)	Alania *et al.* (1964)
Akmolinsk region, northern Kazakhstan	17 (302)	25 (2027)	Mikulin (1959a)
Altai mountains	19 (1332)	8 (1834)	Sapegina *et al.* (1981)
California	4 (407)	13 (307)	Davis *et al.* (2002)
Central Yakutia	7 (556)	17 (848)	Elshanskaya & Popov (1972)
Dzhungarskyi Alatau, Kazakhstan	15 (5230)	21 (5219)	Burdelova (1996)
East Balkhash desert, Kazakhstan	18 (443)	32 (6507)	Mikulin (1959b)
Idaho	10 (3352)	27 (10,017)	Allred (1968)
Kabarda, northern Caucasus	11 (1632)	18 (1695)	Syrvacheva (1964)
Khabarovsk region, southern Russian Far East	8 (6596)	22 (5192)	Koshkin (1966)
Kustanai region, north-western Kazakhstan	18 (195)	18 (958)	Reshetnikova (1959)
Moyynkum desert, Kazakhstan	30 (45,443)	12 (260,774)	Popova (1967)
Mongolia	3 (844)	13 (2180)	Vasiliev (1966)
North Asian Far East	9 (1374)	13 (1010)	Yudin *et al.* (1976)
North Kyrgyzstan	14 (4750)	31 (6858)	Shwartz *et al.* (1958)
North New Mexico	10 (3941)	23 (2704)	Morlan (1955)
Novosibirsk region, southern Siberia	23 (1841)	27 (4161)	Violovich (1969)
Pavlodar region, eastern Kazakhstan	12 (256)	16 (74)	Sineltschikov (1956)
Selenga region, central Siberia	9 (974)	13 (1045)	Pauller *et al.* (1966)
Slovakia	14 (9825)	18 (10,525)	Stanko *et al.* (2002)
Tarbagatai region, eastern Kazakhstan	22 (318)	31 (1124)	Mikulin (1958)
Turkmenistan	11 (234,257)	36 (906,797)	Zagniborodova (1960) and unpubl. data
Tuva	9 (2450)	26 (25,665)	Letov *et al.* (1966)
Volga-Kama region	30 (32,932)	34 (33,619)	Nazarova (1981)

species group), genus, tribe, subfamily, family, superfamily, infraorder and order (Siphonaptera). We restricted our use of taxonomic levels to these basic ones because they are the only ones available for all flea taxa included here. The maximum value that the index Δ^+ can take is thus 8 (when all flea species belong to different infraorders), and its lowest value is 1 (when all flea species belong to the same subgenus or species group). However, as the index cannot be computed for hosts exploited by a single flea species, we assigned a Δ^+ value of 0 to these host species, to reflect their extremely species-poor flea assemblages. The variance in Δ^+, Λ^+, provides information on any asymmetries in the taxonomic distribution of flea species in assemblages (Clarke & Warwick, 1998, 1999; Warwick & Clarke, 2001; Poulin & Mouillot, 2003a); it can only be computed when a flea assemblage comprises three or more flea species (it always equals zero with two flea species). To calculate Δ^+ and Λ^+, DM and RP developed a computer program using Borland C++ Builder 6.0 (available at http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2).

The number of flea species exploiting a host species was significantly positively correlated (albeit weakly) with both Δ^+ and Λ^+ ($r = 0.45$, $n = 254$ and $r = 0.27$, $n = 176$; respectively, $P < 0.05$ for both), indicating that these measures were influenced by the number of species in a host's flea assemblage. Therefore, in the subsequent analyses Δ^+ and Λ^+ were corrected for the flea species richness in an assemblage. In addition, Δ^+ and Λ^+ did not covary with each other ($r = 0.01$, $n = 174$ $P > 0.05$).

Repeatability analysis

To determine whether species diversity of flea assemblages expressed either as the number of flea species found on a host species (species richness), average taxonomic distinctness among fleas in an assemblage of a host species, Δ^+, or its variance, Λ^+, is a true host species attribute, 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 & Mouillot, 2004). Using host species for which at least two samples were available, we analysed the variation in the number of flea species, taxonomic distinctness among fleas, Δ^+, and its variance, Λ^+ in three 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 & Rohlf (1995). First, we carried out the repeatability analysis using all flea species in the data set. Then, we re-analysed the data using flea genera instead, using the repeatability analysis to see if the composition of flea assemblages at the generic level is repeatable within host species. For this part of the analysis, fleas were fitted into a taxonomic structure of six hierarchical levels above genus (tribe, subfamily, family, superfamily,

infraorder and order) and Δ^+, and its variance, Λ^+ were calculated as described above.

Similarity analysis

To examine how the species composition of flea assemblages on a host species varies with geographical or 'faunal' distance among host populations, we selected 11 host species that occurred in at least six regions. These were *Neomys fodiens* Pennant, *Apodemus agrarius* Pallas, *Apodemus uralensis* Pallas, *M. musculus*, *Arvicola terrestris* L., *Clethrionomys glareolus* Schreber, *Clethrionomys rutilus* Pallas, *Microtus arvalis* Pallas, *Microtus gregalis* Pallas, *Microtus oeconomus* Pallas and *Cricetulus migratorius* Pallas. For each host species, similarity in flea species composition, as well as geographical and 'faunal' distances, were computed for all possible pairs of host populations. To evaluate similarity in flea species composition we used both the Jaccard and Morisita–Horn similarity indices. The Jaccard index is based on presence/absence data. It represents the number of flea species shared by two host populations divided by the total number of flea 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 flea species). In contrast to the Jaccard index, the Morisita–Horn index is quantitative. It is based on relative abundance of different species in the assemblages and has been found to be insensitive to species richness and sample size (Magurran, 1988). Similarity indices were computed using EstimateS 5.0 software (Colwell, 1997).

The geographical distance between pairs of host populations was calculated as the linear distance between the centres of each region (described in the respective sources), obtained from a map using the ArcView 3.2 software. 'Faunal' distance between pairs of regions was calculated as the reciprocal of the Jaccard similarity between the small mammal (Insectivora, Lagomorpha and Rodentia) faunas of these regions. Faunal lists were compiled based on the respective sources as well as Hall (1981); Panteleev *et al.* (1990) and Gromov & Erbaeva (1995). Similarity values for the composition of flea assemblages were log-transformed, and the transformed values were regressed against either log-transformed or untransformed values of both geographical and faunal distance (Poulin, 2003) using stepwise multiple regression. Linear regressions of the transformed similarity values on untransformed distance values gave the best overall fit of data and, thus, we present only these results. Following Poulin (2003), the significance of each regression model was tested using a randomization approach (Manly, 1997) using the RT 2.1 software (Western EcoSystems Technology, Inc., Cheyenne, Wyoming) because the pairwise similarity values and distances were not truly independent in a statistical sense. All regression probabilities are based on 10,000 permutations.

In addition, we examined the effect of geographical and 'faunal' distance on the similarity of flea assemblages using the whole set of host species that occurred in at least two regions and for which at least 10 individuals were examined per region

(60 species). To control for the effects of host phylogeny, we used the method of independent contrasts (Felsenstein, 1985). The phylogenetic tree of hosts was derived from various sources (see details in Krasnov et al., 2004). For hosts with more than one pairwise value (i.e. those occurring in more than two regions) we calculated the across-region mean similarity of flea assemblages and the mean geographical and 'faunal' distances. To compute independent contrasts, we used the PDAP:PDTREE program (Garland et al., 1993; Midford et al., 2003) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison & Maddison, 2004). Contrasts were standardized following Garland et al. (1992). To test for the correlation between similarity in flea species composition and geographical or 'faunal' distance between host populations, we regressed standardized contrasts of log-transformed values of the Jaccard or Morisita–Horn indices of similarity between flea assemblages on standardized contrasts of geographical or 'faunal' distance using major axis regression forced through the origin (Garland et al., 1992; Pagel, 1992).

Analyses of determinants of geographical variation in host specificity

To determine the possible climatic causes of geographical variation in species diversity and composition of flea assemblages within a host species, we calculated parameters that characterized climate for each region. These were annual precipitation, mean surface air temperature of January and mean surface air temperature of July. These variables where calculated for each region using 30′ grid data, and then averaged across all grids within a region (Kineman et al., 2000). For each of 11 host species occurring in at least six different regions, we regressed measures of flea assemblage diversity in a region (species richness, Δ^+ and Λ^+) against the mean regional values of the climatic parameters. We avoided an inflated Type I error by performing sequential Bonferroni corrections of the significance level.

RESULTS

Repeatability of species richness and composition of flea assemblages within host species

The repeatability analysis for 69 mammal species occurring in at least two regions demonstrated that the species richness of flea assemblages can be considered as a host species character. Estimates of the number of flea species from the same host species were more similar to each other than expected by chance and varied significantly among host species ($F_{68,185} = 2.48$, $P < 0.0001$), with 32.8% of the variation among samples accounted for by differences between host species. However, this was not the case for either Δ^+ or Λ^+ (Fig. 1). Estimates of taxonomic distinctness of flea assemblages (Δ^+) and of asymmetry of this distinctness (Λ^+) were too variable within-host species ($F_{68,185} = 1.25$ and $F_{44,114} = 1.08$, respectively, $P > 0.3$ for both), and only 6.9%
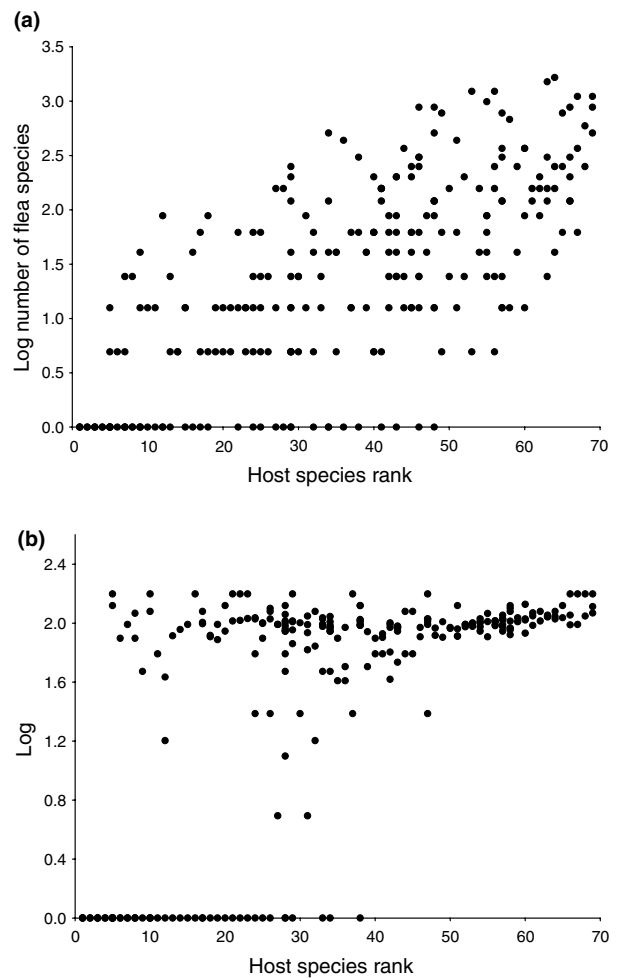

Figure 1 Rank plots of number of flea species, or species richness (a), and average taxonomic distinctness (Δ^+) between fleas (b) in flea assemblages on small mammals. The 69 host species recorded in at least two regions are ranked according to their mean log-transformed values of either number of flea species (controlled for sampling effort) or Δ^+ (controlled for number of flea species), with rank 1 given to the species with the lowest mean value; all sample estimates are plotted for each species. If variation is small within compared to between flea species, we expect the points to fall in a region of the plot stretching from the lower left to the upper right corner, with few or no points in either the upper left or lower right corner.

and 2.4%, respectively, of the variation among samples could be accounted for by differences between host species. Thus, estimates of flea species richness, but not of their taxonomic distinctness appeared to be repeatable within the same host species. The number of flea genera in the assemblages was also repeatable across host species ($F_{41,275} = 3.01$, $P < 0.001$), with 21.7% of the variation among samples originating from between-host differences. However, the taxonomic distinctness (Δ^+) and asymmetry (Λ^+) of flea assemblages considered at the generic level were, again, not repeatable within host species and were as variable across as within host species ($F_{41,275} = 1.33$ and $F_{30,174} = 1.12$, $P > 0.09$ for both).

Similarity of flea assemblages within host species

The results of regression analyses of two measures of similarity in species composition of flea assemblages on 11 host species against geographical or 'faunal' distances between pairs of host populations are summarized in Table 2. No relationship between either similarity measure and either distance measure was found in one host species, the insectivore *N. fodiens* ($r^2 = 0.09$, $F_{1,8} = 1.99$ for the Jaccard similarity of flea assemblages and $r^2 = 0.43$, $F_{2,7} = 2.60$ for the Morisita–Horn similarity of flea assemblages, $P > 0.1$ for both). In the other 10 species, at least one of the similarity measures was negatively correlated with at least one of the distance measures. Similarity in species composition of flea assemblages decreased with an increase in both distance measures in two species (*A. uralensis*, *C. glareolus*). 'Faunal', but not geographical, distance determined dissimilarity in species composition of flea assemblages in four species (*A. agrarius*, *M. musculus*, *M. arvalis* and *C. migratorius*). Finally, in *A. terrestris*, *C. rutilus*, *M. gregalis* and *M. oeconomus*, similarity in species composition of flea assemblages decreased with increasing geographical distance but was not affected by 'faunal' distance.

Regression analyses using independent contrasts demonstrated that, across 60 host species, average similarity in flea species composition between any two host populations calculated with the Jaccard but not the Morisita–Horn index was negatively correlated with average 'faunal' distance between these two populations ($r = -0.38$, $P < 0.003$; Fig. 2 and $r = -0.42$, $P > 0.1$, respectively). Two points with sharply higher and sharply lower than expected similarity (Fig. 2) correspond to contrasts between *Apodemus flavicollis* Melchior and *Apodemus sylvaticus* L. and between *Spermophilopsis leptodactylus* Lichtenstein and *Spermophilus* spp., respectively. In contrast, n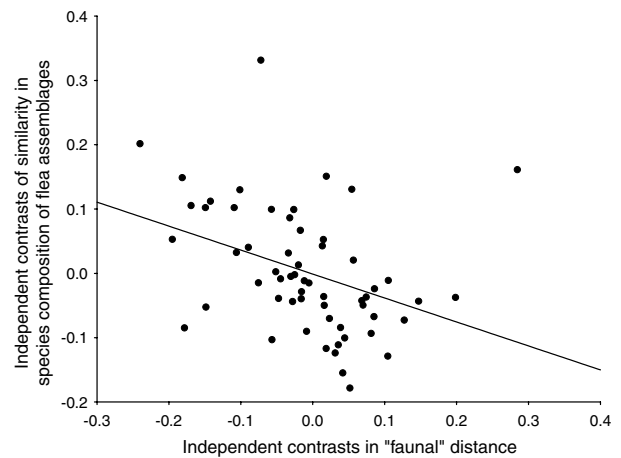o relationship between average similarity in flea species composition and geographical distance between any two host populations was found across host species using independent contrasts ($r = -0.18$–0.05, $P > 0.16$). Stepwise multiple regressions of the similarity of flea assemblages against both geographical and the 'faunal' distances forced through origin provided essentially the same results.

Diversity of flea assemblages and climate variables

In nine of the 11 host species examined, at least one measure of flea diversity correlated positively or negatively with at least one of the climatic parameters (Table 3). One measure of flea

Figure 2 Relationship between average similarity in flea species composition calculated using the Jaccard index and average 'faunal' distance between two host populations ($r = -0.38$, $P < 0.003$). The relationship was computed across 60 mammalian host species using independent contrasts.

Table 2 Summary of the significant ($P < 0.005$) multiple regression analyses of the effect of geographical and 'faunal' distance on similarity in flea assemblages in 10 mammal species. For geographical distance, slope values are in units of log similarity per 1000 km distance. The sample size (n) is the number of similarity values and distances in each analysis, i.e. the number of pairwise comparisons between host populations

Host species	n	Similarity in flea assemblages	Spatial distance	Intercept	Standardized slope (beta coefficient)	r^2
Apodemus agrarius	28	Jaccard	'Faunal'	0.47	−0.60	0.38
		Morisita–Horn	'Faunal'	0.45	−0.51	0.26
Apodemus uralensis	15	Jaccard	Geographical	0.48	−0.35	0.84
			'Faunal'		−0.68	
		Morisita–Horn	'Faunal'	0.51	−0.80	0.64
Mus musculus	91	Morisita–Horn	'Faunal'	0.61	−0.37	0.12
Arvicola terrestris	28	Jaccard	Geographical	0.38	−0.42	0.38
		Morisita–Horn	Geographical	0.49	−0.57	0.32
Clethrionomys glareolus	10	Jaccard	'Faunal'	0.57	−0.75	0.85
		Morisita–Horn	Geographical	0.44	−0.68	0.47
Clethrionomys rutilus	21	Jaccard	Geographical	0.31	−0.79	0.64
		Morisita–Horn	Geographical	0.54	−0.77	0.60
Microtus arvalis	36	Morisita–Horn	'Faunal'	0.55	−0.47	0.16
Microtus gregalis	15	Jaccard	Geographical	0.44	−0.50	0.55
		Morisita–Horn	Geographical	0.72	−0.66	0.61
Microtus oeconomus	21	Jaccard	Geographical	0.21	−0.44	0.20
		Morisita–Horn	Geographical	0.30	−0.53	0.28
Cricetulus migratorius	28	Jaccard	'Faunal'	0.25	−0.59	0.35

Table 3 Summary of significant ($P < 0.05$) correlations between regional characteristics of flea assemblages and climatic factors across regions for nine mammal species. The factors are mean temperature of January (TJA) and July (TJU) and mean annual precipitation (P)

Species	Characteristics of flea assemblage	Climatic factor	r
Apodemus agrarius	Δ^+	TJA	−0.98
	Δ^+	P	−0.90
Apodemus uralensis	Species richness	TJA	−0.73
	Δ^+	TJA	−0.90
Mus musculus	Species richness	TJA	0.68
	Λ^+	TJU	0.83
Arvicola terrestris	Δ^+	TJA	−0.86
	Δ^+	P	0.80
	Λ^+	TJA	−0.83
	Λ^+	P	0.82
Clethrionomys rutilus	Δ^+	TJU	−0.92
	Λ^+	TJU	0.86
Microtus arvalis	Species richness	TJA	−0.49
	Δ^+	TJA	0.49
	Λ^+	P	0.52
Microtus gregalis	Species richness	TJA	−0.98
	Species richness	TJU	−0.79
	Δ^+	TJU	0.82
	Λ^+	P	0.99
Cricetulus migratorius	Δ^+	TJA	0.69
Neomys fodiens	Species richness	TJA	0.73

assemblage diversity or another was correlated with the mean multiannual temperature in January in the majority of these host species (eight of 11 species), whereas a correlation between any measure of diversity of flea assemblages and the mean annual temperature of July or annual precipitation was found in three host species only.

DISCUSSION

The results of this study demonstrated that: (a) flea species richness but not their taxonomic distinctness was repeatable within a host species, (b) similarity in flea assemblages among different populations of the same host decreased with increases in either geographical or 'faunal' (or both) distances between these populations, and (c) in general, local environmental conditions, measured as climatic variables, influenced the diversity of flea assemblages on a host species.

Flea species richness is a true host species attribute

The repeatability of flea species richness among populations of the same host species suggests that the number of flea species that can be supported is a true attribute of a host species. This suggests the existence of some threshold of defence against parasites in a host species that limits the host's ability to cope with multiple parasite species (e.g. because of presumably costly defence systems; Schmid-Hempel & Egert, 2003) but instead maintains their pressure (expressed as a number of parasite species) at a 'tolerable' level (Combes, 2001). If we use the encounter and compatibility filter concept of Combes (2001) that was originally proposed for the host spectrum of a parasite, we can adapt it to the array of parasite species that a

host can support. In this case, the encounter filter excludes all parasites that cannot encounter the host for ecological and behavioural reasons (e.g. host occurs in a very specific habitat), whereas the compatibility filter excludes all parasites that cannot withstand the host immune defenses. Consequently, for each host species, there may be a threshold of encounter and/or a threshold of compatibility that determine the particular number of parasites capable of exploiting this host.

In contrast with flea species richness, the taxonomic distinctness of flea assemblages and its variance were not repeatable within a host species. This means that whenever a new exploiter is added to a host's parasite community, this exploiter is a random addition from the regional pool of exploiter species that manages somehow to adapt itself to the new host species. This can happen, for example, when a new host (supporting its own parasite set) invades an area that is already inhabited by a certain array of exploiter species, and one or more of the resident parasites succeed in attacking and establishing themselves on this new resource. For example, introduced fish rapidly accumulate a rich assemblage of parasite species from the resident fish species (Poulin & Mouillot, 2003b). Alternatively, the parasites of a host invading a new area can succeed in attacking and establishing themselves on one or more resident hosts (e.g. Combes & Le Brun, 1990). From an ecological perspective, this can also mean that each host species is characterized by a certain number of flea species at which the community it can support becomes saturated; the lack of repeatability in taxonomic distinctness would suggest that different flea species are ecologically interchangeable and contribute equally to this saturation. In any case, the results are consistent with a co-evolutionary history dominated mainly by independent

colonization of new hosts (host switching events) (Poulin & Mouillot, 2004). Indeed, the evolutionary history of mammal-flea associations has been shown to involve mainly association by colonization with frequent host switching rather than association by descent (Traub, 1980; Krasnov & Shenbrot, 2002; Lu & Wu, 2003).

Distance decay of similarity in flea assemblages

In most mammal species examined, as well as in the across-species analysis, similarity in flea assemblages within a host species decreased with one or another measure of distance. This suggests that the pattern of distance decay of similarity found in communities of other organisms is universal (Nekola & White, 1999; Poulin, 2003). Furthermore, a negative exponential function provided the best fit to the distance decay of similarity in flea assemblages, as was the case for plant communities (Nekola & White, 1999) and helminth assemblages in fish and mammals (Poulin, 2003). This means that similarity in flea assemblages declines constantly and proportionally per unit distance. Moreover, slope values of the relationship between the Jaccard similarity and the 'faunal' distance were similar for all species in which this relationship was significant. The same was true for the slope values of the relationship between the Jaccard similarity and geographical distance, except for *C. rutilus*, which was rather high. With the exception of *C. rutilus*, slope values for the relationship between Jaccard similarity and geographical distance observed here for flea assemblages were roughly the same as those found for communities of helminth parasites in mammals (Poulin, 2003). In general, slope values for geographical distance were lower than those for the 'faunal' distance suggesting that, perhaps, difference in the surrounding 'milieu' between host populations is a more important determinant of the composition of flea assemblages than mere physical distance. This is supported also by the significant correlation between similarity in flea assemblages and the 'faunal', but not geographical, distance, found in the across-species analysis, and by the absence of repeatability in taxonomic distinctness of flea assemblages among different populations of the same host (see above).

Slope values of the regressions using the Morisita–Horn similarity appeared to be more variable than those using the Jaccard similarity. Perhaps, similarity calculations based on the presence/absence data (the Jaccard index) are more appropriate for comparisons using multiple data sets collected at different times by different researchers, than calculations using the abundance data (the Morisita–Horn index) because the latter can be influenced by some methodological differences between studies (but see Wolda, 1981). In addition, the Jaccard index is effective in detecting underlying ecological gradients (Faith *et al.*, 1987).

Another aspect of the results of this study that requires an explanation is the difference between host species in the effect of either the 'faunal' or 'geographical' distance on the similarity of their flea assemblages. This difference can be related to either differences in the structure of geographical ranges of different species or in patterns of sampling across the geographical range of a species, or both. Indeed, all species for which the relationship between the similarity in flea assemblages and the 'faunal', but not geographical, distance was found are characterized either by continuous geographical ranges (*M. musculus*, *M. arvalis*, *C. migratorius*) or they were sampled in the continuous part of their geographical range (*A. agrarius*) that is situated in the same biome or group of biomes. For these species, environmental variability across the geographical range is likely lower than the 'faunal' variability. In contrast, species for which the relationship between the similarity in flea assemblages and geographical, but not the 'faunal', distance was found are either characterized by a fragmented geographical range (*M. gregalis*) or were sampled in those parts of their geographical ranges where they are distributed patchily in intrazonal habitats (*A. terrestris*, *C. rutilus* and *M. oeconomus*). For these species, environmental variability can be higher than the 'faunal' variability (*M. gregalis*, *M. oeconomus* and *C. rutilus*) and, thus, geographical distance plays the major role in determining similarity between different populations.

Climatic effect on flea diversity

In spite of flea species richness being a true host character, this character varied across the geographical range in many hosts, indicating that diversity of flea assemblages is also influenced by local factors. Variation across regions in the diversity of flea assemblages was found to be linked with climatic conditions in nine of 11 studied host species. This suggests the occurrence of a causal association between flea diversity and local ecological factors. The effect of climatic variables on flea diversity is likely related to the microclimatic preferences of the off-host stages of fleas (eggs, larvae and/or pupa) as well as adult individuals. For example, the jird *Meriones crassus* Sundevall demonstrates sharply different flea assemblages in different locations in the Negev desert of Israel (Krasnov *et al.*, 1997). The reason for this was shown to be the unsuitability of microclimatic and substrate conditions in *M. crassus* burrows for the successful survival of eggs, larvae and newly-emerged imago of either *Xenopsylla ramesis* Rothschild or *Xenopsylla conformis* Wagner in different areas (Krasnov *et al.*, 2001, 2002).

Winter temperature appeared to be the most important correlate of flea diversity. In most species studied, flea diversity decreased with increasing winter temperature. These species have boreal and/or temperate distributions, and, thus, regions with relatively warm winters represent the southern periphery of their geographical ranges. Peripheral host populations may be small and isolated (Carson, 1959) and may lose some of their parasites as is, for example, the case with island host populations (e.g. Goüy de Bellocq *et al.*, 2002). However, in *M. musculus*, *C. migratorius* and *N. fodiens* the correlation between flea diversity and winter temperature appeared to be positive. *Cricetulus migratorius* inhabits mainly steppe and desert regions and, thus, can display a pattern opposite to what

was found in boreal species. Northern populations of this species are at the periphery of their geographical range, they can be small and isolated with decreased parasite species richness. The increase of flea diversity with increasing winter temperature in *M. musculus* can be explained by the fact that this species is synanthropous in northern regions and inhabits natural habitats in southern regions. Consequently, *M. musculus* is mainly nature-dwelling in regions with relatively warm winters, where it can easily get fleas from sympatric rodent species (Krasnov & Khokhlova, 2001). *Neomys fodiens* inhabits boreal and temperate biomes. Changes in the diversity of flea assemblages of this species with increasing winter temperature could be the same as in other boreal species (see above). However, in our data set, samples of *N. fodiens* were taken from the central part of its geographical range. This can explain the apparent increase of flea diversity from north to south. In addition, this explains also why we did not find any relationship between similarity in flea assemblages of different populations of this species and either geographical or 'faunal' distance.

In conclusion, our results suggest that the diversity of flea assemblages on small mammalian hosts is: (a) a true species character, (b) affected by the availability of taxonomically-related host species in the region, and (c) to an important extent mediated by local climatic conditions.

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BIOSKETCHES

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