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RESEARCH PAPER

Deconstructing spatial patterns in species composition of ectoparasite communities: the relative contribution of host composition, environmental variables and geography

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ABSTRACT

Aim We determined whether dissimilarity in species composition between parasite communities depends on geographic distance, environmental dissimilarity or host faunal dissimilarity, for different subsets of parasite species with different levels of host specificity.

Location Communities of fleas parasitic on small mammals from 28 different regions of the Palaearctic.

Method Dissimilarities in both parasite and host species composition were computed between each pair of regions using the Bray–Curtis index. Geographic distances between regions were also calculated, as were measures of environmental dissimilarity consisting of the pairwise Euclidean distances between regions derived from elevation, vegetation and climatic variables. The 136 flea species included in the dataset were divided into highly host-specific species (using 1–2 host species per region, on average), moderately host-specific species (2.2–4 hosts per region) and generalist species (>4 hosts per region). The relative influence of geographic distance, host faunal dissimilarity and environmental dissimilarity on dissimilarity of flea species composition among all regions was analysed for the entire set of flea species as well as for the three above subsets using multiple regressions on distance matrices.

Results When including all flea species, dissimilarity in flea species composition was affected by all three independent variables, although the pure effect of dissimilarity in host species composition was the strongest. Results were different when the subsets of fleas differing in host specificity were treated separately. In particular, dissimilarity in species composition of highly host-specific fleas increased solely with environmental dissimilarity, whereas dissimilarity for both moderately specific and non-specific fleas increased with both geographic distance and dissimilarity in host species composition.

Main conclusions Host specificity seems to dictate which of the three factors considered is most likely to affect the dissimilarity between flea communities. Counter-intuitively, environmental dissimilarity played a key role in determining dissimilarity in species composition of highly host-specific fleas, possibly because, although their presence in a region relies on the occurrence of particular host species, their abundance is itself mostly determined by climatic conditions. Our results show that deconstructing communities into subsets of species with different traits can make it easier to uncover the mechanisms shaping geographic patterns of diversity.

Keywords

Deconstruction, dissimilarity, fleas, geographic distance, Palaearctic, small mammals, species composition.

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INTRODUCTION

A variety of spatial patterns of diversity and composition of biological communities have been documented (e.g. Rosenzweig, 1995; Gaston & Blackburn, 2000). However, although there is consensus about the occurrence of many of these patterns, this is not the case for the mechanisms underlying them (e.g. Rohde, 1992; see Willig *et al.*, 2003, for latitudinal gradient of diversity). The reasons for this lack of consensus are that: (1) there can be several mechanisms responsible for the same pattern, and (2) species composing a community may differ drastically in many traits and thus respond differently to their environment. In other words, pooling a variety of species and then searching for integrated explanations of diversity or community composition patterns may obscure the real patterns and impede our understanding of underlying processes. For example, pooling species that have different levels of requirements may explain why patterns of species turnover at broad scales remain poorly understood (Buckley & Jetz, 2008).

Among the many spatial patterns of community composition, a very few are highly ubiquitous and similar to patterns observed in the physical, geological and social sciences. This similarity has even led to the suggestion that they may be general statistical patterns characteristic of complex dynamical systems rather than unique properties of biological entities (Nekola & Brown, 2007). One of these, the distance decay of similarity, captures the way similarity in plant or animal community composition between any two localities decreases with increasing geographic distance between them (Nekola & White, 1999). The wide variety of taxa for which distance decay of similarity has been reported includes plants and animals, free-living and parasitic, and terrestrial and aquatic groups (Oliva & González, 2005; Steinitz *et al.*, 2006; Soininen *et al.*, 2007; La Sorte *et al.*, 2008).

Although at first glance this pattern seems to be obvious and trivial, the mechanisms that underlie it are still debated (Thompson & Townsend, 2006; Morlon *et al.*, 2008). Soininen *et al.* (2007) distinguished three main groups of mechanisms that may act separately or together to produce the distance decay of similarity: (1) a decrease in environmental (abiotic and/or biotic) similarity with increasing distance, (2) the probability that a hard geographic barrier blocks dispersal increases with increasing distance, and (3) the limited mobility of many species may restrict dispersal even in a homogeneous environment without hard geographic barriers. The latter mechanism is thought to prevail in the framework of the neutral theory (Bell, 2001; Hubbell, 2001) in which the species comprising a community are assumed to be ecologically equivalent and to have the same dispersal abilities. Under neutral scenarios, the distance decay is thought to result from ecological drift, random dispersal and random speciation. However, the results of recent studies suggest that the species making up a community are not equivalent with respect to: (1) their role in generating the distance decay pattern, (2) their rate of decrease of similarity with increasing distance, and (3) mechanisms underlying their distance decrease of similarity. Furthermore, studies of distance decay of similarity have demonstrated that the manifestation of this pattern may differ between species depending on their abundance or dispersal ability (Nekola & White, 1999; Thompson & Townsend, 2006; Morlon *et al.*, 2008).

Recently, Marquet *et al.* (2004) suggested that applying a 'deconstructive' strategy based on the ecological and/or life-history characteristics of species comprising a community may be a useful approach in studies of a variety of spatial diversity patterns (see also Blamires *et al.*, 2008; Terribile *et al.*, 2009). They argued that patterns of diversity or community composition should be considered separately for subsets of species extracted from the entire community based on some traits or requirements. This approach allows one to disentangle the different mechanisms that together may blur the overall spatial pattern. However, the application of the 'deconstruction' approach requires the selection of relevant traits according to which the community will be 'deconstructed'. For example, when spatial patterns of diversity/community composition are considered, the size of species geographic ranges, their dispersal ability and their level of abundance all seem to be relevant (Terribile *et al.*, 2009).

Parasites form a large proportion of the diversity of life, and parasite communities represent convenient models for investigations of spatial diversity patterns (Poulin, 2003). However, although the number of studies aiming to explain spatial patterns of parasite species richness has increased in the past decade, the results of many of these studies are inconsistent (see Poulin & Morand, 2004, and references therein). Applying a 'deconstruction' strategy may allow an understanding of the reasons behind these inconsistencies. One of the inherent properties of parasites, host specificity, is correlated with other traits such as, for example, geographic range (Krasnov *et al.*, 2005a) and mean abundance (Poulin, 1998; Krasnov *et al.*, 2004a). Furthermore, although parasites rarely disperse far on their own, indirect dispersal of parasites via host switches may be substantial (Shenbrot *et al.*, 2007). In other words, the degree of host specificity of a parasite can be used as an inverse proxy of its dispersal ability, assuming, that the opportunities for host-specific parasites to disperse to remote locations are generally limited, whereas host-opportunistic parasites are probably capable of broad dispersal. Consequently, spatial patterns of community composition may vary among subsets of parasites having different degrees of host specificity because of differences in the size of their geographic range, abundance and/or dispersal ability.

Recently, numerous studies have reported distance decay of similarity in parasite communities (Poulin, 2003; Fellis & Esch, 2005; Oliva & González, 2005; Krasnov *et al.*, 2005b; Vinarski *et al.*, 2007; Seifertová *et al.*, 2008; Pérez-del-Olmo *et al.*, 2009; Thieltges *et al.*, 2009). The majority of these studies used data from different host populations and thus considered one community to be the parasite assemblage on a particular host species in one locality (e.g. Poulin, 2003; Pérez-del-Olmo *et al.*, 2009), rather than the entire community of parasites exploiting the whole pool of host species in one locality (but see Vinarski *et al.*, 2007). Furthermore, no attempt has been made to date to deconstruct parasite assemblages based on some characteristic of their species.

Here, we examined spatial variation in dissimilarity among assemblages of fleas (Siphonaptera) parasitic on small mammalian hosts across the Palaearctic. Fleas are typical 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. The degree of association between a particular flea species and various host species varies, with flea species ranging from highly host-specific to host-opportunistic (Krasnov, 2008). Earlier, we showed that host community dissimilarity had a strong effect on the similarity of flea assemblages harboured by a particular host species (Krasnov *et al.*, 2005b). Here, we considered the entire flea assemblage in a location (i.e. the supracommunity; see Poulin, 2007) as well as subsets of flea species with different degrees of host specificity, and compared their similarity among different regions with different environmental conditions and host faunas with different species composition. We hypothesized that the key variables shaping the decay of similarity should differ among assemblages of fleas with different host specificity. We predicted that similarity between assemblages of host-specific fleas would be explained mainly by host species composition, whereas that between assemblages of host-opportunistic fleas should be affected mainly by environmental similarity and geographic distance between locations.

MATERIALS AND METHODS

Data collection

Data on fleas collected from the bodies of their hosts were obtained from published surveys that reported flea distribution and abundance on small mammals (Erinaceomorpha, Soricomorpha, Lagomorpha and Rodentia) in 28 different regions of the Northern Palaearctic (see Appendix S1 in Supporting Information). These sources reported data on the number of individual fleas belonging to a particular species found on the number of individuals sampled of a particular small mammal species in a particular location. We included data on those host species for which at least 10 individuals were collected and those flea species for which at least two individuals were collected. In total, the database comprised data on 139,215 individual fleas belonging to 136 species and 150,922 individual mammals belonging to 84 species.

Distance matrices

To examine how the species composition of flea supracommunities varies with geographic 'host' or 'environmental' distance among locations, we constructed matrices of flea, host, geographic and environmental dissimilarity between these locations. Given that estimates of flea abundance per host are not affected by host body size (see Krasnov *et al.*, 2005c, for tests based on roughly the same data), we estimated the abundance of each flea species in a region by averaging the number of fleas per individual host of any small mammalian species. We assumed that the number of examined host individuals belonging to a particular mammal species in a region reflected the relative abundance of this species in this region. In other words, we used the absolute number of examined individuals of a mammalian species in a region as an estimate of its relative abundance. We constructed matrices of pairwise dissimilarity in flea and mammal species composition between regions using the dissimilarity form of the Bray–Curtis index (Bray & Curtis, 1957), which is commonly used in ecological studies (Legendre & Legendre, 1998; Clarke & Warwick, 2001). This distance avoids the pitfall due to the presence of double zeros (absence) and facilitates comparison of our results with many other studies on similarity in species composition. Although this index may be influenced by differences in species composition attributable to species richness gradients (Koleff *et al.*, 2003), our main results are unlikely to be blurred by these possible distortions. The matrix of dissimilarity in mammal species composition therefore represented 'host' distances.

The geographic distances between pairs of regions were calculated as the linear distance between the centres of each region (described in the respective sources), obtained from a map using ArcGIS Desktop 9.2. To calculate 'environmental' distances between regions, we computed elevation (mean, maximum and minimum altitude), green vegetation (normalized difference vegetation indices for winter, spring, summer and autumn) and climatic variables (mean winter, spring, summer and autumn precipitation; mean yearly, July and February surface air temperature, annual and monthly temperature ranges) averaged within a region across 30-arcsec grids (approximately 1 km resolution). Elevation data were extracted from the GOTOPO30 data set distributed with ArcGIS Desktop 9.2. Data on green vegetation were obtained from the VEGETATION Programme (http://www.spot-vegetation.com; http://free.vgt.vito.be; data for 1998–2007, every 10 days' estimations). Climatic variables were obtained as a part of WORLDCLIM Version 1.4 (BIOCLIM) package (Hijmans *et al.*, 2005). As all variables were quantitative and because none deserves more weight than another, we standardized all variables to a mean = 0 and variance = 1. Then we computed the classical Euclidean distance between pairs of regions to provide a measure of environmental distance between regions.

We estimated the host specificity of each flea species as the number of mammalian species on which a flea species was found, averaged across regions where the flea was recorded. On average, a flea species in a region exploited from 1–10 host species. We divided the 136 flea species in three approximately equal groups according to the average size of their host range per region. This resulted in 47 highly host-specific species that exploited on average 1.0–2.0 hosts per region, 48 moderately host-specific species that exploited on average 2.2–4.0 hosts per region and 42 non host-specific (generalist) species that used on average 4.3–10.2 hosts per region.

Regression on distance matrices

We analysed the relative influence of geographic, 'host' and 'environmental' distances on dissimilarity of flea species composition for the entire set of flea species as well as for the subsets of highly host-specific, moderately host-specific and non-host-specific species using multiple regressions on distance matrices (MRM; see Manly, 1986, Legendre *et al.*, 1994, Legendre & Legendre, 1998, and 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 flea species composition) and any number of explanatory distance matrices (in our case, geographic distances, environmental distances and dissimilarity in host species composition) (Lichstein, 2007), which are unfolded into distance vectors. In particular, the advantage of MRM is that it can cope with linear, nonlinear and nonparametric relationships between matrices (Lichstein, 2007). The significance of the model and regression coefficients is tested by permuting a response matrix while the explanatory matrices are held constant. The rows and corresponding columns in the response matrices are permuted simultaneously and the coefficient of determination of the model and regression coefficients are calculated for each permutation to generate a null distribution (Legendre & Legendre, 1998; Lichstein, 2007). One of the limitations of the predecessor of MRM, Mantel analysis, was inflated type I error in the presence of spatial autocorrelation, even if a geographic distance matrix was included in the analysis (Raufaste & Rousset, 2001; Lichstein, 2007). However, it is still unknown if MRM has the same problem (Lichstein, 2007).

Since complete independence between explanatory matrices is rarely met, we implemented additional partial multiple regressions on distance matrices to estimate the 'pure' effect of each explanatory matrix. This is especially important for our data assuming that the spatial pattern of species composition of flea supracommunities may have 'pure' spatial (dispersal limitation), environment-related (e.g. microclimatic preferences) and host-related (host preference) components. Similarly, environmental dissimilarity may have a spatial component, and patterns of host species composition may have 'pure' spatial and environment-related components. More precisely, we extracted a 'pure' effect for each independent variable as follows. For each subset of flea species (all fleas and highly, moderately and non-host-specific fleas), 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 & 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, while we express the fraction of variation explained by each 'pure' effect as a percentage. In general, the application of MRM to species composition data represents a level-3 analysis *sensu* Tuomisto & Ruokolainen (2006) because it aims to evaluate to what extent the variation in one group of distances can be explained by variation in another group of distances. It should be noted, however, that Legendre *et al.* (2005) argued that the variance of the dissimilarity matrix is not the same as the variance of the raw-data table, and that there is no simple relationship between the two variances. In other words, if the explained variation in community similarity is partitioned into, for example, spatial and environmental components, this variation in community similarity may be distinct from the variation in species abundances (Legendre *et al.*, 2005). Nevertheless, Tuomisto & Ruokolainen (2006) disagreed with Legendre *et al.* (2005) and suggested that distance-based variation partitioning is appropriate when the goal is analysing (as opposed to 'explaining' *sensu* Legendre *et al.*, 2005) beta diversity (a level-3 question *sensu* Tuomisto & Ruokolainen, 2006). This is because distance-based variation partitioning can indicate what proportions of the variation in beta diversity of fleas are explained by variation in geographic distances alone, variation in the differences in environment alone, variation in the differences in host species composition alone, as well as the joint variation in the three factors.

We tested the significance of regression coefficients and r^2 using permutations as described above. All probabilities were based on 10,000 permutations. Analyses were performed using the library 'ecodist' (Goslee & Urban, 2007) implemented in the R Package (R Development Core Team, 2005).

To test whether data points for flea dissimilarity are significantly concentrated in a triangular area of the bivariate space when plotted against geographic or environmental dissimilarity (see Results), we used the boundary test implemented in the EcoSim 7 software (Gotelli & Entsminger, 2009). This test uses a null-model approach and calculates: (1) the number of points that fall beyond the boundary, and (2) the sum of squares of those points for observed and simulated (1000 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. EcoSim creates a null data set by reshuffling the observed values of both variables. In other words, it retains the variances of both variables and any significant results are thus due to patterns in the covariance of these variables (Gotelli & Entsminger, 2009). Outliers and asymmetric data distributions are fully retained. We considered the data distributions in the boundary tests as asymmetric because the distributions of flea composition dissimilarity, geographic distance and environmental dissimilarity demonstrated non-zero skewness (–3.53, –1.52, 0.91 and 0.97, respectively), although a rerun of the boundary tests assuming symmetric distribution produced similar results.

RESULTS

Results of MRM linking the flea species composition dissimilarity matrix to geographic distance, environmental distance and host species composition dissimilarity matrices are presented in Table 1. When all fleas were included independently of their degree of host specificity, dissimilarity in flea species composition appeared to be affected by all three independent variables (Fig. 1), although the pure effect of dissimilarity of host species composition was the strongest (Table 1). In general, dissimilarity in flea species composition between regions increased with

Table 1 Results of multiple regressions on distance matrices using a permutation method with the matrix of pairwise dissimilarity in flea species composition between regions as the dependent matrix and matrices of pairwise geographic distance (GD), environmental dissimilarity (ED) and dissimilarity in host species composition (HD) between regions as independent matrices (IM).

Subset	IM	Coefficient	R^2 of the entire model	Percentage of explained variation due to 'pure' effect
AF	GD	0.001**		4.37
	ED	0.90**		4.48
	HD	0.38**		38.77
			0.32**	
HHS	GD	-0.0003^{ns}		1.24
	ED	1.58**		57.57
	HD	0.05^{ns}		2.42
			0.08**	
MHS	GD	0.001**		14.69
	ED	-0.03^{ns}		0.01
	HD	0.24**		43.50
			0.19**	
NHS	GD	0.01**		5.90
	ED	0.70*		2.58
	HD	0.41**		41.13
			0.27*	

**$P < 0.001$, *$0.001 = P \leq 0.05$, ns, not significant ($P > 0.05$). See text for details about explained variation due to the 'pure' (i.e. completely independent) effect.

AF, all fleas; HHS, MHS and NHS, highly, moderately and non-host-specific fleas, respectively.

an increase in geographic distance as well as environmental and host compositional dissimilarity between these regions.

However, when highly host-specific, moderately host-specific and non host-specific fleas were considered separately, dissimilarity between regions in flea species composition was found to be affected by different factors. Dissimilarity in species composition of highly host-specific fleas was related solely to, and correlated positively with, environmental dissimilarity (Table 1, Fig. 2), whereas that of both moderately host-specific and non-host-specific fleas were related to, and correlated positively with, both geographic distance and dissimilarity in host species composition (Table 1, Figs 3 & 4), although the percentage of variation explained by dissimilarity in host species composition was higher than that explained by geographic distance (Table 1). In addition, the positive relationship between dissimilarity in species composition of non-host-specific fleas and environmental dissimilarity was only marginally significant.

Comparison of the r^2 values of the model that included geographic, environmental and host composition distances among subsets of fleas with different degrees of host specificity showed that the model explained dissimilarity in the species composition of non-host-specific and moderately host-specific fleas much better than for highly host-specific fleas.

Table 2 Results of the boundary tests for a predominant scatter of data points in the upper left corner of the scatterplot of dissimilarity in flea species composition against geographic distance (GD) or environmental dissimilarity (ED).

Independent variable	Subset of flea species	Number of points P		Sum of squares P	
		O > S	O < S	O > S	O < S
GD	All	0.96	0.04	0.99	0.001
	Moderately host-specific	0.99	0.001	0.99	0.001
	Non-host-specific	0.97	0.03	0.99	0.001
ED	All	0.99	0.001	0.99	0.001
	Highly host-specific	0.98	0.03	0.97	0.02

The tests were based on 1000 simulations. O > S, observed greater than simulated; O < S, observed lower than simulated.

In cases where the effects of geographic (all fleas, moderately host-specific fleas and non-host-specific fleas) and environmental distances (all fleas and highly host-specific fleas) were significant, the distributions of data points in the scatterplots were clearly triangular (Figs 1a & 3a,b). The boundary number of points and the boundary sum of squares tests confirmed the statistical significance of a predominant scatter of data points in the upper left corner of the space (Table 2). This suggests that two geographically distant or environmentally different regions cannot have similar flea assemblages, while close or environmentally similar regions can have either very similar or dissimilar flea assemblages.

DISCUSSION

The results of this study did not contradict our main hypothesis, although our specific predictions have not been supported. Our main result is that the set of explanatory variables for between-region dissimilarity in flea species composition differed depending on which subset of flea species (in terms of the level of host specificity) was taken into account. Thus, pooling together all species comprising a community may mask important patterns, and the deconstruction strategy proposed by Marquet *et al.* (2004) is a better approach.

Indeed, when we considered all fleas in the analysis, the spatial pattern of similarity was found to reflect the combined effect of geographic distance, environmental variation and host species composition. However, when fleas with different degrees of host specificity were treated separately, it appeared that the effect of the environment on flea dissimilarity was mainly due to host-specific fleas, whereas the effects of geographic distance and host species composition were mainly due to host-opportunistic species. The evaluation of dissimilarity in species composition between locations is based on the number of species and their relative abundances in these locations. Consequently, dissimilarity represents a composite variable that encompasses a variety of species as if they were equivalent except for their abundance

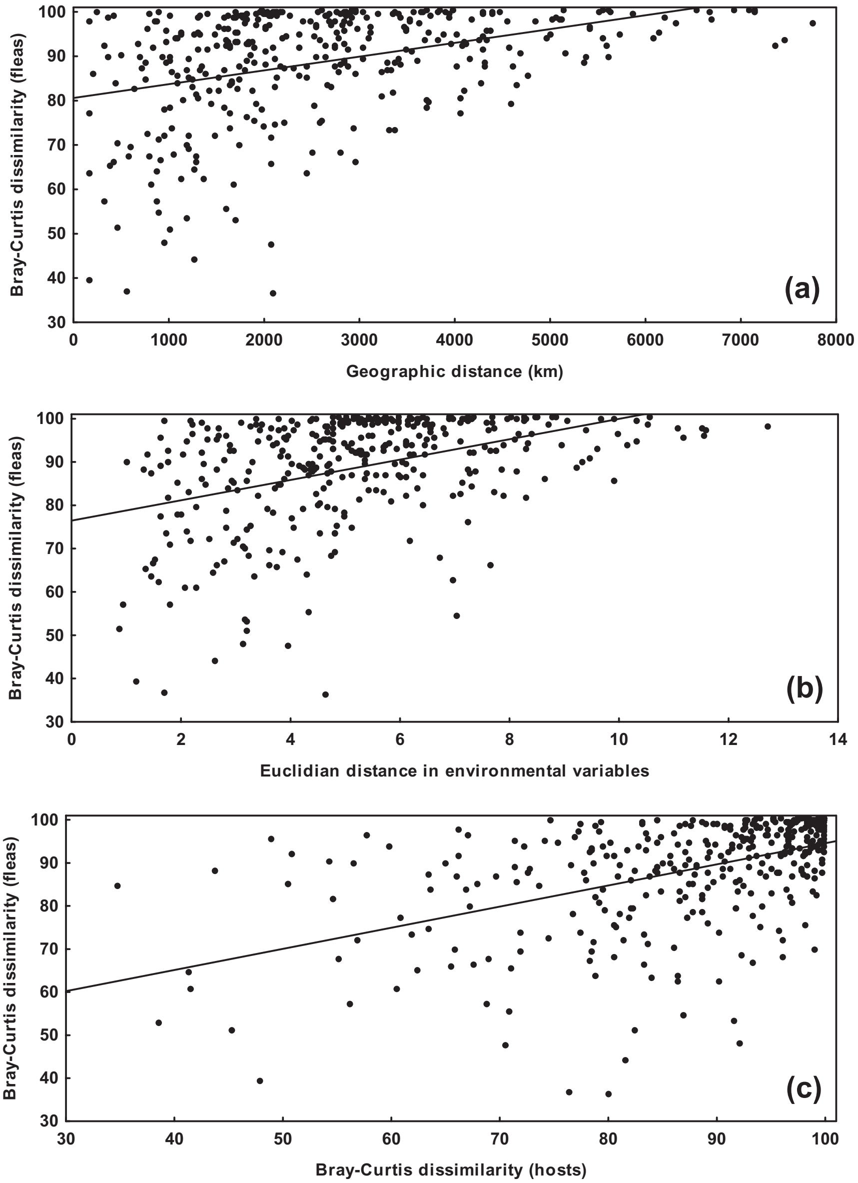


Figure 1 Relationship between Bray–Curtis dissimilarity in total flea species composition and (a) geographic distance, (b) environmental dissimilarity and (c) Bray–Curtis dissimilarity in host species composition.

(Marquet *et al.*, 2004). However, nobody would deny that even closely related species can differ in many traits. These differences may cause differential responses of subsets of species to extrinsic factors and, thus, different spatial patterns.

Contrary to our expectation, similarity in species composition of highly host-specific fleas between locations did not depend on either host species composition or geographic distance, but depended, albeit weakly, on similarity in the 'physical' environment. The non-significance of host species composition for the similarity of the assemblages of highly host-specific fleas between regions may stem from at least three non-mutually exclusive reasons. First, if a highly host-specific flea occurs in a region, it is clearly because at least one of the hosts it needs occurs there as well, so the identity of other hosts in the local pool may not matter to the presence or abundance of this flea. Second, the identity of the principal host used by a host-specific flea may change across its geographic range (Shenbrot *et al.*, 2007). For example, the principal (and only) host of *Amphipsylla kuznetzovi* across the largest part of its geographic range is *Microtus gregalis*, but this host is substituted by *Chionomys gud* in the Main Caucasus and by *Chionomys nivalis* in the Trans-Caucasus. In other words, a flea may be host specific on a local scale, but host opportunistic on a global scale (Krasnov *et al.*, 2008). However, such local specialists/global generalists represent a minority among fleas, with most species being either host specialists or host generalists independently of spatial scale (Krasnov *et al.*, 2008). Nevertheless, the ability of a flea to switch from one principal host to another in different geographic regions may explain why neither host composition dissimilarity nor geographic distance affects dissimilarity in species composition of highly host-specific fleas. Third, some highly host-specific fleas exploit hosts distributed across the whole or most of the Palaearctic (e.g. *Tarsopsylla octodecimdentata* on *Sciurus vulgaris*, *Leptopsylla segnis* on *Mus musculus*, *Ceratophyllus*

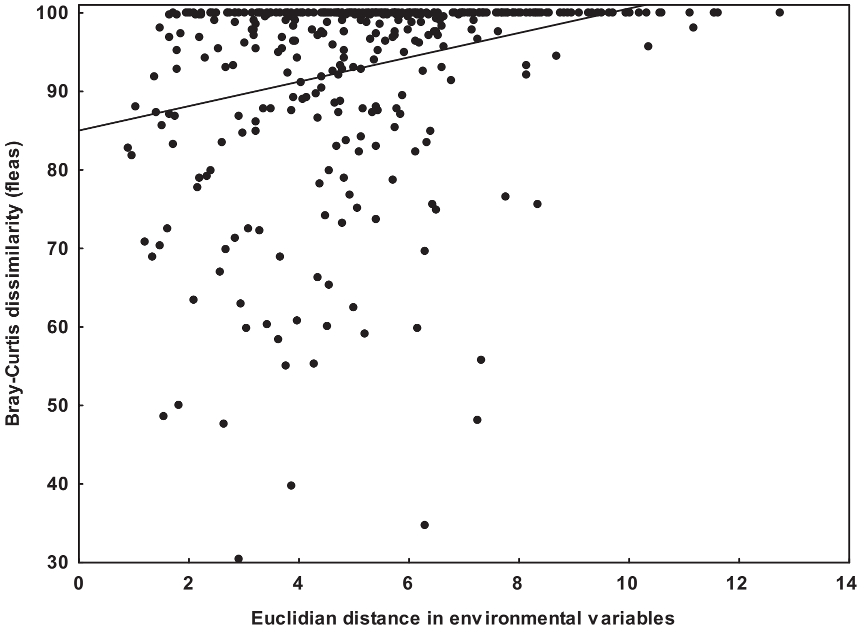


Figure 2 Relationship between Bray–Curtis dissimilarity in species composition of highly host-specific fleas and environmental dissimilarity.

indages on *Eutamias sibiricus*). The effect of environmental dissimilarity on dissimilarity in flea species composition is undoubtedly related to the microclimatic preferences of the off-host stages of fleas (eggs, larvae and/or pupae) as well as adult individuals (Krasnov *et al.*, 2001, 2002; Krasnov, 2008). The reason behind the weak effect of environmental dissimilarity may be the fact that the influence of microclimatic variables on survival and duration of development of pre-imago fleas is similar in all studied flea species, although their effect on reproductive parameters such as egg production and rate of oviposition varies among flea species and is associated with seasonal patterns of activity (Krasnov, 2008). In addition, the triangular distribution of data points in Fig. 2 (locations with a similar environment may have either similar or dissimilar assemblages of highly host-specific fleas, though locations with highly dissimilar environments always have dissimilar flea assemblages) may be caused by this different effect of microclimate on pre-imago as compared with imago fleas.

Dissimilarity in species composition of both moderately host-specific and non-host-specific fleas was correlated mainly with dissimilarity in host species composition and geographic distance. The former effect may occur because even highly opportunistic parasite species do not achieve the same abundance on all hosts they are able to exploit (Poulin, 2005). For example, the abundance of a flea in its auxiliary hosts has been shown to decrease with increasing taxonomic distance of these hosts from the principal host (Krasnov *et al.*, 2004c). Consequently, host species composition can play an important role as a determinant of the composition and relative abundance of host generalist fleas. Similar arguments can be applied to the effect of geographic distance, because if different hosts are not equivalent resources for an opportunistic flea, its indirect (via hosts) dispersal abilities are probably much lower than we initially thought. The shape of the data swarm when dissimilarity in flea species composition was plotted against geographic distance was clearly triangular. This may be simply because although distance does not prevent a species from dispersing to a nearby location, other factors (such as environmental dissimilarity) can make this unlikely, such that the similarity between nearby regions is not necessarily always high; however, when two regions are very distant, distance alone is sufficient to guarantee they will have different assemblages.

The different effects of different extrinsic factors on dissimilarity in flea community composition between host-specific and host-opportunistic fleas may be explained, at least partly, by our earlier findings on spatial patterns of similarity in species composition of flea and mite assemblages within a host (Krasnov *et al.*, 2005b; Vinarski *et al.*, 2007). In these earlier studies we found that the extrinsic variable (geographic distance, environmental dissimilarity or species composition of the local host fauna) that best explained the similarity in species composition of parasite assemblages between host populations varied among host species. This among-host difference may be related to the fact that parasite assemblages on different host species are often predominantly composed of either host specialists or host generalists (Vázquez *et al.*, 2005), which in turn respond differently to different extrinsic factors.

After its pioneering introduction by Marquet *et al.* (2004), the deconstruction approach has been successfully used to gain insight into the determinants of various patterns of diversity in different plant (Svenning & Skov, 2007) and animal (Thompson & Townsend, 2006; Blamires *et al.*, 2008; Diniz-Filho *et al.*, 2008; Real *et al.*, 2008; Terribile *et al.*, 2009) taxa. Our study broadens the application of this approach and demonstrates that it can be used to elucidate the mechanisms underlying diversity patterns in parasites.

There is no commonly accepted way of performing the deconstruction. It is clear that it should be based not only on

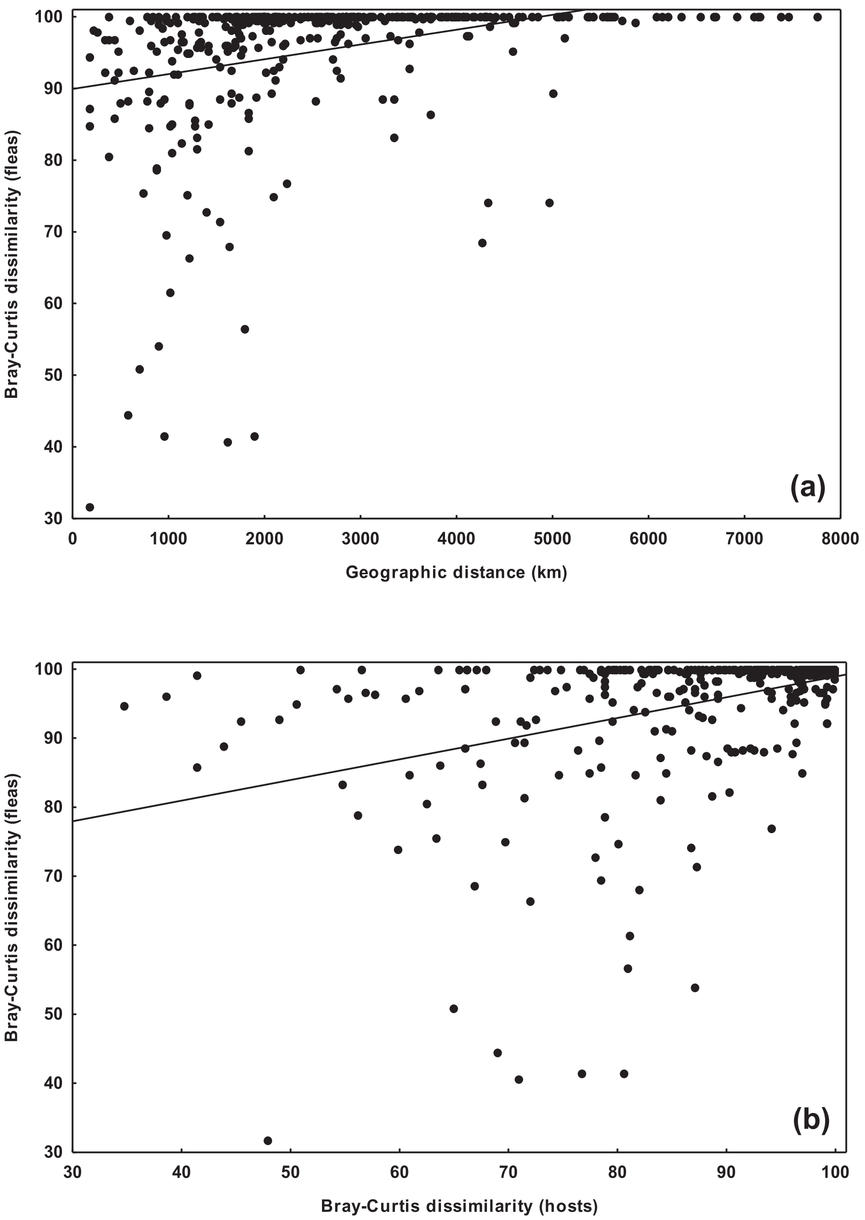
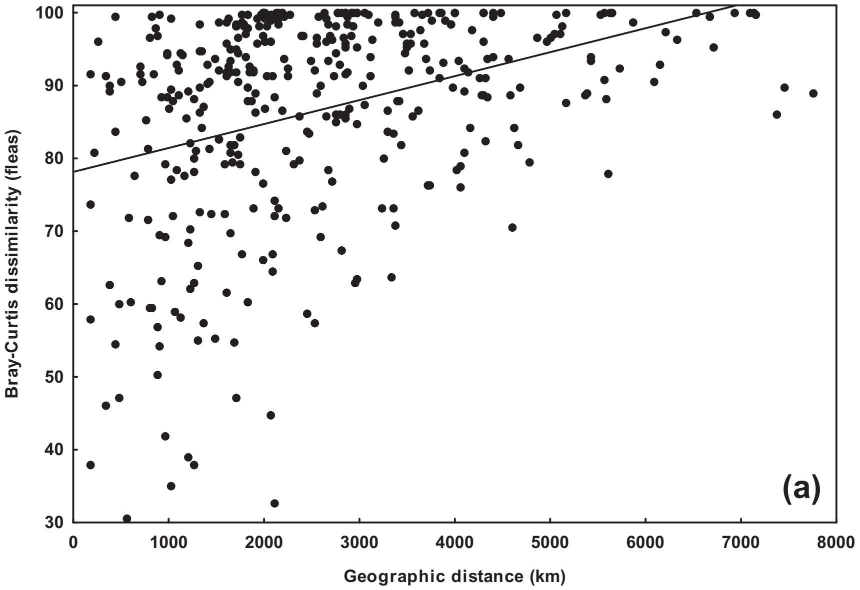


Figure 3 Relationship between Bray–Curtis dissimilarity in species composition of moderately host-specific fleas and (a) geographic distance and (b) Bray–Curtis dissimilarity in host species composition.

theory but also on empirical knowledge of the species of interest (Marquet *et al.*, 2004), and thus the deconstruction criteria should differ depending on the biological properties of the taxon under study. For example, the deconstruction of communities has been done based on geographic range (Svenning & Skov, 2007; Terribile *et al.*, 2009), body size (Terribile *et al.*, 2009) and habitat use (Blamires *et al.*, 2008). In the case of parasites, the deconstruction of communities according to the level of host specificity seems to be a productive approach. Host specificity is one of the most fundamental properties of parasitic organisms. From an evolutionary perspective, it reflects the parasite's historical associations with its hosts (Poulin, 2007), whereas from an ecological perspective, it mirrors the diversity of resources used by a parasite, or the breadth of its niche (Futuyma & Moreno, 1988; Poulin, 2007). Host specificity correlates with various other traits. For example, host specificity of a parasitic species correlates negatively (see Poulin, 1998, for helminths parasitic on teleost fish) or positively (see Krasnov *et al.*, 2004a, for fleas parasitic on small mammals) with mean abundance achieved on the host (but see Morand & Guégan, 2000). In fleas, the degree of host specificity was found to be negatively correlated with the size of their geographic range (Tripet *et al.*, 2002; Krasnov *et al.*, 2005a). Moreover, host specificity in fleas is, to a large extent, phylogenetically constrained and, in general, does not vary within a species on any spatial scale (i.e. it can be considered as a true character of a flea species) (Krasnov *et al.*, 2004b, 2008). In other words, host specificity is a trait subjected to natural selection, although the evolution of host specificity is reversible and thus not unidirectional (Poulin *et al.*, 2006). However, it is difficult, at present, to



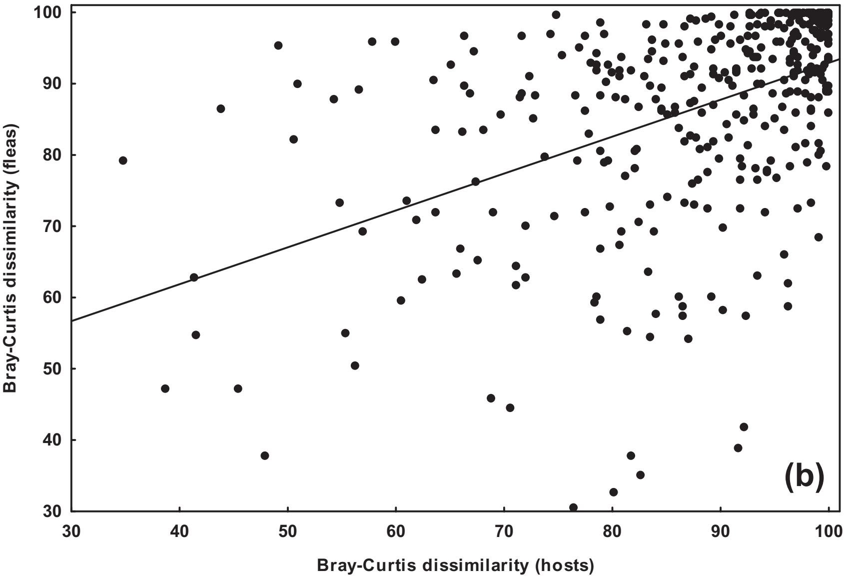


Figure 4 Relationship between Bray–Curtis dissimilarity in species composition of non host-specific fleas and (a) geographic distance and (b) Bray–Curtis dissimilarity in host species composition.

state explicitly which of the various facets of host specificity plays the most important role as a determinant of spatial diversity patterns in a particular subset of fleas. Nevertheless, the use of niche breadth as a deconstruction criterion may be useful not only in studying parasites, but free-living species as well.

The deconstruction approach in studies of parasite communities can be useful not only from purely theoretical but also from applied points of view. For example, it has been shown that the level of host specificity may correlate with the ability of a parasite to serve as a vector of infectious disease (e.g. Krasnov *et al.*, 2006, for fleas and plague). Consequently, deconstructing parasite communities into subsets of species according to their host specificity in geographic studies of parasite diversity patterns may help in further understanding the mechanisms shaping geographic patterns of diseases which, in turn, may help in their control and prevention.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data on mammals and fleas used in the analyses.

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BIOSKETCHES

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