Phylogenetic structure of host spectra in Palaearctic fleas: stability versus spatial variation in widespread, generalist species

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SUMMARY

We investigated spatial variation in the phylogenetic structure of host spectra in fleas parasitic on small mammals. Measures of phylogenetic host specificity ((phylogenetic species clustering (PSC) and phylogenetic species variability (PSV)) varied significantly more between than within flea species, but the proportion of variation which accounted for among-species differences was low. In 13 of 18 common flea species, at least one of the indices of the phylogenetic structure of regional host spectra revealed a significantly positive association with the phylogenetic structure of regional host assemblage, while relationships between PSC or PSV of the regional host spectrum and the distance from either the region of a flea's maximal abundance or latitude were not supported. Overall, results of this study demonstrated that although the degree of phylogenetic host specificity in fleas can be considered as a true attribute of a flea species, it is highly spatially variable, with phylogenetic structure of the surrounding host pool being the main reason behind this variation.

Key words: host specificity, fleas, spatial variation, phylogenetic structure.

INTRODUCTION

The degree of resource specialization (= resource niche breadth) is one of the most important properties of any species (Fox and Morrow, 1981; Futuyma and Moreno, 1988). The main resources for a parasite are its hosts. Consequently, the degree of resource specialization of a parasitic species is considered in terms of its host specificity; that is, the extent to which a parasite can exploit different host species (Poulin, 2007; Poulin *et al*. 2011). One of the most important challenges regarding evolution of resource specialization in general and host specificity of parasites in particular is to understand what are the relative roles of evolutionary *vs* ecological (e.g. local environment) constraints in shaping a given level of specialization (Fox and Morrow, 1981; Poulin, 2007; Antonovics *et al*. 2013). In parasites, several studies demonstrated that although host specificity is to a large extent phylogenetically constrained and thus is undoubtedly a product of natural selection, it is still strongly influenced by local environmental conditions and varies across populations of the same parasite species (Krasnov *et al*. 2004*a*; Korallo-Vinarskaya *et al*. 2009; Poulin *et al*. 2011). This spatial variation might be caused by a variety of factors such as: (a) spatial variation in the availability of resources (= abundance and diversity of hosts) (Fox and Morrow, 1981); (b) relationships between latitude, geographical range size and the level of specialization (Brown, 1984; Ruggiero and Hawkins, 2006); and (c) relationship between latitude, species richness and the effect of the latter on the level of specialization (Vázquez and Stevens, 2004). However, the relative roles of different factors determining spatial variation in the level of specialization are still poorly understood.

Recently, it has been recognized that host specificity is a multi-faceted trait that reflects (a) how many host species a parasite exploits and what are the relative abundances of parasite individuals in different hosts (structural specificity); (b) how closely related these host species are to each other (phylogenetic specificity); and (c) how consistently different hosts are used across a parasite's geographical range (spatial specificity) (see review in

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Poulin *et al*. 2011). Thus, investigation of factors explaining variation of host specificity in a parasite species requires deconstructing this trait into its structural, phylogenetic and spatial components (Poulin *et al*. 2011). Only two studies (Krasnov *et al*. 2004*a*; Korallo-Vinarskaya *et al*. 2009) have specifically investigated spatial variation of parasite host specificity while attempting to deconstruct host specificity into structural and taxonomic components. These studies, indeed, demonstrated that spatial variation in different components of host specificity might be affected by different factors. For example, the number of hosts exploited by a gamasid mite species in a region (i.e. structural host specificity) correlated positively with regional host species richness (Korallo-Vinarskaya *et al*. 2009). In contrast, taxonomic diversity of the regional host spectrum (i.e. phylogenetic host specificity; see Poulin and Mouillot, 2003 for details of the index) within a mite species did not demonstrate any clear trend in its association with regional host species composition (Korallo-Vinarskaya *et al*. 2009). In fleas, the degree of structural host specificity within a region did not depend on the number of available hosts in a region (Krasnov *et al*. 2004*a*). Phylogenetic host specificity, measured as taxonomic diversity of host spectrum, was also not affected by taxonomic diversity of regional host assemblages (= regional host pools). However, comparison between taxonomic diversity of the regional host spectrum and that of the regional host assemblage demonstrated that some fleas utilized host species that were more closely related to each other than on average across the regional pool (Krasnov *et al*. 2004*a*). The latter inconsistency can be related to the fact that the phylogenetic component of host specificity in the Krasnov *et al*. (2004*a*) study was evaluated via an earlier proposed measure of phylogenetic host specificity, taxonomic distinctness of host spectrum (Poulin and Mouillot, 2003), that relied on the Linnaean classification of host species rather than on true phylogenetic information. In other words, it took into account phenotypic similarities among species rather than their true phylogenetic relatedness. Obviously, the phylogenetic relatedness among host species is more relevant for understanding the evolutionary and ecological factors underlying a given degree of host specificity in a parasite population.

Phylogenetic information has been introduced into community ecology and biogeography in recent years and appears to be a powerful tool in providing a better understanding of evolutionary processes involved in the assembly of communities and their spatial variation (Webb *et al*. 2002; Morlon *et al*. 2011; Cooper *et al*. 2012). Here, we take advantage of the recently proposed indices of phylogenetic structure (phylogenetic species clustering (PSC) and phylogenetic species variability (PSV); see Helmus *et al*. 2007 for details) to investigate factors determining spatial patterns of variation in the phylogenetic component of host specificity in fleas parasitic on small mammals in the Palaearctic. Values of both indices indicate whether a host assemblage is composed of phylogenetically distant (that is, low phylogenetic host specificity) or phylogenetically close (that is, high phylogenetic host specificity) species (see details below).

The aims of this study were twofold. First, we asked: (a) whether the degree of host specificity, measured as phylogenetic structure of host spectrum, is repeatable across populations of the same flea species; and (b) what proportion of variation is accounted for by differences among flea species? Second, we asked: what are the factors explaining spatial variation in the degree of phylogenetic host specificity within flea species? To answer these questions, we tested the effect of three factors on the estimate of phylogenetic host specificity of a flea population. These were: (a) phylogenetic structure of the regional host pool; (b) distance from the region where a flea attains maximal abundance; and (c) latitude. The association between the phylogenetic structure of hosts utilized by a flea and that of the entire host pool may arise when a species-specific degree of host specificity is modified by local restrictions in host availability (Fox and Morrow, 1981; Krasnov and Poulin, 2010). Positive relationships between phylogenetic structure of the regional host pool and phylogenetic structure of the regional host spectrum of a parasite would suggest that a certain host lineage is added to or omitted from the host spectrum which is dependent on its availability. In addition, we expected that there would be an effect of distance from the region of maximal abundance on phylogenetic component of host specificity according with the 'abundance optimum' hypothesis (Gaston, 2003; Poulin and Dick, 2007; Krasnov *et al*. 2008). This hypothesis states that species abundance peaks in the locality with the most favourable conditions and decreases with an increasing distance from that locality. Among parasites, this pattern, albeit not especially strong, was supported for fleas and gamasid mites on mammalian hosts (Krasnov *et al*. 2008) and monogeneans and larval trematodes (but not cestodes, parasitic crustaceans, nematodes and acanthocephalans) in freshwater fish (Poulin and Dick, 2007; Seifertová *et al*. 2008). Higher local abundance may be associated with lower local host specificity merely because parasites in dense populations would have higher probability of contact with multiple and phylogenetically more diverse host species than conspecifics in sparse populations. This, however, may not be true for highly host-specific parasites and/or for parasites in which abundance varies synchronously with that of their preferred hosts. Similarly, a latitudinal gradient in phylogenetic component of host specificity was expected due to relationships found earlier for fleas between local abundance and

Table 1. Mean values (M) and coefficients of variation (CV) of indices of phylogenetic structure (PSC and PSV; see text for explanations) of the regional host spectra in 18 flea species. PSV indices for *C. agyrtes* are not presented because in the majority of regions they did not differ from expected by chance

Species	Number of regions	PSC		PSV	
		M	CV	M	CV
Amalaraeus penicilliger	18	0·75	0·16	0·41	0·41
Amphypsylla rossica	7	0·74	0·09	0·26	0·26
Citellophilus tesquorum	7	0·64	0·16	0·10	0·10
Corrodopsylla birulai	9	0·72	0·23	0·23	0·23
Ctenophthalmus agyrtes	7	0·73	0·07	–	–
Ctenophthalmus assimilis	12	0·73	0·09	0·62	0·19
Frontopsylla elata	12	0·69	0·19	0·52	0·28
Hystrichopsylla talpae	13	0·73	0·09	0·61	0·16
Leptopsylla segnis	8	0·68	0·15	0·48	0·23
Megabothris rectangulatus	12	0·74	0·10	0·54	0·17
Megabothris turbidus	12	0·73	0·15	0·56	0·21
Megabothris walkeri	8	0·72	0·11	0·51	0·33
Neopsylla mana	9	0·63	0·22	0·63	0·16
Neopsylla pleskei	9	0·74	0·07	0·45	0·21
Nosopsyllus consimilis	9	0·68	0·16	0·54	0·22
Palaeopsylla soricis	11	0·75	0·14	0·71	0·07
Peromyscopsylla bidentata	9	0·69	0·26	0·61	0·21
Peromyscopsylla silvatica	7	0·82	0·06	0·41	0·52

latitude (Krasnov *et al*. 2006). However, individual flea species differed in the direction of correlation between abundance and latitude suggesting that this pattern was related to climatic correlations of latitude and depended on species-specific environmental preferences. Consequently, we expected that the degree of phylogenetic clustering and/or variability (see below) of regional host spectra would decrease with latitude in some species and increase with latitude in other species.

MATERIALS AND METHODS

Data on composition of host spectra

Data on species composition of host spectra were taken from a database compiled from published surveys of fleas parasitic on small mammals (insectivores, rodents and pikas) across the Palaearctic (60 surveys in 52 regions). Each survey reported the number of fleas of a particular species collected from a given number of individuals of a particular host species. The list and geographical locations of surveys can be found in Krasnov *et al*. (2010). Initially, we selected flea species that were recorded in at least two regions while infesting at least four host species per region. This resulted in the dataset on regional host spectra for 74 fleas which was used for the analyses of repeatability of phylogenetic host specificity within *vs* among flea species (see below). Then, to understand the possible causes of geographical variation in phylogenetic host specificity within a flea species, we selected 18 species that were recorded in at least seven regions (Table 1).

Phylogenetic structure of host spectra

A phylogenetic tree for hosts was constructed using the global phylogenetic supertree for mammals (Bininda-Emonds *et al*. 2007). We modified topology of the tree branches for voles as described in Krasnov *et al*. (2011).

Various metrics of the phylogenetic structure of a species assemblage indicate whether species in an assemblage are either more (phylogenetic clustering) or less (phylogenetic overdispersion) related phylogenetically than expected by chance or else represent a phylogenetically random set (Webb *et al*. 2002). As mentioned above, we used two indices of phylogenetic structure for a regional set of host species used by a flea, namely PSV and PSC (Helmus *et al*. 2007). Calculation of these indices involves a comparison between (a) the expected variance of a neutral trait evolving under Brownian motion along the actual phylogenetic tree of species composing an assemblage; and (b) the variance of a neutral trait expected under star phylogeny (that is, the case when these species evolved simultaneously from the same ancestor, so that their pairwise phylogenetic distances are equal). However, the two indices capture somewhat different components of phylogenetic structure because PSV considers all species while PSC takes only close relatives into account. Values of both indices vary between zero and 1 where values of 1 indicate an assemblage of phylogenetically independent species while values close to zero indicate high phylogenetic relatedness (Helmus *et al*. 2007). Indices of phylogenetic structure were calculated using the package 'picante' (1·5–2)

(Kembel *et al.* 2010) implemented in R 2.15 (R Development Core Team, 2011).

To test whether the phylogenetic structure of a regional host spectrum of a flea differed significantly from that expected by chance, we compared the observed index with the average of 500 indices calculated for randomly generated host spectra. Each null spectrum was generated by random sampling of the observed number of host species from the total pool of host species exploited by a flea across all regions where it was found. In further analyses, we used only data on those regional assemblages in which phylogenetic structure differed significantly from that expected by chance.

Data analyses

To determine whether phylogenetic host specificity is repeatable within flea species, that is, a parameter that varies less among populations of the same flea species than among host species, we performed a repeatability analysis following that of Arneberg *et al.* (1997). Using flea species for which data from at least two regions were available, we analysed the variation in PSC and PSV of the host spectrum using a one-way ANOVA in which flea species was the independent factor. A significant effect of flea species would indicate that PSC and PSV of the host spectrum are repeatable within flea species, that is, they are more similar across populations of the same flea than across flea species. We estimated the proportion of the total variance originating from differences among flea species, as opposed to within species, following Sokal and Rohlf (1995).

Then, we selected 18 flea species recorded in at least seven regions and applied Generalized Linear Models (GLM) with normal distribution and a log-link function (separately for each flea species) to test for the relationships between the phylogenetic structure of the host spectrum of a flea in a region and (a) the phylogenetic structure of the entire regional host assemblage; (b) latitudinal position of a region (distance to the equator); and (c) distance of a region to the region where a given flea attains maximal abundance (see below). Both distance measures were log-transformed prior to analyses. We selected the best model using Akaike's Information Criterion (AIC). Then, we further investigated the best models and tested for significance of coefficients using Wald statistics.

To identify the region where each flea species attains maximal abundance, we used the mean number of fleas per individual host of a given host species as a measure of abundance for each host in each region where at least 15 individual hosts from this region were examined. For each flea species, we selected the region where its abundance peaked and calculated the geometric distance between this region and each of the remaining regions where this flea was recorded (see details in Krasnov *et al.* 2008).

We used the values of the coefficients of the models and their respective standard errors to test for the general trends in the effects of either phylogenetic structure of the regional host assemblage or latitudinal position of a region or distance of a region to the region of maximal abundance of a flea on the phylogenetic structure of the regional host spectra of a flea using meta-analyses separately for each independent variable. The meta-analyses that used either fixed or random effects models produced the same results. Here, we report the results of the analysis that used the fixed effects model only. Meta-analyses were carried out using the computer program Comprehensive Meta-Analysis 2.2 (Biostat Inc., Englewood, NJ, USA). Selection of flea species recorded in at least seven regions and calculation of abundances on those host species for which at least 15 individuals were examined allowed comparability of data taken from different sources.

RESULTS

The phylogenetic structure in terms of both PSV and PSC of the majority of within-host local flea assemblages differed significantly from that expected by chance (in 336 for PSC and 340 for PSV of 391 flea-region samples). Mean values of indices of phylogenetic structure varied for PSC between a low of 0·34 in *Paraneopsylla ioffi* and a high of 0·82 in *Peromyscopsylla silvatica* and for PSV between a low of 0·40 in *Nosopsyllus turkmenicus* and a high of 0·79 in *Ctenophthalmus bisoctodentatus*. The distribution of mean PSC values was strongly left-skewed ($\gamma = -0{\cdot}76$; Fig. 1), while that of mean PSV values was roughly symmetrical ($\gamma = 0{\cdot}29$; Fig. 1).

The repeatability analysis for flea species recorded in at least two regions demonstrated relative stability of phylogenetic host specificity measured as PSC or PSV within a flea species. Estimates of phylogenetic structure of host spectra from the same flea species were closer to each other than expected by chance, and varied significantly among flea species ($F_{68,257} = 1{\cdot}99$ for PSC and $F_{73,261} = 1{\cdot}83$ for PSV, respectively, $P < 0{\cdot}001$ for both), with 17·8 and 16·3%, respectively, of the variation among samples accounted by differences between flea species.

In 18 common flea species, PSC and PSV for regional host spectra varied spatially with coefficients of variation ranging between a low of 6% in *P. silvatica* and a high of 26% in *Peromyscopsylla bidentata* for PSC and between a low of 7% in *Palaeopsylla soricis* and a high of 52% in *P. silvatica* for PSV (Table 1). Coefficients of variation of regional indices of the phylogenetic structure of host spectra of a flea did not correlate with the number of regions in which this flea was recorded (Spearman's rank order correlation; $r = 0{\cdot}21$ and

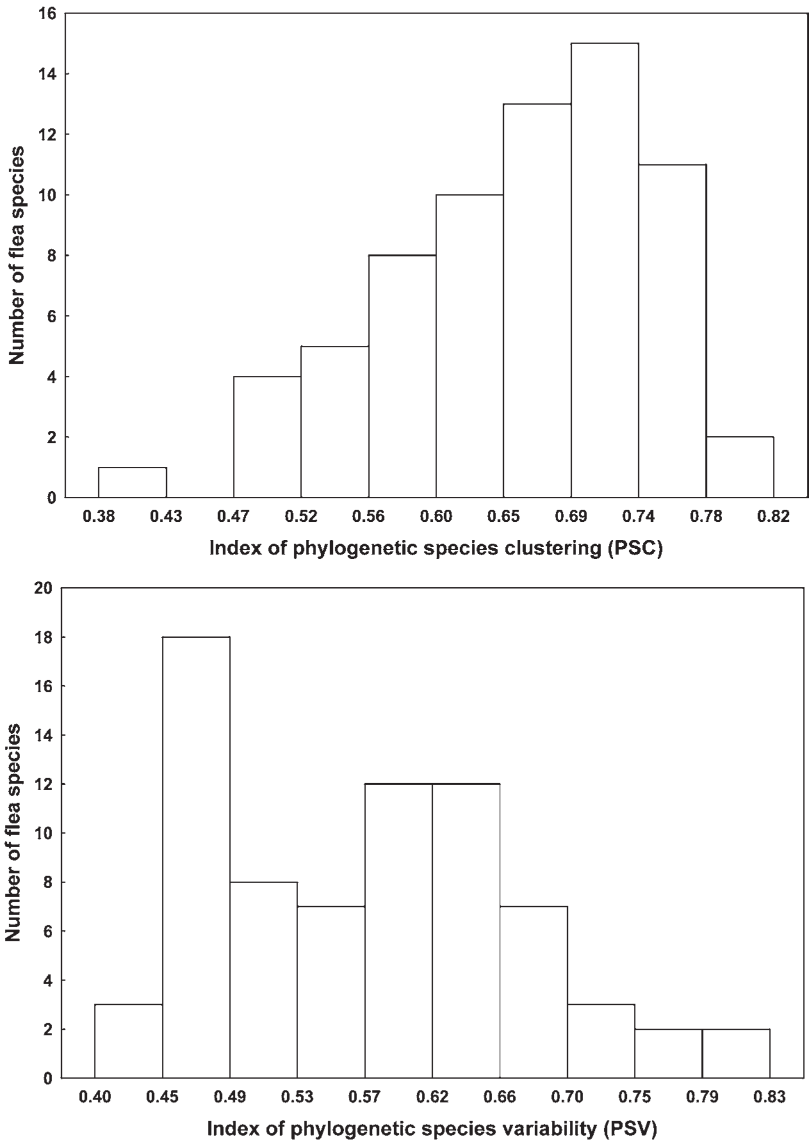

Fig. 1. Frequency distributions of mean values of the indices of phylogenetic structure (PSC and PSV, see text for explanations) of the regional host spectra across 74 flea species.

$r = -0{\cdot}20$ for PSC and PSV, respectively; $P > 0{\cdot}05$ for both).

Results of the GLM of the relationships between PSC and PSV of the regional host spectra and the respective index of the phylogenetic structure of the regional host assemblage, distance of a region from the region where a flea attains maximal abundance and distance of the region from the equator are presented in Tables 2 (PSC) and 3 (PSV). In 13 of 18 flea species, at least one index of the phylogenetic structure of regional host spectra showed a significant positive association with the phylogenetic structure of regional host assemblage (see illustrative example with *Amalaraeus penicilliger* in Fig. 2). Significant relationships between PSC or PSV of the regional host spectrum and the distance from the region where a flea attained maximal abundance were found in only three flea species (*A. penicilliger, Amphipsylla rossica, Neopsylla mana*) with a higher degree of phylogenetic clustering (lower PSC or PSV; see example with PSC in *A. penicilliger* in Fig. 3) in the regions farther from the region of maximal abundance. However, the relationships of PSC and PSV of the regional host spectra and distance to the region of maximal abundance in either *A. rossica* or *N. mana* became non-significant after a single data point (index of phylogenetic structure of host spectrum in the region of maximal abundance) was removed from the analysis. Significant effect of latitude (measured as distance to the equator) on the phylogenetic structure of the regional host spectra was found in six flea species with no consistency in the direction of this effect. Higher latitudes were associated with either a higher (lower PSC or PSV) or lower (higher PSC or PSV) degree of phylogenetic clustering of the hosts exploited (see illustrative examples with *Frontopsylla elata* and *Nosopsyllus consimilis* in Fig. 4). Moreover, in two fleas (*A. penicilliger* and *N. consimilis*), the two

Table 2. Best models explaining the relationships between the phylogenetic structure (measured as PSC; see text for explanations) of the regional host spectrum of a flea and the phylogenetic structure of the regional assemblage of host species (PSCh), distance of the region from the region where the flea attains maximal abundance (MA) and position of the region relative to the equator (DE). AIC, Akaike Information Criterion; L-l χ^2, log-likelihood χ^2. Asterisks denote terms with non-significant coefficients. Only significant intercept terms are shown

Species	Model	AIC	L-l χ^2	*P*
A. penicilliger	PSC = −5·97 + 1·33PSCh + 0·05MA* + 1·20DE	−32·26	12·72	< 0·01
A. rossica	PSC = −5·23 + 1·45PSCh − 0·07MA + 1·09DE	−18·39	10·86	0·03
C. tesquorum	PSC = 3·39PSCh	−14·76	4·71	0·03
C. birulai	PSC = 2·16PSCh*	−4·57	0·71	0·40
C. agyrtes	PSC = 0·14PSCh	−22·91	4·82	0·04
C. assimilis	PSC = 1·41PSCh	−33·75	4·91	0·03
F. elata	PSC = −9·02 + 2·51DE	−17·73	5·31	0·02
H. talpae	PSC = 1·13DE*	−31·16	1·05	0·30
L. segnis	PSC = −10·28 + 2·22DE	−16·07	4·95	0·03
M. rectangulatus	PSC = 1·12PSCh + 0·06MA*	−33·10	10·02	< 0·01
M. turbidus	PSC = 1·18PSCh	−18·76	4·81	0·04
M. walkeri	PSC = 1·06DE*	−17·02	2·52	0·11
N. mana	PSC = −0·11MA	−10·75	4·48	0·04
N. pleskei	PSC = 0·58PSCh	−29·26	4·95	0·03
N. consimilis	PSC = 6·62 − 1·37PSCh* − 0·04MA* − 1·60DE	−19·08	11·29	0·01
P. soricis	PSC = 2·58PSCh − 1·62DE*	−24·10	10·56	< 0·01
P. bidentata	PSC = 5·53PSCh	−7·34	4·66	0·03
P. silvatica	PSC = −0·62PSCh*	−20·60	2·20	0·14

Table 3. Best models explaining the relationships between the phylogenetic structure (measured as PSV; see text for explanations) of the regional host spectrum of a flea and the phylogenetic structure of the regional assemblage of host species (PSVh), distance of the region from the region where the flea attains maximal abundance (MA) and position of the region relative to the equator (DE). AIC, Akaike Information Criterion; *L*-l χ^2, log-likelihood χ^2. Asterisks denote terms with non-significant coefficients. Only significant intercept terms are shown. Analysis were not carried out for *C. agyrtes* because phylogenetic structure of host spectra of this flea did not differ from that expected by chance in the majority of regions

Species	Model	AIC	*L*-l χ^2	*P*
A. penicilliger	PSV = 11·43 + 2·95PSVh − 0·25MA − 3·55DE	−15·42	18·15	< 0·01
A. rossica	PSV = 4·09PSVh	−14·52	6·31	0·01
C. tesquorum	PSV = 1·85PSVh	−24·47	8·72	< 0·01
C. birulai	PSV = 2·14PSVh	−10·60	4·45	0·03
C. assimilis	PSV = 1·89PSVh	−22·99	8·63	< 0·01
F. elata	PSV = −1·53DE*	−9·55	0·41	0·52
H. talpae	PSV = −8·23 + 1·22PSVh	−25·50	8·75	0·01
L. segnis	PSV = 1·78PSVh + 0·48MA*	−14·84	7·15	0·03
M. rectangulatus	PSV = 0·94PSVh*	−20·40	0·79	0·37
M. turbidus	PSV = 2·53PSVh	−18·78	9·15	< 0·01
M. walkeri	PSV = −9·09DE	−7·08	4·94	0·03
N. mana	PSV = −9·86 + 2·28DE*	−12·42	1·25	0·26
N. pleskei	PSV = −0·34MA*	−16·18	2·23	0·13
N. consimilis	PSV = −8·12 + 2·01PSVh + 1·67DE	−28·30	20·63	< 0·01
P. soricis	PSV = −0·02MA*	−31·28	1·20	0·27
P. bidentata	PSV = −1·36PSVh*	−10·21	2·97	0·08
P. silvatica	PSV = −0·19MA*	−1·38	2·78	0·09

indices of phylogenetic structure of the regional host spectra showed contrasting patterns of the relationships with the distance of the region to the equator.

Meta-analyses across all 18 flea species demonstrated a significant trend of the coefficients of PSC and PSV of the regional host pools in the models to be positive (Table 4). In contrast, meta-analytic estimates of the coefficients of both distance measures did not differ significantly from zero (Table 4).

DISCUSSION

This study demonstrated that although the degree of phylogenetic host specificity was repeatable within

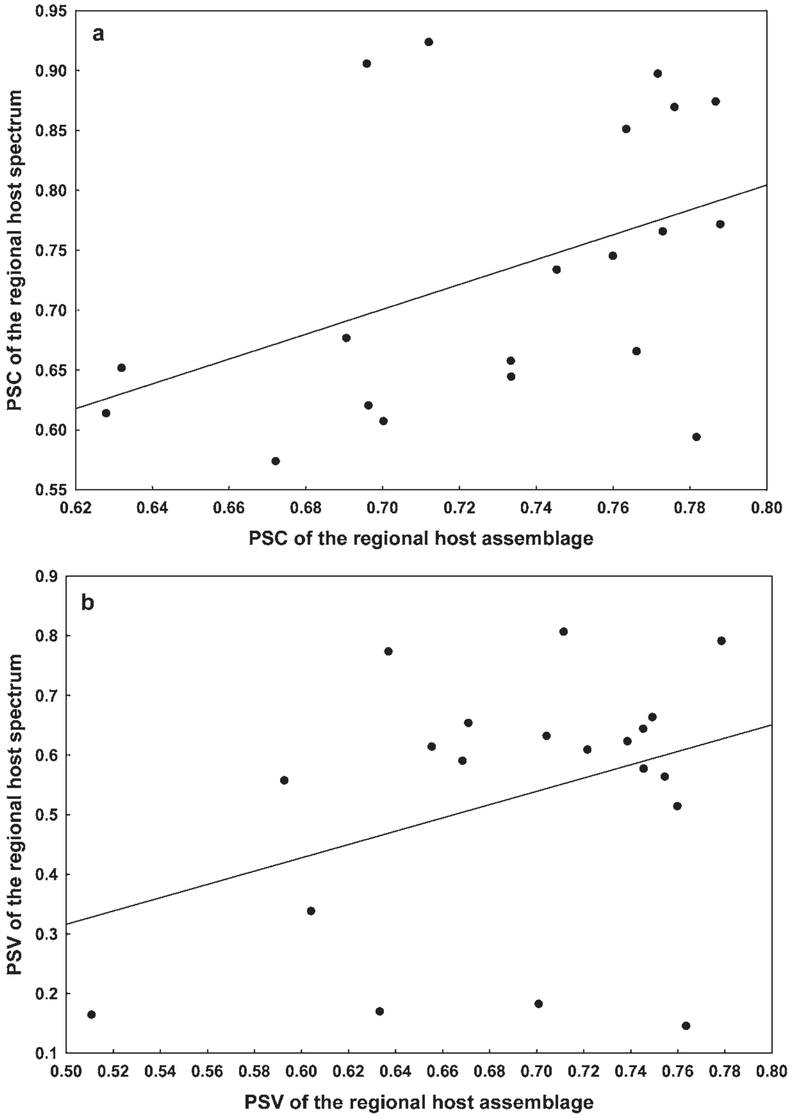

Fig. 2. Relationships between the phylogenetic structure of the regional host spectra and the phylogenetic structure of the regional host assemblages in *Amalaraeus penicilliger*; (a) PSC; (b) PSV.

flea species, the proportion of variation accounted for by among-flea species as opposed to within-flea species differences was rather low, so that the degree of phylogenetic host specificity of a flea was highly variable across space. Furthermore, spatial variation in the phylogenetic component of host specificity depended mainly on spatial variation in the phylogenetic composition of host assemblages in a locality, while the spatial effects associated with flea abundance were, at most, of minor importance. Finally, the effect of latitude on phylogenetic structure of host spectra across localities was found in a few flea species only. Moreover, patterns of this effect appeared to be inconsistent not only between flea species, but also in the same flea species between different measures of phylogenetic structure.

Repeatability of PSC and PSV values within flea species suggests that the degree of phylogenetic relatedness among host lineages utilized by a flea may be considered as a true attribute of flea species that was shaped by natural selection (Krasnov and Poulin, 2010). In some fleas, this set may be composed of closely related hosts (high values of PSC and/or PSV), while in other species, the fleas exploit hosts belonging to different lineages (low values of PSC and/or PSV). Furthermore, left-skewed frequency distribution of PSC values (Fig. 1) suggests the host spectra of the majority of flea species include distantly related hosts. However, frequency distribution of the PSV values is more symmetric (Fig. 1). PSC and PSV capture somewhat different facets of phylogenetic structure with PSC focusing on a shallow phylogenetic level (taking into account close relative) and PSV focusing on a deep phylogenetic level (taking into account all species) (Helmus *et al.* 2007). Frequency distributions of PSC and PSV values showed thus that the host spectra of the majority of fleas were characterized by low level of relatedness of close relatives (PSC) and intermediate level of overall relatedness (PSV). The difference in frequency

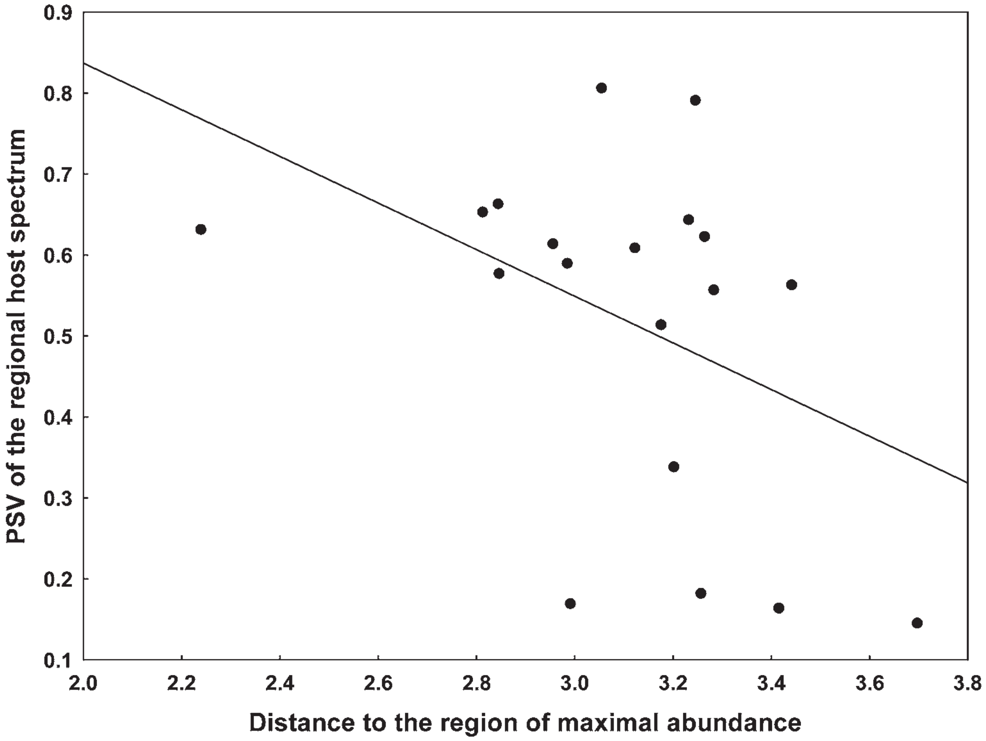

Fig. 3. Relationships between the phylogenetic structure of the regional host spectra (measured as PSV) of *Amalaraeus penicilliger* and distance to the region where it attains the highest abundance.

distribution of PSC and PSV of host spectra indicates that a host spectrum of a flea species at different phylogenetic levels was shaped by different processes (Villalobos *et al*. 2013). These processes remain to be studied.

Among 86 flea species studied by Krasnov *et al*. (2004*a*), about 30% were found to use a subset of host species taxonomically different from the random subset taken from the regional host species pool. In this study, the lack of association between the phylogenetic structure of the regional host spectrum and phylogenetic structure of the available host pool was found in roughly the same proportion in all species. This suggests that local host availability influences the realized degree of phylogenetic host specificity for the majority, albeit not all flea species. This can partly explain why the distribution of the degree of specialization in fleas is much less right-skewed than in other parasite taxa (Poulin *et al*. 2006).

The effect of the phylogenetic structure of the regional host pool and the phylogenetic structure of the host spectrum of a flea population advocates the possible substitutability of resources (i.e. hosts) across locations as one of the main mechanisms underlying spatial variation of resource specialization in general and host specificity in particular (Hughes, 2000). This may be especially true for consumers that utilize a resource provided by numerous sources. Indeed, fleas are non-specialized omnivores as larvae and specialized haematophages as adults, but both resources (organic matter in burrows for larvae and blood of a host for adults) are shared by a variety of host species. Moreover, although the reproductive performance of fleas depends heavily on the identity of a host species they exploit, fleas are able to produce offspring even when feeding on non-preferable hosts (Khokhlova *et al*. 2012). As a result, fleas may track not a host per se but rather a resource provided by a host, so that they may expand or shift their geographic ranges to geographic areas where the resource (e.g. blood) is present, but where its ‘original source’ (that is, the original host species) does not occur. In a broader context, this phenomenon is described as ‘ecological fitting’ (Janzen, 1985; Brooks *et al*. 2006). In some cases, this new host may be close phylogenetically to the original host, while in other cases the original and the new host may be related only distantly. For example, *Ceratophyllus ciliatus* changes its preferred hosts from south to north along the northwest Pacific coast of North America but all these hosts belong to the same phylogenetic lineage (sciurids: *Tamias townsendii*, *Tamiasciurus douglasii*, *Tamiasciurus hudsonicus* (Krasnov, 2008)). Across the largest part of its geographical range, the principal host of a Palaearctic flea *Amphipsylla kuznetzovi* is a vole *Microtus gregalis*, while this host is substituted by *Chionomys* voles in the Caucasus (Shenbrot *et al*. 2007). In contrast, *Hoplopsyllus anomalus* is a flea distributed in the western USA and is normally associated with sciurids across the largest part of its geographical range. However, in the southern part of San Joaquin Valley of California, the heteromyid kangaroo rat, *Dipodomys ingens*, was found to be almost exclusively infested with *H. anomalus*

Table 4. Results of meta-analytic generic point estimate of the coefficients of independent variables in the models explaining the relationships between the phylogenetic structure (measured as PSC or PSV) of the regional host spectrum of a flea and the phylogenetic structure of the regional assemblage of host species (PSCh and PSVh, respectively), distance of the region from the region where the flea attains maximal abundance (MA) and position of the region relative to the equator (DE). PE, point estimate; SE, standard error; LL, lower limit; UL, upper limit

Dependent variable	Independent variable	PE ± S.E.	LL	UL	*Z*-value	*P*
PSC	PSCh	0·74 ± 0·15	0·44	1·04	4·82	< 0·001
	MA	− 0·005 ± 0·01	− 0·02	0·01	− 0·56	0·57
	DE	− 0·03 ± 0·05	− 0·13	0·08	− 0·49	0·62
PSV	PSVh	0·21 ± 0·06	0·08	0·34	3·24	0·001
	MA	− 0·009 ± 0·01	− 0·03	0·01	− 0·87	0·38
	DE	0·09 ± 0·24	− 0·38	0·56	0·37	0·71

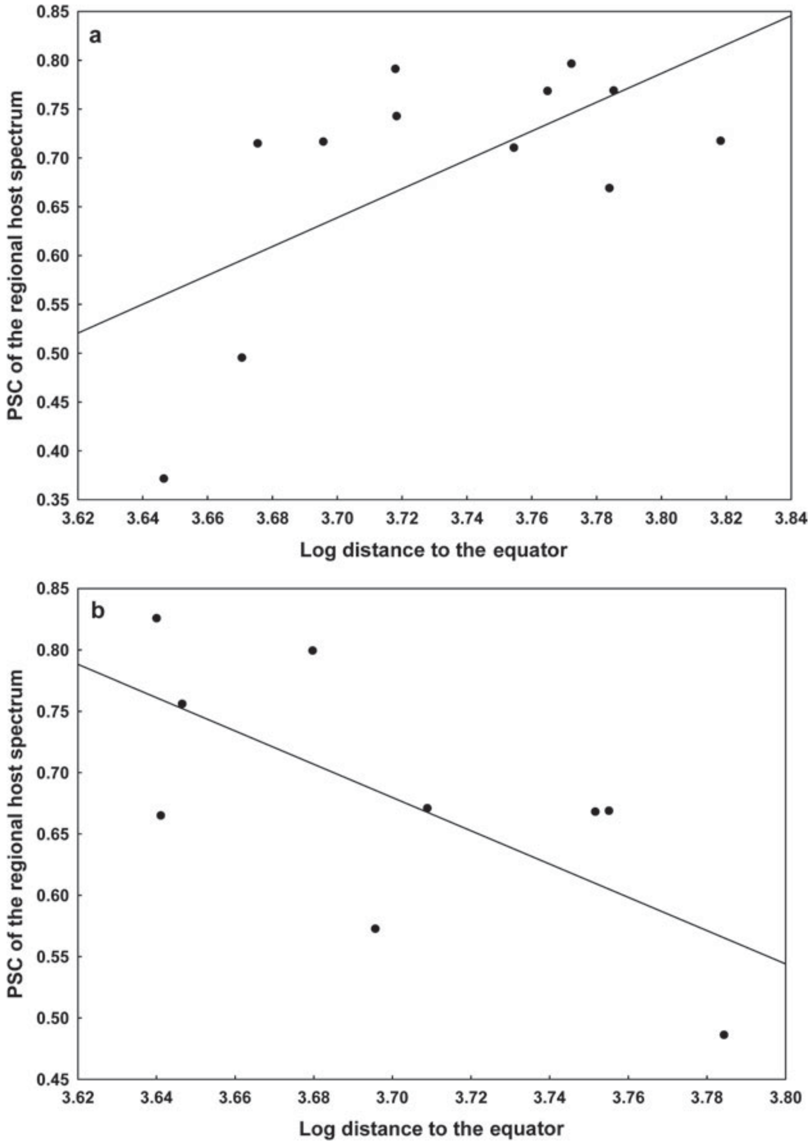

Fig. 4. Relationships between the phylogenetic structure of the regional host spectra (measured as PSC) of *Frontopsylla elata* (a) and *Nosopsyllus consimilis* (b) and distance to the equator.

(Tabor *et al*. 1993). Replacement by *D. ingens* in the niche ordinarily filled by the ground squirrels was proposed as an explanation for this host shift (Tabor *et al*. 1993).

As mentioned above, some flea species did not show any effect of phylogenetic structure of the surrounding host pool on phylogenetic structure of their host spectra. This may happen if these fleas are adapted to a particular way of blood acquisition from a particular host species or a particular set of closely related host species (sharing morphological, physiological and/or behavioural traits). Indeed, although all hosts provide blood for fleas, the pattern of acquisition of this resource may differ substantially between host species depending on their morphological (e.g. skin thickness, hair density), physiological (e.g. pattern of immune response) and/or behavioural (e.g. capability of self-grooming) characters. This is often reflected in strong links between skin morphology, hair structure and/or grooming behaviour of a host, on the one hand, and morphology of mouthparts, pattern of sclerotized structures (bristles and helmets) and/or behaviour (preference for the least accessible for grooming areas of a host's body) of a flea, on the other hand (see review in Krasnov, 2008). In addition, nesting habits of hosts (e.g. communal *vs* solitary nesting) may affect the attacking behaviour of a flea with some fleas being able to survive only on communally nested hosts (Krasnov *et al*. 2002*a*). Microclimate of hosts' shelters (e.g. difference between burrows *vs* aboveground nests) may also be a limiting factor for exploitation of a particular host species by some fleas because of narrow environmental preferences of both imago and preimaginal stages (e.g. Krasnov *et al*. 2002*b*). We recognize that the above statements require solid justification or, at least, examples. However, there is still a lack of detailed knowledge on specific adaptations to parasitism on a given host for most flea species.

From an evolutionary perspective, dependence of phylogenetic structure of the host spectrum on that of the entire host pool may be associated with some advantages of exploitation of multiple hosts. First, parasites that add host species to their repertoire reduce their dependence on a given host and, thus, decrease their chances of extinction (Futuyma and Moreno, 1988). Second, exploitation of a host related distantly to the usual host species may provide a parasite with an immediate fitness benefit because this host may not possess defences against this parasite (Krasnov *et al*. 2007; Khokhlova *et al*. 2012). Although in fleas, as in other parasites, the abundance achieved on new or secondary hosts is lower than that on the main host with the difference being proportional to the taxonomic or phylogenetic distance between the secondary hosts and the main host (Krasnov *et al*. 2004*b*; Poulin, 2005; Khokhlova *et al*. 2012), this may not hold for hosts very distant from the main host (Khokhlova *et al*. 2012).

This study emphasized the necessity to deconstruct host specificity into structural and phylogenetic components for better understanding of forces shaping resource specialization in parasites (Poulin *et al*. 2011). For example, the structural and phylogenetic composition of host specificity in fleas demonstrated contrasting patterns of their association with structural and phylogenetic composition of the available host assemblages, respectively, with no association in the former (Krasnov *et al*. 2004*a*) and a positive association in the latter (this study). In addition, the use of true phylogenetic information instead of simplified taxonomic classification for estimation of the phylogenetic component of host specificity should be encouraged. This may allow the identification of trends that, otherwise, might be obscured. Admittedly, this was not the case for the Palaearctic fleas parasitic on mammals. Indeed, proportions of variation in the phylogenetic component of host specificity accounted for by differences between flea species were similar for host specificity measured as taxonomic distinctness (14·4%; Krasnov *et al*. 2004*a*) and as PSV or clustering (17·8 and 16·3%, respectively) of the host spectrum. However, patterns of taxonomic and phylogenetic structures of host spectra may differ for parasites, other than fleas, and/or for hosts, other than mammals.

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