

Similarity in ectoparasite faunas of Palaearctic rodents as a function of host phylogenetic, geographic or environmental distances: Which matters the most?

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ABSTRACT

Different host species harbour parasite faunas that are anywhere from very similar to very different in species composition. A priori, the similarity in the parasite faunas of any two host species should decrease with increases in either the phylogenetic distance, the distinctness of the environments occupied or the geographical distance between these hosts. We tested these predictions using extensive data on the faunas of fleas (Insecta: Siphonaptera) and gamasid mites (Acari: Parasitiformes) parasitic on rodents across the Palaearctic. For each pair of host species, we computed the similarity in parasite faunas based on both species composition as well as the phylogenetic and/or taxonomic distinctness of parasite species. Phylogenetic distances between hosts were based on patristic distances through a rodent phylogeny, geographic distances were computed from geographic range data, and environmental dissimilarity was measured from the average climatic and vegetation scores of each host range. Using multiple regressions on distance matrices to assess the separate explanatory power of each of the three dependent variables, environmental dissimilarity between the ranges of host species emerged as the best predictor of dissimilarity between parasite faunas, especially for fleas; in the case of mites, phylogenetic distance between host species was also important. A closer look at the data indicates that the flea and mite faunas of two hosts inhabiting different environments are always different, whilst hosts living in similar environments can have either very similar or dissimilar parasite faunas. Additional tests showed that dissimilarity in flea or mite faunas between host geographic ranges was best explained by dissimilarity in vegetation, followed by dissimilarity in climatic conditions. Thus, external environmental factors may play greater roles than commonly thought in the evolution of host–parasite associations.

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1. Introduction

A host's parasite fauna is the entire set of parasite species exploiting all populations of that host species across its entire geographic range (Poulin, 2007). Although a variety of evolutionary events have shaped the parasite faunas of modern hosts (Brooks, 1988; Paterson et al., 1993; Paterson and Gray, 1997; Page and Charleston, 1998; Beveridge and Chilton, 2001; Paterson and Banks, 2001; Roy, 2001), the evolution of a parasite fauna is, in general, influenced by two main processes, namely the acquisition and loss of parasite species over time. Acquisition of parasites

occurs either by inheritance from ancestors or via shifts from related or unrelated hosts (see Brooks et al., 2006a). Loss of parasites occurs due to either historical accidents (e.g., “missing the boat” sorting events, see Paterson and Gray, 1997 for definition) or host dispersal to new environments which may be unfavourable for some parasites (e.g., suboptimal climatic conditions for free-living stages or the absence of appropriate intermediate hosts). As a result, the composition of the parasite fauna of a given host is partly due to host phylogenetic identity, whereas another part is due to its environment (Kennedy and Bush, 1994). The effect of host identity on the composition of parasite faunas is manifested by similar parasite assemblages in phylogenetically-related hosts (e.g., Munoz Cerda et al., 2006), whereas the effect of the environment is seen as similar parasite assemblages in phylogenetically

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distant but co-occurring hosts (e.g., Szymanski and Lovette, 2005; Poulin, *in press*). The latter phenomenon may indicate ecological fitting, i.e., situations in which an organism interacts with its environment in a way that suggests a shared evolutionary history, when in reality the traits relevant to the interaction evolved elsewhere and in response to a different set of conditions (Janzen, 1985). Ecological fitting applies well to parasites and their hosts. In particular, it may explain incongruities between parasite and host phylogenies (Brooks et al., 2006a). Using case studies on trematodes in amphibian hosts, Brooks et al. (2006a,b) showed that if the main requirement of a parasite is the resource itself rather than its “representation” in nature (a particular host species; see also Brooks and McLennan, 2002) and if this resource is shared by many host species, then a parasite tracking the resource may invade new geographic areas where the resource is present, but where its “original representation” (the host species in which the parasite evolved and is adapted to) does not necessarily occur. Thus, similarity in parasite assemblages between host species is determined not only by host phylogenetic relatedness *per se* (i.e., is a result of parasite–host co-speciation), but to a great extent by their morphological, physiological and/or environmental similarity unrelated to their phylogeny (i.e., is a result of ecological fitting). Recently, Poulin (*in press*) tested for the relationship between similarity of parasite faunas and host phylogenetic distance using data on metazoan parasites of freshwater fishes. It was found that phylogenetically close hosts tended to share most of their parasites, whilst phylogenetically distant hosts have roughly equal chances of harbouring very similar or very dissimilar parasite faunas. This suggested that the effect of environmental similarity might play an important role. However, neither the effect of environmental similarity on similarity of parasite faunas nor the relative importance of phylogenetic, geographic and environmental factors for the similarity in parasite species composition has ever been studied.

An additional and potentially important factor affecting between-host similarity in parasite assemblages is the difference between their occurrences in geographic space. This pattern, commonly known as the distance decay of similarity, corresponds to a decrease in the similarity of species composition between biological communities in two localities with increasing geographical distance between these localities. It is one of the most ubiquitous spatial patterns in ecology and biogeography (Nekola and White, 1999; Nekola and Brown, 2007). In particular, a distance decay of similarity has been reported for various parasites in various hosts (Poulin, 2003; Fellis and Esch, 2005; Krasnov et al., 2005a; Oliva and González, 2005; Vinarski et al., 2007; Pérez-del-Olmo et al., 2009; Thieltges et al., 2009). Although at first glance the mechanism underlying this pattern seems to be related to the aforementioned effect of the environment (i.e., a decrease in environmental similarity with increasing distance), this may not always be the case. Instead, the mechanism of distance decay in community similarity may have a “pure” spatial component because of (i) the probability of a hard geographic barrier blocking dispersal increases with increasing distance, and (ii) the low mobility of many species restricts dispersal even in a homogenous environment (Soininen et al., 2007).

The aim of this study was to understand the relative influence of phylogenetic distance, environmental dissimilarity and geographic distance amongst host species on the dissimilarity in species composition of parasite faunas amongst these hosts. We investigated dissimilarity in faunas of fleas (Insecta: Siphonaptera) and gamasid mites (Acari: Parasitiformes) parasitic on rodent hosts across the Palaearctic. Fleas are obligate hematophagous ectoparasites, most abundant and diverse on small and medium-sized mammals. In most fleas, all stages of the life cycle are spent off the host, except for the adults that feed intermittently on the host. In contrast,

gamasid mites vary in their ecology and feeding modes. Here we focused on mites collected from host body surfaces which include both facultative and obligatory haemato- and/or lymphophages. Earlier, we reported that host community dissimilarity had a strong effect on the similarity of flea assemblages (Krasnov et al., 2005a), whereas mite assemblages were mainly affected by similarity in local environmental conditions (Vinarski et al., 2007). Furthermore, the hosts seem to be the main vehicle of dispersal for both fleas and mites. Consequently, we predicted that between-host dissimilarity in the composition of their flea faunas should be mainly related to between-host phylogenetic distance, whereas between-host dissimilarity in the composition of their mite faunas should be mainly related to differences in the environments in which these hosts occur. We expected the effect of geographic distances to be similar for both parasite taxa.

In this study, we considered not only compositional but also taxonomic and phylogenetic (for fleas) dissimilarity between flea and mite faunas. These measures represent another facet of assemblage dissimilarity that focus on the presence or absence of flea or mite lineages rather than on individual species. In other words, these measures consider evolutionary rather than ecological components of parasite faunas.

2. Materials and methods

2.1. Parasite data sets

Data on fleas and gamasid mites collected from the bodies of rodent hosts in different regions of the Palaearctic were obtained from published surveys (60 surveys in 52 regions for fleas and 25 surveys in 25 regions for mites) and unpublished data (four surveys in one region for mites) that reported the number of fleas or mites of each species found on a given number of individuals of each rodent species in a particular location (Supplementary Fig. S1). Four of these surveys reported data on both fleas and mites. Rodents for which fewer than 10 individuals were examined were excluded from the analyses. In addition, we excluded from the analyses (i) commensal rodents (*Rattus rattus*, *Rattus norvegicus* and *Mus musculus*), (ii) a recently introduced rodent (*Ondatra zibethicus*) and (iii) rodents of unclear taxonomic affinity, i.e., those that had the status of a species during the survey period but that have subsequently been split into two or more species (e.g., *Arvicola terrestris*, *Sicista subtilis*). Commensal rodents were excluded from the analyses because their geographic ranges cannot be explicitly defined, and because the main habitats of these rodents (e.g., human settlements) have not been sampled in the majority of surveys. *Ondatra zibethicus*, which has been recently introduced in the Palaearctic, was excluded from the analysis because (i) it acquired parasites from resident hosts, i.e., during ecological time only, as opposed to other rodents that acquired parasites over both evolutionary and ecological time scales, and (ii) the flea and mite faunas of *O. zibethicus* in its original area (North America) differ from those in the area of introduction (Eurasia). Consequently, defining the parasite fauna and geographic range of this host in the present context is problematic. Single findings of a flea or mite species on one individual of a host species or in a region were considered accidental and were not included in the analyses. In total, we used data on 208 flea and 60 mite species collected from 90 and 36 rodent species, respectively (Supplementary Data S1).

2.2. Distance matrices

All flea or mite species found on a host species in any locality within its geographic range were considered as the flea or mite faunas of this host, respectively (Poulin, 2007). We determined

these faunas using the presence/absence of each flea or mite species on each host species across all regions. From these data, we constructed matrices of compositional, taxonomic and phylogenetic dissimilarity in flea or mite faunas between each pair of host species. Matrices of compositional dissimilarity of parasite faunas were constructed using the reciprocal Jaccard index, one of the most commonly used indices of ecological similarity that avoids the pitfall of double absences (Magurran, 1988).

We constructed matrices of pairwise phylogenetic and taxonomic (for fleas) or only taxonomic (for mites) dissimilarity of the parasite faunas of 90 or 36 host species, respectively. We used only taxonomic dissimilarity for mites because no phylogenetic tree is available for these animals.

Phylogenetic dissimilarity was measured as the mean phylogenetic distance (branch length) of all possible pairs of taxa between the flea fauna of one host species and the fauna of another species, using the nearest taxon method. In this method, the routine finds for each taxon in flea fauna A, the nearest phylogenetic neighbour in flea fauna B, records this, and at the end calculates the mean. The phylogenetic tree of fleas was based on the only available molecular phylogeny of fleas, i.e., that recently constructed by Whiting et al. (2008). This tree includes 128 flea species (ca. 6% of global fauna) belonging to 83 genera (ca. 34% of the entire number of flea genera). Our data sets included most of these genera, although this was not the case at the species level. Consequently, the positions of the flea taxa and lineages which were not represented in the original tree of Whiting et al. (2008) were determined using their morphologically-derived taxonomy (see Poulin et al., 2006, for details). All branch lengths were set equal to 1.0. Phylogenetic dissimilarity was calculated for flea faunas between each pair of host species using the programme Phylocom 4.0.1beta (Webb et al., 2008).

The taxonomic dissimilarity of flea and mite faunas between each pair of hosts was calculated using either the Γ^+ index, which is an extension of the Bray–Curtis index based on presence/absence data (Clarke et al., 2006) or the Θ^+ index, which is an extension of Kulczynski dissimilarity (Iszak and Price, 2001). In the calculation of Γ^+ , for each species in sample A, one finds the closest relative in sample B, calculates the distance between them and then averages these distances over all species for both samples. In the calculation of Θ^+ , these averages are calculated separately for both samples and then they are themselves averaged. Consequently, these indices are closely related, so that Γ^+ and Θ^+ calculated for our data set were highly correlated (0.97). We carried out two runs of analyses, one for each index. Both runs produced the same results. Here, we present the results of the analyses using Γ^+ only. To calculate Γ^+ and Θ^+ , all flea species were fitted into a taxonomic structure with eight hierarchical levels above species [subgenus (or species group), genus, tribe, subfamily, family, superfamily, infraorder, and order (Siphonaptera)] (see details in Krasnov et al., 2005a), whereas all mite species were fitted into a taxonomic structure with four hierarchical levels above species [genus, subfamily, family and superfamily (Dermanyssoidea)] (see details in Korallo et al., 2007). Calculations of taxonomic dissimilarities in flea and mite faunas (as well as compositional similarities in faunas of both parasite taxa) were performed using the programme Primer-6 (Clarke and Gorley, 2006).

We used compositional, phylogenetic and/or taxonomic dissimilarities in parasite faunas between hosts as dependent matrices in the analyses, whereas independent matrices consisted of pairwise between-host phylogenetic, spatial (geographic) and environmental dissimilarities. Phylogenetic dissimilarity between host species was calculated as the patristic distance (i.e., the sum of the lengths of the branches that link two nodes in a tree) between each pair of hosts using the global phylogenetic supertree for mammals (Bininda-Emonds et al., 2007).

The geographic pairwise distances between the geographic ranges of hosts were calculated as the standardised distance $D_{St} = D_C / (D_C - D_E)$, where D_C is the distance between the geometric centres of geographic ranges and D_E is the distance between the edges of geographic ranges. Geographic ranges of hosts were constructed as described elsewhere (Poulin et al., 2008). D_C values were measured directly on the projected maps constructed using the ArcGIS Desktop 9.2 software. For non-overlapping geographic ranges, D_E values were measured directly as the minimal distance between the edges of geographic ranges on the projected map. For overlapping geographic ranges, D_E values were calculated as $-\sqrt{(4 * S_{Ov})/\pi}$, where S_{Ov} is the area of overlap of the two ranges. D_{St} equals 0 for geographic ranges of identical configuration, varies from 0 to 1 for partially overlapping geographic ranges, equals 1 for non-overlapping ranges that abut each other, and is greater than 1 for non-overlapping and non-abutting ranges. The maximal possible value of D_{St} is 20,001.6 for two point ranges located on the equator at completely opposite sites on the Earth.

To calculate “environmental” distances between the geographic ranges of host species, the computed relief (slope and mean, maximal and minimal altitude; the latter two variables allow evaluation of the altitudinal range), green vegetation [Normalised Difference Vegetation Indices (NDVI) for winter, spring, summer and autumn] and climatic variables (mean winter, spring, summer and autumn precipitation; mean, maximal and minimal surface air temperature, annual and monthly temperature ranges) were averaged within the geographic range of a given host across 30 arcsecond grids (approximately 1 km resolution). These environmental variables were selected because they have been shown to directly or indirectly affect the composition of ectoparasite assemblages (e.g., Krasnov et al., 2005b,c). Elevation and slope data were extracted from the GTOPO30 data set issued with ArcGIS Desktop 9.2.

Data on green vegetation (NDVI) were obtained from the VEG-ETATION Programme (<http://www.spot-vegetation.com>; <http://free.vgt.vito.be>; data for 1998–2007, estimations every 10 days). NDVI is a measure of photosynthetic activity at the landscape scale. Averaging of NDVI values across large areas provides a general estimation of vegetation abundance, reflecting differences between different biomes (Pettorelli et al., 2005a). Negative values of NDVI (those approaching -1) correspond to water, whereas values close to zero (-0.1 to 0.1) generally correspond to barren areas of rock, sand or snow. Low positive values (0.2 – 0.4) represent shrub and grassland, whilst high positive values indicate temperate and tropical rainforests. Calculation of NDVI in the database we used (see above) is characterised by the automatic exclusion of negative values (the programme returns empty cells instead of negative values). Consequently, when NDVI is calculated across a host's geographic range, the relative area of free-standing water and bare soil is not included, so the index focuses on the “inhabited” portion of its geographic range. NDVI has been shown to correlate with primary production (Pettorelli et al., 2005b), although not without problems when the relationship between NDVI and vegetation productivity is saturated. However, this is the case only for highly productive areas, such as the tropics, which have not been considered in our study. In addition, the use of seasonal NDVIs allowed us to take into account geographic and landscape differences in plant phenology that may be important factor for animals (Pettorelli et al., 2005a).

Climatic variables were obtained as a part of WORLDCLIM Version 1.4 (BIOCLIM) package (Hijmans et al., 2005). Since all variables were quantitative and since none deserves more weight than another, we standardised all variables to a mean = 0 and variance = 1. We selected the mean rather than the mode as a central value since (i) we aimed to take into account the entire range of values and not only their ranks because extreme values may have

an impact on species distributions, and (ii) the species composition of ectoparasite assemblages of a host may vary across its geographic range, being, in particular, substantially different in the margins compared to central parts of the range (Krasnov et al., 2005a). Then, we used these values to compute the classical Euclidean distance between the geographic ranges of each pair of hosts to provide a measure of environmental distance.

2.3. Data analyses

We analysed the relative effect of phylogenetic, geographic and environmental distances between hosts on the compositional, phylogenetic or taxonomic dissimilarity of their flea or mite faunas using multiple regressions on distance matrices (MRM; see Manly, 1986; Legendre et al., 1994; Legendre and Legendre, 1998; Lichstein, 2007, for details). In brief, MRM is an extension of partial Mantel analysis that is used to investigate relationships between a multivariate response distance matrix (in our case, dissimilarity in parasite fauna) and any number of explanatory distance matrices (Lichstein, 2007). We implemented additional partial multiple regressions on distance matrices to estimate the “pure” effect of each explanatory matrix. We extracted a “pure” effect for each independent variable as follows. For each matrix of parasite fauna dissimilarity, we calculated coefficients of determination (r^2) for the entire model with three independent matrices and for the model without one of the matrices (matrix of interest). Then the “pure” effect of this matrix of interest was obtained following the decomposition of Legendre and Legendre (1998) dedicated to multiple fractions of explanations (see also Borcard et al., 1992; Lichstein, 2007). We report r^2 values for the entire models as well as the associated P -values, whilst we express the fraction of the variation explained by each “pure” effect as a percentage.

The significance of regression coefficients and r^2 were tested using permutations. All probabilities were based on 1,000 permutations. Analyses were performed using the library “ecodist” (Goslee and Urban, 2007) implemented in the R Package (R Development Core Team, 2005).

To test whether data points for flea and mite compositional dissimilarity were significantly concentrated in a triangular area of the bivariate space when plotted against environmental dissimilarity between host geographic ranges (see Section 3), we used the boundary test implemented in the EcoSim 7 software (Gotelli

and Entsminger, 2009). This test uses a null-model approach and calculates (1) the number of points that fall beyond the diagonal boundary, and (2) the sum of squares of those points for observed and simulated (1,000 randomizations) data. If some corners of the space are unusually empty, the observed number of points and/or their sum of squares in the observed data set will be significantly lower than in the simulated data sets.

To test which are the most important environmental factors determining between-host similarity in parasite faunas, we constructed separate distance matrices for each group of environmental variables [relief, vegetation (NDVI), precipitation and surface temperature]. To do this, we extracted the first two principal components from each group of variables. The principal components cumulatively explained from 95.8% to 99.9% of the variance and their eigenvalues ranged from 0.88 to 3.14. Then, we used the scores of these principal components to compute the Euclidean distance between the geographic ranges of each pair of hosts. The resulting distance matrices were used as independent matrices in MRM, whereas dependent matrices in these analyses were compositional, phylogenetic and taxonomic dissimilarities of flea or mite faunas. Then, we calculated the “pure” effect of each independent matrix as described above.

3. Results

The multiple regressions of matrices of compositional, phylogenetic and/or taxonomic dissimilarities of flea and mite faunas against matrices of phylogenetic, geographic and environmental distances amongst hosts demonstrated significant effects of all three host-related distance measures (Table 1 and Figs. 1–3). Whatever measure of dissimilarity of flea faunas was used, the percentage of variation explained by environmental dissimilarity between host geographic ranges was at least twice higher than that explained by either phylogenetic (patristic) or geographic distance between hosts (Table 1). The same was true for the compositional dissimilarity of mite faunas; however, when the taxonomic dissimilarity of mite faunas was considered, similar percentages of variation were explained by host phylogenetic and environmental distances (both higher than percentage of variation explained by geographic distance) (Table 1). In addition, host phylogenetic and geographic distances explained a two times greater percentage of

Table 1
Results of multiple regressions on distance matrices, with pairwise compositional (CD) and phylogenetic/taxonomic dissimilarity (PD/TD) in flea and mite faunas between hosts as the dependent matrices, and pairwise patristic distance (PtD), geographic distance (GD) and environmental dissimilarity (ED) between hosts as independent matrices. All regression coefficients and r^2 are significant, $P < 0.001$.

Parasite taxon	Dependent matrix	Independent matrices	Coefficient	r^2 of the entire model	Percentage of explained variation due to “pure” effect
Fleas	CD	PtD	0.0004	0.18	18.42
		GD	0.005		5.40
		ED	0.02		63.27
	TD	PtD	0.001	0.14	24.82
		GD	0.01		12.4
		ED	0.02		47.01
	PD	PtD	0.01	0.08	14.12
		GD	0.32		11.37
		ED	0.56		55.37
Mites	CD	PtD	0.0007	0.24	17.90
		GD	0.04		9.69
		ED	0.02		31.86
	TD	PtD	0.0006	0.21	27.79
		GD	0.05		13.29
		ED	0.01		21.48

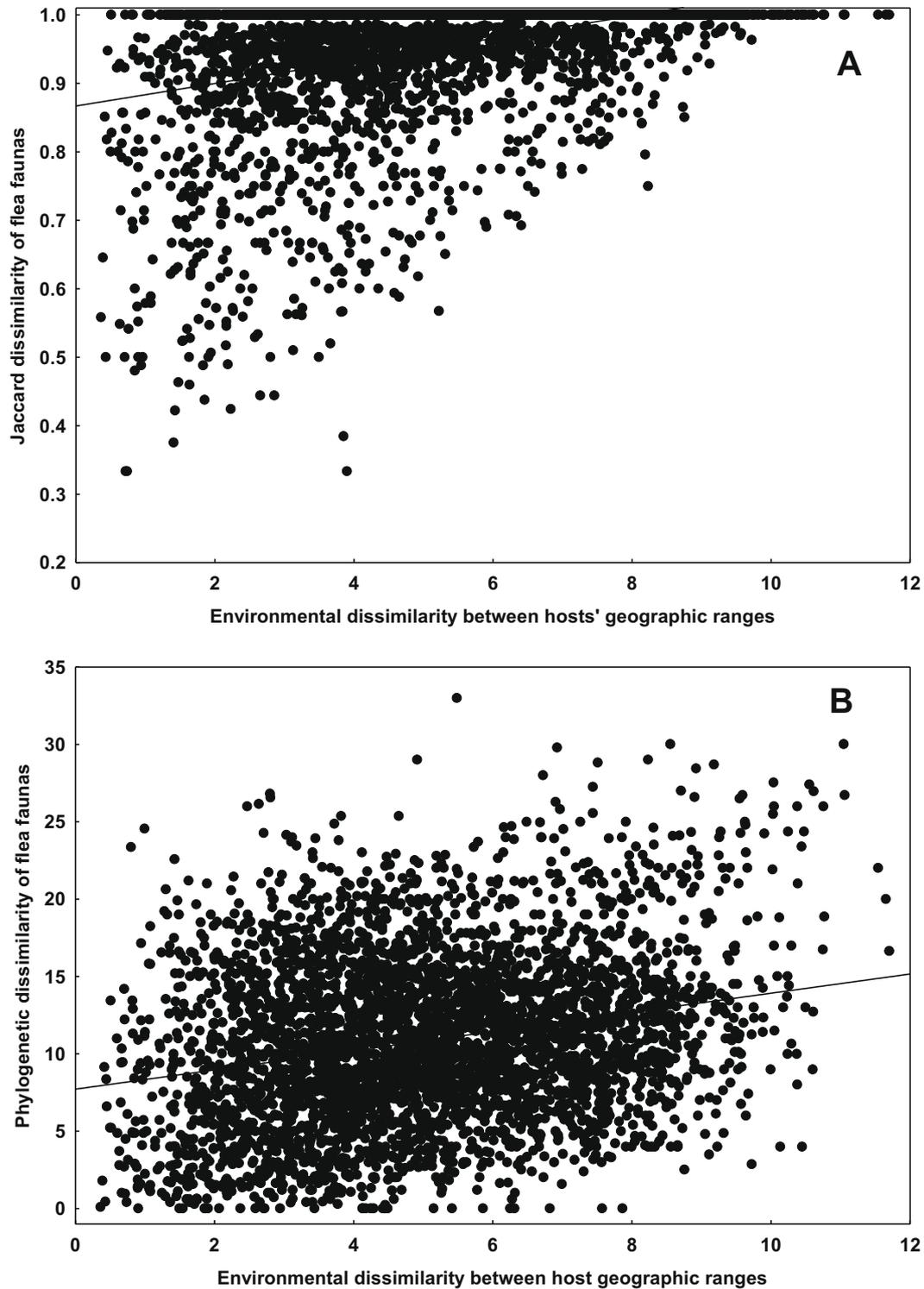


Fig. 1. Relationship between environmental dissimilarity between the geographic ranges of host species and (A) Jaccard dissimilarity and (B) phylogenetic dissimilarity in their flea faunas.

variation in taxonomic dissimilarity of flea faunas compared to their phylogenetic dissimilarity.

Comparison of the r^2 values of the model that included host phylogenetic, geographic and environmental distances amongst host taxa and measures of faunal dissimilarity showed that the model explained equally compositional dissimilarity in both flea and mite faunas amongst hosts, as well as taxonomic dissimilarity in mite faunas. However, the full model was less successful at

explaining taxonomic and, especially, phylogenetic dissimilarities in flea faunas.

The distributions of data points in the scatterplots of compositional dissimilarity of flea and mite faunas against environmental dissimilarity between host geographic ranges were clearly triangular (Figs. 1A and 2). The boundary number of points and the boundary sum of squares tests confirmed the statistical significance of a predominant scatter of data points

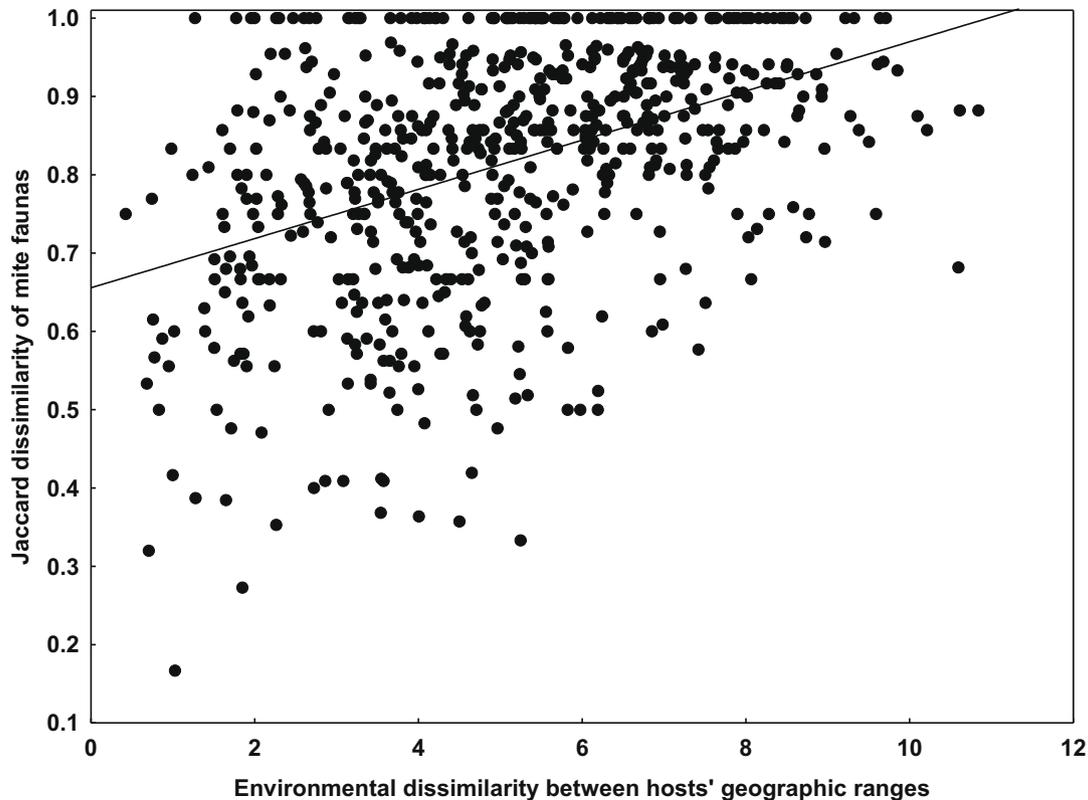


Fig. 2. Relationship between environmental dissimilarity between the geographic ranges of host species and Jaccard dissimilarity in their mite faunas.

in the upper left corner of the space (for both fleas and mites, the observed number of points that fall beyond the boundary and their sum of squares in the observed data set were significantly lower than in simulated data sets; $P < 0.001$ for all). This suggests that the flea and mite faunas of two hosts inhabiting different environments are always different, whilst hosts living in similar environments can have either very similar or dissimilar flea and mite faunas.

The results of multiple regressions of matrices of compositional, phylogenetic and/or taxonomic dissimilarities of flea and mite faunas against distance matrices of separate groups of environmental variables are presented in Table 2. The highest percentage of variation in dissimilarity in flea or mite faunas between host geographic ranges was explained by dissimilarity in vegetation (as indicated by NDVI) followed by dissimilarity in climatic conditions. The only exception was compositional dissimilarity in flea faunas which was affected mainly by dissimilarities in precipitation and surface temperature.

4. Discussion

Our original predictions appeared to be only partially true. On the one hand, and as we predicted, compositional, phylogenetic and/or taxonomic dissimilarity of parasite faunas between hosts correlated with phylogenetic, geographic and environmental distances between these hosts. On the other hand, and contrary to our predictions, the host-related correlates of dissimilarity in parasite faunas were roughly the same for both studied parasite taxa. The strongest effect on this dissimilarity came from between-host environmental distance, followed by phylogenetic distance between hosts; in contrast, “pure” geographic distance between hosts explained only a very small proportion of the variance in dissimilarity of parasite faunas. In addition, between-host environmental and phylogenetic distances had approximately similar

effects on the taxonomic (but not compositional) dissimilarity of mite faunas.

The relatively weak effect of between-host phylogenetic distance on similarity of their parasite faunas suggests that a great proportion of parasites encountered on a host species is a result of ecological fitting (Brooks et al., 2006a,b). Ecological fitting acts if (i) distantly related parasites specialise on the same host resource that is widespread amongst many host species and (ii) a parasite mainly follows the resource provided by a host rather than a host per se (Brooks et al., 2006a). These prerequisites apply well to fleas and mites. Indeed, these parasites use two main resources from a host, namely (i) blood or another body fluid for feeding and (ii) the host's burrow or nest where ectoparasites develop and/or spend most of their lives. The biochemistry of blood is similar amongst mammalian hosts, so many fleas and mites are able to feed on a variety of host species (Radovsky, 1985; Vashchenok, 1988; Krasnov, 2008). The structure and microclimate of the burrow are strongly constrained by the external physical environment, such as soil texture and amount of vegetation (Shenbrot et al., 2002). As a result, many fleas and mites may, for example, be acquired when a host expands or otherwise changes its geographic range. It could be found suitable by local ectoparasites because its blood may likely be used by many flea or mite species and because its shelters in the new environment will likely be similar to those of local hosts. However, the role of subtle adaptations (i.e., resulted from co-speciation) between a host and a parasite evolved during a long history of association cannot be ruled out. For example, a strong link between the morphology of the mouth apparatus of a flea and the skin structure of a host (see Krasnov, 2008) may prevent exploitation of some hosts by a flea. These hosts may provide a parasite with necessary resources, but if a parasite is unable to acquire these resources, then it will not switch between the “original” host and a new host. These parasites may thus be responsible for a significant, albeit weak, effect of between-host

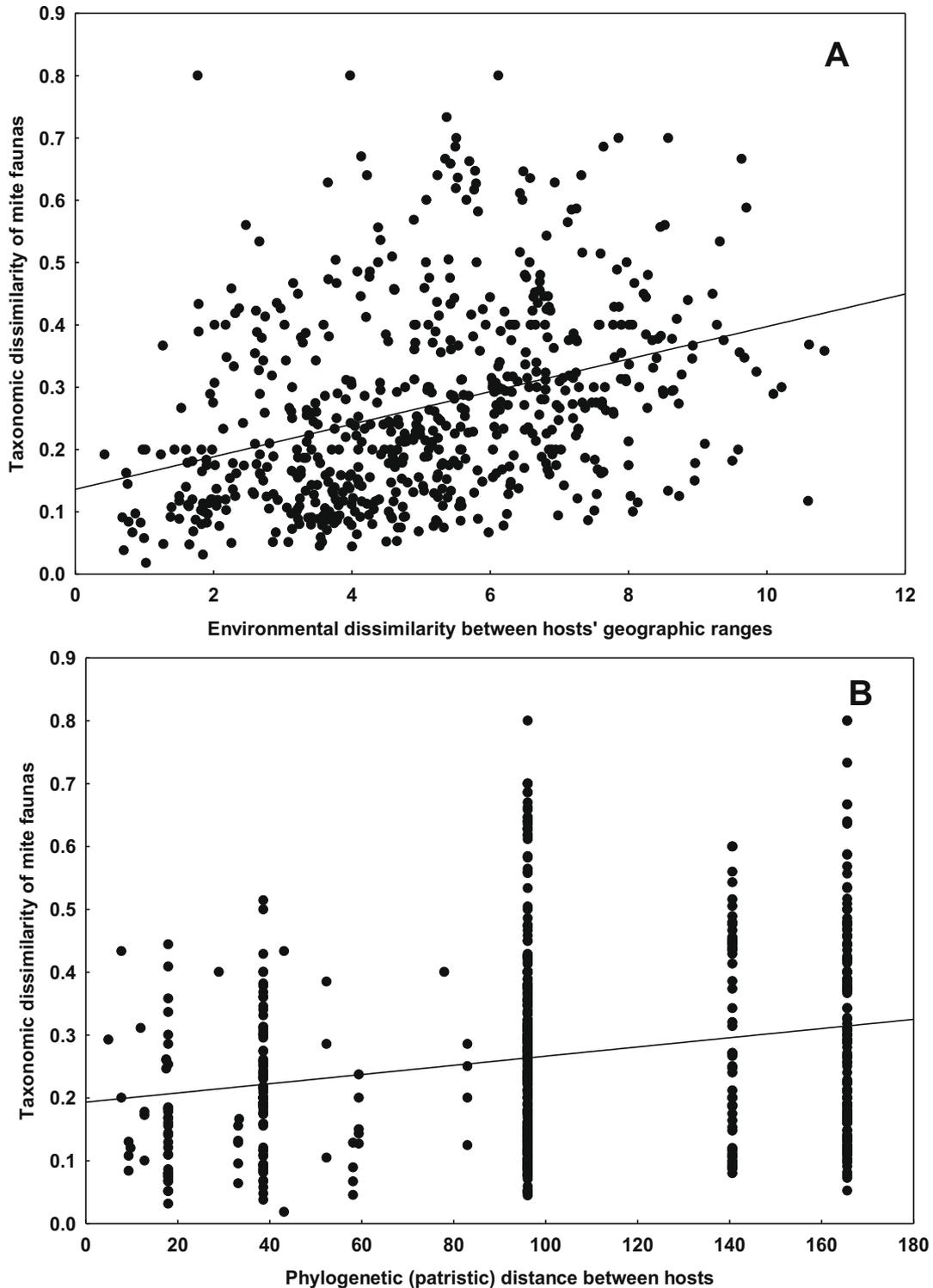


Fig. 3. Relationship between taxonomic dissimilarity in mite faunas and (A) environmental dissimilarity between the geographic ranges of their hosts and (B) phylogenetic distance between hosts.

phylogenetic distance on dissimilarity of their parasite faunas (see below).

The most obvious reason for dependence of between-host similarity in the composition of the flea and mite faunas on between-host similarity in the physical environment is that both fleas and mites are ectoparasitic and therefore spend much time off-host. Consequently, they are substantially influenced not only by their hosts but also by the off-host environment. Indeed, it is commonly

known that both fleas and mites strongly respond to environmental factors that affect their feeding activity (Gong et al., 2004 for fleas and Cross and Wharton, 1966 for mites), reproduction (Vashchenok, 1988 for fleas and Sikes and Chamberlain, 1954 for mites), development (Edney, 1945 for fleas and Kozlova, 1983 for mites) and survival (Krasnov et al., 2002a for fleas and Maurer and Baumgärtner, 1992 for mites). Moreover, some parasite species are adapted to a particular environment but not to any par-

Table 2
Results of multiple regressions on distance matrices, with pairwise compositional (CD) and phylogenetic/taxonomic dissimilarity (PD/TD) in flea and mite faunas between hosts as the dependent matrices, and pairwise distances in relief (R), vegetation (V), precipitation (P) and temperature (T) variables between hosts' geographic ranges as independent matrices. Only significant regression coefficients and r^2 ($P < 0.001$) are shown.

Parasite taxon	Dependent matrix	Independent matrices	Coefficient	r^2 of the entire model	Percentage of explained variation due to "pure" effect	
Fleas	CD	R	0.01	0.15	5.40	
		V	0.01		5.40	
		P	0.01		12.16	
		T	0.02		12.16	
	TD	V	0.04		27.38	
		P	0.01		8.45	
		T	0.02		8.68	
	PD	R	0.27		0.11	12.50
		V	1.13			28.75
P		0.56	55.37			
Mites	CD	R	0.02	0.08	5.81	
		V	0.05		11.95	
		P	0.03		5.53	
	TD	R	0.01		0.25	4.02
		V	0.05			23.46
		P	0.03			6.70
						0.18

ticular host. For example, the flea *Synosternus cleopatrae* in deserts of the Middle East has been recorded on a variety of small mammals, but only in sandy habitats (Krasnov et al., 1999). Some gamasid mites are also host generalists but have restricted habitat distribution (e.g., Korneev, 2003). These environmental specialist/host generalist parasites may thus be responsible for the relationship between between-host compositional dissimilarity in parasite faunas and between-host environmental distance. Other parasites, although they occur in the same environments, demonstrate strikingly different host preferences (see Krasnov et al., 1997 for fleas and Luo et al., 2007 for mites). These species may be responsible for the triangular scatter of points seen in Figs. 1A and 2 for regressions of parasite compositional dissimilarity against host environmental distance.

The preference of a parasite for particular environmental conditions could be inherited from its ancestors. If so, then closely-related parasites are expected to demonstrate similar environmental preferences. To the best of our knowledge, no study has aimed to specifically test this question in either fleas or mites, although other ecological traits of ectoparasitic arthropods have been shown to be evolutionarily conservative (Mouillot et al., 2006). Nevertheless, indirect observations suggest that this also may be the case with environmental preferences. For example, the flea genus *Stenoponia* includes 16 species, all of which reproduce only during the cold season (Vashchenok, 1988). Phylogenetic conservatism in the response to the physical environment might be one of the reasons behind the effect of between-host environmental distance on the dissimilarity of their parasite fauna measured as phylogenetic/taxonomic dissimilarity.

We found that the most important environmental factor was a composite factor measured via NDVI. Because NDVI, in general, allows to distinguish between different landscapes (Pettorelli et al., 2005a,b; see also above), our results suggest that hosts inhabiting similar biomes harbour similar ectoparasite faunas. In particular, these biomes differ in the amount and composition of vegetation and soil texture. These factors may have stronger effects on architecture, soil structure and microclimate (temperature and relative humidity) of rodent burrows and nests than, for example, precipitation or surface temperature does (Shenbrot et al., 1997, 2002). In turn, microclimate and soil texture of rodent burrows strongly affect survival and developmental rate of ectoparasites

(e.g., Krasnov et al., 2002b). As a result, populations of the same host species but occurring in different habitats may harbour quite different ectoparasite assemblages (Krasnov et al., 1998, 2005a).

The strong effect of environmental dissimilarity, mainly measured via NDVI, on between-host dissimilarity in parasite faunas found in this study may not only be direct (via direct effects of environmental factors on parasites), but also indirect (via effect of the environment on the composition of small mammal communities). Indeed, it is known that small mammals (rodents, soricomorphs, erinaceomorphs and lagomorphs) may share substantial proportions of their flea and mite infra- and component communities (e.g., Radovsky, 1985 for mites; Krasnov, 2008 for fleas). This is because co-occurring host species often exchange their ectoparasites via direct contacts or during visits to each other's burrows (e.g., Krasnov and Khokhlova, 2001). Mammal species composition is likely similar in similar environments and, thus, between-host dissimilarity in parasite faunas may be caused by dissimilarity in the species composition of mammals co-habiting with these hosts across their geographic ranges rather than by direct effects of the environment. Disentangling direct environmental and "host compositional" effects on between-host dissimilarity of parasite faunas undoubtedly deserves further investigation. However, such an investigation will be possible only after data on geographic ranges for the majority of Palaeartic species of Erinaceomorpha, Soricomorpha, Lagomorpha and Rodentia become available.

Although between-host phylogenetic distance explained the dissimilarity of their parasite faunas relatively poorly compared with environmental distance, the effect of the former was significant, indicating a trend for phylogenetically-related hosts to harbour similar parasite faunas (see also Poulin, in press). There can be at least two non-mutually-exclusive mechanisms underlying this trend. Firstly, hosts could inherit some of their parasites from common ancestors (Brooks, 1988; Hafner and Nadler, 1988; Clayton and Johnson, 2003). Secondly, closely-related hosts are expected to have similar physiological and ecological characters (Harvey and Pagel, 1991), so that they would be equally suitable for and/or share their habitats with the same parasite species or group of species that may switch to them from another host lineage. For example, two closely-related woodmice (*Apodemus flavicollis* and *Apodemus sylvaticus*) have been shown to harbour almost identical parasite assemblages (Klimpel et al., 2007). How-

ever, this similarity may be related to the fact that these two rodents have similar environmental requirements, live in the same habitats and construct similar shelters (shallow burrows and above-ground nests). It would probably be fair to say that the similarity in parasite faunas of phylogenetically-related hosts arises partly due to shared ancestry and partly due to shared environment.

The reason behind the weak effect of “pure” geographic distance and overlap between host geographic ranges on their parasite dissimilarity may be the scale of our study. Here we dealt with parasite faunas rather than with local parasite assemblages, i.e., we focused on processes that presumably occurred over long evolutionary time scales. In contrast, geographic distances between hosts may reflect present-day distributions, which may change rapidly due to climate fluctuations or anthropogenic disturbances (see Parmesan, 2006, for review). An alternative explanation is the quasi-absence of dispersal limitation or neutral processes in the distribution of parasite species and a predominance of niche-related processes (host and environment) (Thompson and Townsend, 2006).

In general, the increase in the dissimilarity of parasite faunas as a function of host environmental, phylogenetic and geographic distances appeared to be not particularly strong, with coefficients of determination of regressions ranging from 0.08 to 0.24 (Table 1). This suggests that other factors may be generating dissimilarity between parasite faunas. Firstly, dissimilarity in parasite faunas between closely-related hosts may be magnified by historical events such as biogeographic dispersal. For example, the majority of allactagine jerboas are not exploited by pulicid fleas probably because the Pulicidae have an African origin (Medvedev, 2005), whereas allactagine jerboas originated in central Asia (Shenbrot et al., 2008). However, the single allactagine that harbours pulicids is *Allactaga tetradactyla* which dispersed from Asia to Africa where it acquired these parasites before becoming isolated from other allactagines, presumably at the Pliocene–Pleistocene boundary (Krasnov and Shenbrot, 2002; Shenbrot et al., 2008). Secondly, highly dissimilar parasite faunas between closely-related hosts may arise due to purely ecological causes. An example for this again comes from the flea fauna of *A. tetradactyla* which is the only allactagine to harbour *Hopkinsiopsylla occulta* (Krasnov and Shenbrot, 2002). This flea is active only during winter, and *A. tetradactyla* is the only non-hibernating allactagine. Thirdly, the relatively low coefficients of determination of the regressions may result merely from our still incomplete knowledge of the flea and mite faunas of rodents. Parasitological surveys have not been carried out everywhere, although they have to date covered many geographic locations.

Furthermore, models that included environmental, phylogenetic and geographic dissimilarity between hosts explained the compositional dissimilarity in their parasite faunas better than their phylogenetic and/or taxonomic dissimilarity. This suggests that along host-related environmental, phylogenetic and/or geographic gradients, the turnover of flea and mite species was higher than the phylogenetic turnover of these taxa. Amongst host species, parasite species are substituted for one another at a higher rate than parasite lineages (i.e., genera). In other words, the main phylogenetic/taxonomic branches of both parasite taxa were present in the majority of hosts and in the majority of environments and locations, i.e., everywhere along those gradients (Ferrier et al., 2007; Bryant et al., 2008).

Finally, between-host environmental and phylogenetic distances affected to the same extent the taxonomic dissimilarity of mite faunas, but the effects of environmental distance on flea taxonomic and phylogenetic dissimilarities were much stronger than that of phylogenetic distance. However, comparison of the “pure” effects of explanatory matrices (Table 1) suggests that

the main reason for this difference is the very strong effect of between-host environmental distance, rather than the weak effect of between-host phylogenetic distance in fleas as compared to mites. This difference between the two ectoparasite taxa may stem from differences in their life histories. All fleas are obligate haematophages when at the imago stage, but larval fleas of most species are not parasitic, feed on various kinds of organic matter and occur off-host in its burrow or nest. Although mites may feed on host blood either obligatorily or facultatively, both nymphal and imaginal stages in many gamasids are haematophagous and some species spend their entire life cycle on the host body (Zemskaya, 1969; Radovsky, 1985). Consequently, the stronger effect of the off-host environment on fleas than on mites can be, at least in part, responsible for the stronger effect of between-host environmental distance on the dissimilarity of faunas for fleas.

Overall, our results indicate that for these ectoparasitic taxa, differences between the environments occupied by their hosts are more important for the convergence or divergence of parasite faunas over time than the phylogenetic relatedness of host species. The latter is assumed to lead to similar faunas via a process of inheritance of parasites from a common ancestor (Brooks, 1988; Paterson and Gray, 1997). Amongst parasites of fish, the decay in the similarity of parasite faunas with increasing phylogenetic distances between hosts is generally weak, and not more apparent in endoparasites, which are only exposed to environmental conditions during transmission, than for ectoparasites (Poulin, in press). Thus external environmental factors may play greater roles than commonly thought in the evolution of host–parasite associations. In other words, our results suggest that ecological fitting may be more important than co-speciation in shaping faunas of haematophagous ectoparasitic arthropods.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ijpara.2009.12.002.

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