Beta-specificity: The turnover of host species in space and another way to measure host specificity

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ARTICLE INFO

ABSTRACT

Host specificity is often measured as the number of host species used by a parasite, or as their phylogenetic diversity; both of these measures ignore the larger scale component of host use by parasites. A parasite may exploit very few host species in one locality but these hosts may be substituted for completely different species elsewhere; in contrast, another parasite may exploit many host species in one locality, with the identity of these hosts remaining the same throughout the parasite's geographical range. To capture these spatial nuances of host specificity, we propose to use an index for host species turnover across localities, or beta-specificity (β_{SPF}), that is derived from studies of spatial patterns in plant and animal diversity. We apply this index to fleas parasitic on small mammals to show that: (i) it is statistically independent of traditional or "local" measures of host specificity as well as of "global" measures of host specificity, and (ii) it is also independent of the size of the geographical area studied or the sampling effort put into collecting hosts and parasites. Furthermore, the distribution of β_{SPF} values among flea species shows a significant phylogenetic signal, i.e. related flea species have more similar β_{SPF} values than expected by chance. Nevertheless, most possible combinations of either local specificity (alpha-specificity) or global (gamma-specificity) and beta-specificity are observed among flea species, suggesting that adding a spatial component to studies of host use reveals a new facet of specificity. The measure presented here provides a new perspective on host specificity on a scale relevant to studies on topics ranging from biogeography to evolution and may underlie the rate and extent of disease transmission and population dynamics.

1. Introduction

Host specificity is one of the most fundamental properties of any parasitic species. Highly host-specific parasites exploit a single host species, whereas host-opportunistic parasites use hosts belonging to several different species. Consequently, from an ecological perspective, host specificity represents a component of the breadth of a parasite's ecological niche, i.e. the one reflecting the diversity of resources it uses (Futuyma and Moreno, 1988). From an evolutionary perspective, the host specificity of a parasite is not merely a function of how many host species it can exploit, but also of the identity of these hosts and how closely related they are to each other (Poulin and Mouillot, 2003). Therefore, the species composition of a parasite's host spectrum reflects both the position and the breadth of one of the dimensions of its ecological niche within the multi-dimensional ecological space (Hutchinson, 1957).

Several methods to measure host specificity in parasites have been suggested (see Poulin, 2007 for review). Some of these methods rely on the number of host species used by a parasite or the relative abundance of the parasite in its different host species (e.g., Rohde, 1994), whereas other methods take into account the phylogenetic relatedness of a parasite's host spectrum (Caira et al., 2003; Poulin and Mouillot, 2003, 2005). Importantly, all of these methods estimate host specificity on a local scale; that is, in a particular locality or region where parasites may choose their hosts from the pool of available species. This specificity can be defined as alpha-specificity, similarly to the way species diversity is classically divided across scales into alpha (local), beta (between localities) and gamma (global) components (Whittaker, 1972; Crist and Veech, 2006).

The resource specialization of a species depends on two interrelated factors, namely local resource specialization and the extent to

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which these resources can be substituted in space, i.e. among locations (Hughes, 2000), so that the estimation of resource specialization should be scale-dependent (Devictor et al., 2010). In the case of parasites, if we are interested not only in the simple estimation of a parasite's ability to infest either a few or many host species in a particular location (alpha-specificity), but also in, for example, its potential to expand its geographic distribution and infest new host species, then host specificity should be measured at both small and large scales. The former facet of specificity has been extensively studied and quantified, while the latter has been neglected and deserves both an appropriate definition and measurement tools.

The need to estimate the host specificity of parasites at a regional scale has recently been recognized and addressed by measuring it in fleas parasitic on small mammals at local and global scales, i.e. alpha- and gamma-specificity (Krasnov et al., 2008). Adapting ideas from Fox and Morrow (1981), Gaston et al. (1997) and Hughes (2000) to parasites, it was suggested that a parasite might not just be either host-specific or host-opportunistic on both local and global scales. Instead, a parasite may be host-specific on a local scale but host-opportunistic on a global scale, or host-opportunistic locally but host-specific globally. The former would use locally few hosts that are substitutable across locations, so that it shifts hosts from location to location and has a high total number of hosts across its geographic range. The latter exploits locally many hosts that cannot be substituted from one location to the next, so the total number of hosts that it uses across its geographic range is relatively small. Krasnov et al. (2008) showed that, although the majority of flea species are either scale-invariant host specialists or scale-invariant host opportunists (alpha- and gamma-specificity positively correlated), some species, nevertheless, demonstrated scale-dependence in their degree of host specificity, being either local generalists but global specialists (low alpha-specificity but high gamma-specificity), or local specialists but global generalists (high alpha-specificity but low gamma-specificity). Krasnov et al. (2008) measured host specificity as both the number and taxonomic diversity of host species used by a parasite, but the actual identity of host species was not taken into account. Surprisingly, the beta component of specificity has not been introduced yet, although it captures the ability of parasite species to shift their host spectrum across locations. In particular, this ability may underlie the rate and extent of disease transmission and population dynamics.

Consequently, a measure of host specificity that mirrors spatial variation in host species composition is needed. In other words, the pattern of spatial variation in the species composition of the host spectrum represents another facet of host specificity that has not been considered in earlier studies.

Here we evaluated host specificity of parasites across a large spatial scale using deconstruction of the beta-diversity of host species composition into two components, namely "pure" spatial turnover and dissimilarity due to nestedness (Baselga, 2010). The concept of beta-diversity was originally developed to estimate variation in the species composition of assemblages of free-living organisms (Whittaker, 1960). Spatial turnover is the replacement of some species by others from locality to locality (e.g., Harrison et al., 1992), whereas nestedness represents a pattern in which species comprising depauperate assemblages constitute non-random subsets of the species occurring in successively richer assemblages (e.g., Patterson and Atmar, 1986). Recently, Baselga (2010) proposed a technique to disentangle the contributions of spatial turnover and nestedness to total beta-diversity based on the fact that these two facets are additive and antithetic (Baselga et al., 2007). We proposed to use the turnover component of beta-diversity (that is, beta-diversity free from the effect of nestedness) as a new measure of host specificity (="beta-specificity") because it reflects the "pure" ability of a parasite to shift hosts from one region

to another independently of any non-random and/or any nested pattern (Fig. 1). Indeed, nestedness tends to inflate beta-diversity (and thus beta-specificity) but this component does not tell us whether a parasite is able to shift host composition across scales, only that this parasite infests subsets of hosts that are nested within the broader host spectrum in one location. We recognize that the dissimilarity in host species composition due to nestedness is important to study spatial or temporal variation in the species composition of a parasite's host spectrum. However, a truly host-specific parasite is expected to demonstrate low turnover of host species composition whatever the degree of dissimilarity due to nestedness. Therefore, beta-specificity is an inverse indicator of the degree of host specialization across scales.

We calculated beta-specificity using fleas (Siphonaptera) parasitic on small Palaearctic mammals as a case study. In addition to presenting the new measure of host specificity, our aims were threefold. First, we tested whether the pattern of spatial variation in the composition of the host spectra of a flea species follows that of the assemblage of all available host species. This was done by comparing "the pure" turnover component of beta-diversity of the host spectra of a flea species with that of the assemblages of small mammalian hosts that are exploited by any flea species.

Second, we studied the phylogenetic dependence of beta-specificity in fleas by testing whether phylogenetically related fleas resemble one another in the degree of their beta-specificity. The pattern of resemblance among phylogenetically-related species is commonly known as "phylogenetic signal" (Blomberg and Garland, 2002; Blomberg et al., 2003). The detection and estimation of phylogenetic signals in any ecological trait (including host specificity) is important because a significant signal necessitates control for the confounding effect of phylogenetic dependence in further comparative analyses (Freckleton et al., 2002).

Third, we tested whether beta-specificity is independent of other measures of host specificity such as the number and
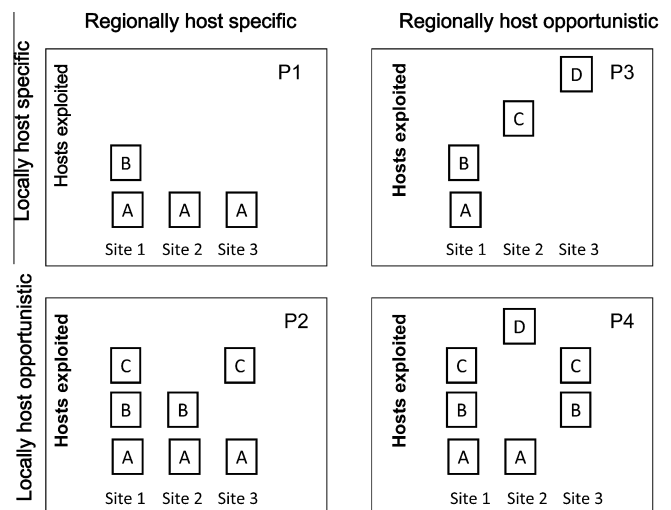

Fig. 1. Hypothetical examples involving four parasite species (P1–P4), three locations (Site 1–Site 3) and four host species (A–D). Parasite P1 is overall (that is, both locally and regionally) host-specific because it exploits few host species in each location and its host spectra in locations where it exploits fewer hosts are subsets of the host spectrum in the location where it exploits the highest number of hosts. Parasite P2 is locally host-opportunistic but regionally host-specific because it exploits many hosts in each location but, similarly to P1, its poorer local host spectra are subsets of the richest host spectrum. Parasite P3 is locally host-specific but regionally host-opportunistic because it exploits a few hosts in each location and the shifts of its host spectra among locations are random. Parasite P4 is overall a host opportunist because it exploits many hosts in each location and the shifts of its host spectra among locations are random. Note that P3 and P4 exploit the same numbers of hosts across locations.

taxonomic diversity of (i) exploited hosts averaged across locations (that is, alpha-specificity) and (ii) exploited hosts across a flea's geographic range (that is, gamma-specificity). The independence of beta-specificity from these measures would support the usefulness of this new index. In addition, we asked whether beta-specificity is sensitive to the size of a flea's geographic range and/or sampling effort (number of examined host individuals). In particular, the effect of sampling effort on the number of recorded host species is one of the main problems associated with use of host number as a measure of specificity (Poulin, 1992) as is the case with many other diversity measures (Magurran, 2004).

2. Materials and methods

2.1. Flea species and host species

We extracted data from our database compiled from published surveys of fleas parasitic on small mammals (Soricomorpha, Erinaceomorpha, Rodentia and Lagomorpha) across the Palaearctic (60 surveys in 52 regions). These surveys reported the number of fleas of each individual species found on a given number of individuals of each mammal species. The complete list and geographic location of surveys can be found elsewhere (Krasnov et al., 2010a). We selected flea species that were recorded in at least 10 regions and host species from which at least three individuals of a given flea species were collected. This resulted in datasets of regional host species composition for 21 flea species.

2.2. Beta-specificity

To estimate beta-specificity, we used measures of beta-diversity and its components of spatial turnover and nestedness derived by Baselga (2010). In this context, beta-diversity is considered as a measure of dissimilarity between sites (see also Koleff et al., 2003). The total amount of beta-diversity may be estimated using a multiple-site metric (β_{SOR}) based on the Sørensen dissimilarity measure (Baselga et al., 2007; Baselga, 2010). This measure encompasses both spatial turnover and differences in species richness (Fig. 1; Koleff et al. 2003). It can be calculated using the equation: (1).

$$\beta_{SOR} = \frac{\left[\sum_{i<j} \min(b_{i,j}, b_{j,i})\right] + \left[\sum_{i<j} \max(b_{i,j}, b_{j,i})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j} \min(b_{i,j}, b_{j,i})\right] + \left[\sum_{i<j} \max(b_{i,j}, b_{j,i})\right]} \quad (1)$$

where S_i is the total number of species in site i, S_T is the number of species in all sites and $b_{i,j}$ and $b_{j,i}$ are the numbers of species occurring in site i only and site j only, respectively, when compared by pairs (Baselga, 2010). The total amount of beta-diversity can be further partitioned into two components, spatial turnover (β_{SIM}) and dissimilarity due to nestedness (β_{NES}). The measure of multi-site spatial turnover free from the influence of richness (β_{SIM}) is based on the Simpson dissimilarity index (Lennon et al., 2001; Baselga et al., 2007; Baselga, 2010) and involves construction of multiple-site equivalents of the matching components of indices (that is, species shared and not shared by assemblages; see Baselga et al., 2007 for details). The equation to calculate multiple-site spatial turnover is (2)

$$\beta_{SIM} = \frac{\left[\sum_{i<j} \min(b_{i,j}, b_{j,i})\right]}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j} \min(b_{i,j}, b_{j,i})\right]} \quad (2)$$

where variables are the same as in equation (1) (Baselga 2010). If assemblages are composed of equal numbers of species, then their dissimilarity is due to "pure" turnover because nestedness is not possible. Consequently, the total amount of beta-diversity will be equal to the amount of turnover ($\beta_{SOR} = \beta_{SIM}$). The difference between β_{SOR} and β_{SIM} is thus dissimilarity due to nestedness or $\beta_{NES} = \beta_{SOR} - \beta_{SIM}$ (Baselga, 2010). A detailed description of the behaviors of these indices under various simulated scenarios can be found in Baselga (2010).

For each flea species, we constructed presence-absence matrices in which rows were regions, while columns were either (i) hosts that this flea exploited in a region or (ii) hosts that were exploited by any flea species in a region. Thus, for each flea, we obtained two matrices that reflected (i) variation in species composition of its host spectrum (realized host spectrum) and (ii) variation in species composition of all hosts that are suitable for fleas (potential host spectrum). Then, we calculated β_{SOR} and β_{SIM} using the function "beta-multi.R" for the R software environment (R Development Core Team, 2009) compiled by Baselga (2010). Following Baselga et al. (2007) and to make measures computed for fleas occurring in different numbers of regions comparable with each other, we calculated β_{SOR} and β_{SIM} for fleas occurring in more than 10 regions using resampling procedures. For each of these fleas, we took 100 random samples of 10 host spectra and averaged metrics across these samples. Initially, we estimated beta-specificity (β_{SPF}) for each flea as the spatial turnover component of beta-diversity of hosts used by this flea across locations. In addition, for each flea species, we estimated the spatial turnover component of beta-diversity of all hosts used by any flea species across locations where this flea occurred (β_{SIM}). However, β_{SPF} might be not only an intrinsic property of a parasite, but may also be affected by the beta-diversity of the available hosts. This was not the case in our dataset (see Results), but it may well be the case for other datasets. If β_{SPF} of parasites and β_{SIM} of available hosts are related, then positive and negative deviations from the regression line between these two metrics would indicate turnover either in excess of or lower than that expected due to the structure of host communities. Thus, these deviations would reflect properties of the parasites themselves that are free from the effects of host communities. Consequently, we plotted β_{SPF} against β_{SIM} and visually identified a single species that obviously accounted for the lack of the relationship between these two measures (see Results). We removed this species from the dataset. Then, we substituted original values of β_{SPF} with their residual deviations from the regression on β_{SIM} (β_{SPFR}) and re-ran all analyses.

2.3. Local host specificity, global host specificity and geographic range

For each of the 21 flea species, we calculated two measures of alpha- (that is, local) and two measures of gamma- (that is, global) host specificity: (i) the number of mammalian species on which the flea species was found, and (ii) an index of specificity, S_{TD} (Poulin and Mouillot, 2003). At a local scale, we took into account the number and taxonomic diversity of all host species exploited by a given flea in a geographic region, while at the global scale we included all host species exploited by that flea across its entire geographic range. The index S_{TD} is based on the taxonomic or phylogenetic affinities of the host species and measures the average taxonomic distinctness of all host species used by a parasite species. Thus, this measure emphasises the phylogenetic diversity of a flea's host spectrum, providing a different perspective on host specificity. The greater the taxonomic distinctness between host species, the higher the value of S_{TD}: thus this index is inversely proportional to specificity. Details of calculation of S_{TD} for fleas are published elsewhere (Krasnov et al., 2004a). For each flea species, we calculated S_{TD} (i) within each region for all host species and then averaged the resulting values across regions, and (ii) for all

host species across all regions. Obviously, all these measures are inverse indicators of host specificity.

For each flea species, we calculated the size of its geographic range. We estimated the size of the geographic range from a flea's distribution map based on published maps (e.g., Traub et al., 1983) and/or various literature sources and museum records using ArcView 9.2 software and a combination of the minimal convex polygon method (MCP; Fortin et al., 2005) and the GARP algorithm (Stockwell and Peters, 1999) (see details in Krasnov et al., 2008). Geographic range size was log-transformed prior to further analyses.

Across flea species, the mean number of host species per region and the total number of host species on which a flea was recorded did not correlate with the mean number of host individuals examined in a region or with the total number of hosts examined in all regions (Pearson's product-moment correlation $r = -0.30$ and $r = -0.06$, respectively, $P > 0.20$ for both). In contrast, within-region S_{TD} and S_{TD} for the entire host assemblage were positively correlated with the number of host species used by flea species within a region and across regions, respectively (Pearson's product-moment correlations $r = 0.81$ and 0.62, $P < 0.001$), indicating that this measure was influenced by the number of host species in a flea's repertoire (see Poulin and Mouillot, 2003). In subsequent analyses, values of S_{TD} were corrected for the number of host species exploited by a flea in a region or across regions by substitution of the original values with their residual deviations from the linear regressions of these variables in log–log space. Values of host specificity in terms of number of host species exploited were log-transformed prior to analyses.

2.4. Data analyses

Distributions of the variables β_{SIM}, β_{SPF} and β_{SPFR} did not significantly deviate from normality (Kolmogorov–Smirnov tests, $P > 0.20$ for all).

We used Pagel (1999) λ to detect phylogenetic signal in β_{SPF} and β_{SPFR}. This method involves maximum likelihood optimization to assess the degree to which a trait exhibits a phylogenetic signal. The measure λ is a multiplier of the off-diagonal elements of the variance/covariance matrix describing tree topology and branch lengths. It ranges from zero to 1 and thus gradually eliminates phylogenetic structure. A zero value indicates that the evolution of the trait is independent of phylogeny, while $\lambda = 1$ indicates a Brownian motion model of evolution of the trait on a given phylogenetic tree. Under this model, evolutionary changes along branches are expected to have zero values. Their distribution is normal with a variance proportional to branch length (Felsenstein, 1985). We calculated λ using the package "geiger" implemented in the R software environment (Harmon et al., 2008). We tested the significance of any phylogenetic signal by comparison of log-likelihood obtained from the observed tree topology and log-likelihood obtained from a tree without phylogenetic signal (that is, when $\lambda = 0$ or a star phylogeny) using log-likelihood ratio tests. The only available molecular phylogeny of fleas (Whiting et al., 2008) was used as a source of topological relationships among fleas with branch length arbitrarily set to an equal length of 1.

Significant phylogenetic signal in β_{SPF} and β_{SPFR} (see Results) necessitated controlling for the confounding effects of phylogeny in subsequent analyses. We tested for the relationships across flea species between β_{SPF} or β_{SPFR} and mean local (alpha-) host specificity (number of host species and S_{TD}), global (gamma-) host specificity (number of host species and S_{TD}), geographic range size, and sampling effort (number of host individuals examined). Among several available methods that allow controlling for phylogeny, the method of independent contrasts (Felsenstein, 1985) and Generalized Least-Squares (GLS) analysis (Martins and Hansen, 1997; Pagel, 1997, 1999; Freckleton et al., 2002; Gage and Freckleton, 2003) are the most widely used. We applied both of these methods

and found that they produced similar results. Consequently, we present here the results of GLS only.

In brief, GLS analysis tests for the relationships between original character values rather than between contrasts. This method controls for the confounding effect of phylogeny by incorporating the phylogenetic autocorrelation of the data in the structure of errors (Martins and Hansen, 1997; Freckleton et al., 2002). The significance of the regression coefficients between the dependent variable and independent variable(s) was tested using maximum likelihood (Pagel, 1997, 1999). GLS analyses were carried out using the package "ape" (Paradis et al., 2004) implemented in R.

We re-ran the analyses after obtaining values of β_{SPFR} via GLS rather than conventional statistics. These analyses produced the same results, so we do not report them here. P-values < 0.05 were considered significant.

3. Results

Among the 21 flea species, values of total amount of beta-diversity for the host spectra and communities of available host ranged from 0.79 to 0.92 and from 0.76 to 0.86, respectively (Table 1). The spatial turnover component of the total amount of beta-diversity in the host spectra (that is, β_{SPF}) varied from 0.46 in *Mesopsylla hebes* to 0.87 in *Neopsylla setosa* and *Amphipsylla primaris*, while spatial turnover component of beta-diversity of available hosts (that is, β_{SIM}) varied from 0.59 in *Ceratophyllus sciurorum* to 0.82 in *A. primaris, A. rossica* and *N. pleskei*; the rest being due to nestedness.

Across fleas, β_{SPF} did not correlate with β_{SIM} (conventional statistics: Pearson product-moment correlation 0.36, $P > 0.05$; GLS: coefficient = 0.45 ± 0.37, $\lambda = 0.66$, $t = 1.23$, $P > 0.20$) (Fig. 2A). However, this lack of correlation was obviously due to *M. hebes* (Fig. 2B). When this flea was omitted from the analyses, correlation between β_{SPF} and β_{SIM} became significant (conventional statistics: Pearson product-moment correlation 0.51, $P < 0.05$; GLS: coefficient = 0.80 ± 0.29, $\lambda = -0.16$, $t = 2.76$, $P < 0.05$).

In both β_{SPF} and β_{SPFR}, a significant phylogenetic signal was detected ($\lambda = 0.90$, log-likelihood ratio = −3.96 and $\lambda = 0.79$, log-likelihood ratio = −3.88, respectively, $P < 0.05$), i.e. values from related flea species tend to be more similar than expected by chance. GLS analyses detected no relationship between β_{SPF} or β_{SPFR} and either

Table 1
Total amount of beta-diversity (β_{SOR}) and its spatial turnover component for the host spectra of 21 flea species (β_{SPF}) and small mammal communities co-occurring with these fleas (β_{SIM}).

Flea species	Flea host spectrum		Small mammal community	
	β_{SOR}	β_{SPF}	β_{SOR}	β_{SIM}
Amalaraeus penicilliger	0.88	0.78	0.85	0.79
Amphipsylla primaris	0.92	0.87	0.86	0.82
Amphipsylla rossica	0.88	0.78	0.85	0.82
Catallagia dacenkoi	0.87	0.78	0.79	0.64
Ceratophyllus indages	0.8	0.57	0.81	0.7
Ceratophyllus sciurorum	0.87	0.71	0.76	0.59
Citellophilus tesquorum	0.91	0.84	0.85	0.8
Corrodopsylla birulai	0.83	0.64	0.80	0.72
Ctenophthalmus assimilis	0.81	0.7	0.79	0.73
Frontopsylla elata	0.9	0.84	0.85	0.8
Hystrichopsylla talpae	0.83	0.65	0.82	0.77
Megabothris calcarifer	0.87	0.8	0.80	0.69
Megabothris rectangulatus	0.83	0.69	0.82	0.75
Megabothris turbidus	0.84	0.71	0.82	0.77
Mesopsylla hebes	0.79	0.46	0.83	0.78
Neopsylla mana	0.91	0.83	0.85	0.81
Neopsylla pleskei	0.92	0.85	0.86	0.82
Neopsylla setosa	0.91	0.87	0.84	0.8
Oropsylla ilovaiskii	0.9	0.85	0.82	0.78
Oropsylla silantiewi	0.89	0.85	0.84	0.78
Palaeopsylla soricis	0.83	0.64	0.79	0.73

of the two traditional measures of host specificity at either scale, the size of a flea's geographic range, or host sampling effort. All coefficients of independent variables were non-significant (Table 2).

The distributions of species data points in bivariate space for β_{SPF} against either alpha- (the mean number of hosts exploited locally or mean local S_{TD}) or gamma-specificity (the total number of hosts exploited or total S_{TD}) are presented in Figs. 3 and 4, respectively. The respective scatterplots of β_{SPFR} showed similarities independent of scale. In terms of host number, the majority of fleas used in our study were either local specialists or local generalists with a high spatial turnover of hosts among locations, whereas only two fleas (M. hebes and C. indages) were locally host-specific with concomitantly low β_{SPF}, and no locally host-opportunistic flea was characterized by low β_{SPF} (Fig. 3A). When local host specificity was evaluated via the taxonomic diversity of host assemblages, it appeared that the majority of species data points were scattered along β_{SPF} but mainly in the right portion of the bivariate space. This means that fleas that exploited local host spectra of high taxonomic diversity were characterized by either a high or low turnover of these hosts from one locality to another (Fig. 3B). In addition, two fleas that predominantly used taxonomically-related hosts were characterized by either high (Oropsylla ilovaiskii) or low (M. hebes) β_{SPF}. Fleas with relatively large or taxonomically diverse global host spectra (e.g., N. mana and Ctenophthalmus assimilis, respectively) were mainly characterized by high spatial host turnover (Fig. 4). In contrast, fleas with global host spectra of a small size (e.g., Oropsylla silantiewi) and/ or low taxonomic diversity (e.g., N. setosa) demonstrated twofold variation in their degree of spatial host turnover (e.g., O. silantiewi versus M. hebes) (Fig. 4).
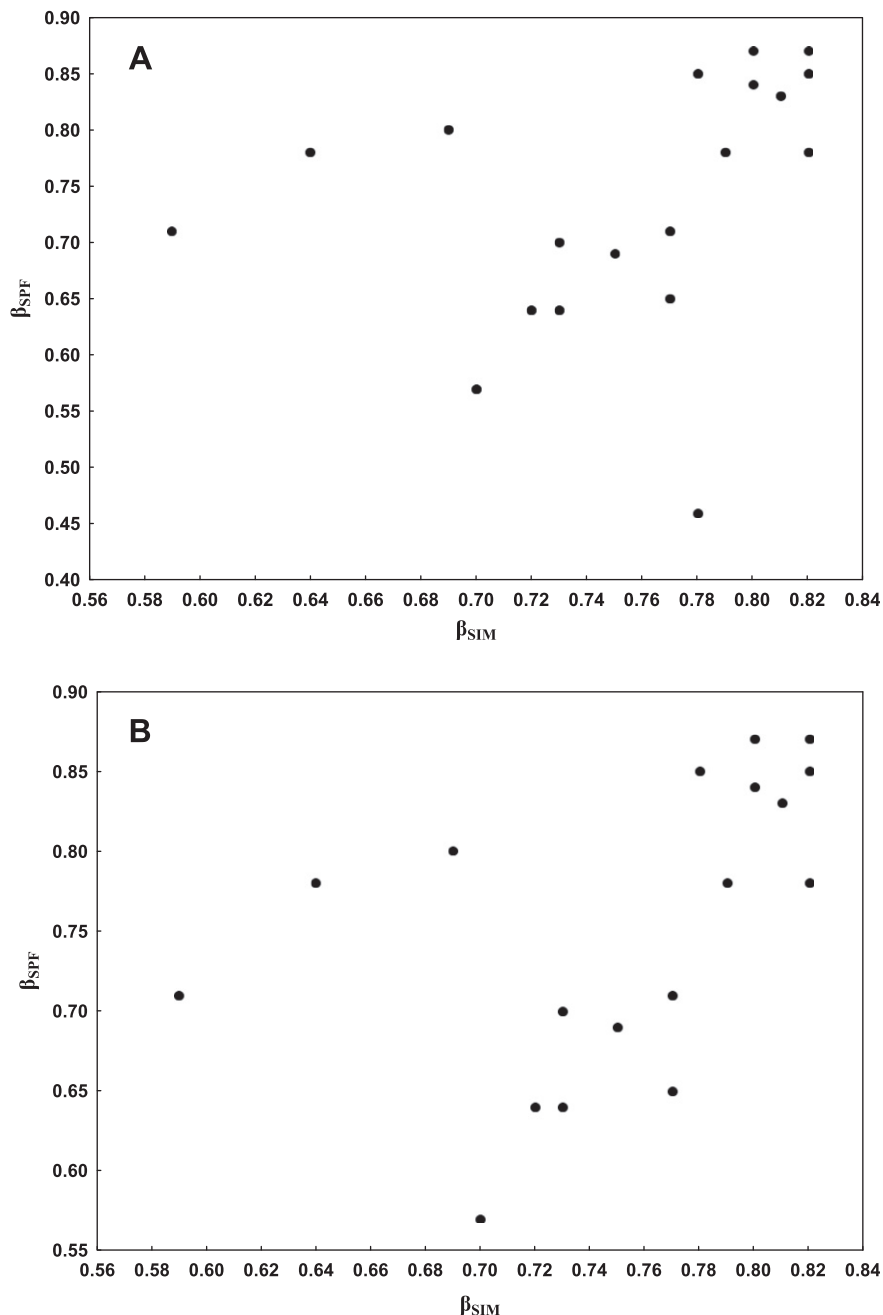

Fig. 2. Relationships between spatial turnover component of beta-diversity of flea host spectra (β_{SPF}) and spatial turnover component of beta-diversity of small mammal communities co-occurring with these fleas (β_{SIM}) before (A) and after (B) removal of Mesopsylla hebes.

Table 2
Summary of generalized least-squares of the relationships between β_{SPF} or β_{SPFR} and alpha-host specificity [α-NHS (number of host species) and α-S_{TD}], gamma-host specificity [γ-NHS (number of host species) and γ-S_{TD}], geographic range size (GRS), and sampling effort (SEF; number of host individuals examined).

Dependent variable	Independent variable	Coefficient ± S.E.	t	P
β_{SPF}	α-NHS	−0.34 ± 0.30	−1.13	0.27
	α-S_{TD}	0.48 ± 0.38	1.27	0.22
	γ-NHS	0.14 ± 0.25	0.58	0.57
	γ-S_{TD}	0.28 ± 0.20	1.44	0.17
	GRS	−0.17 ± 0.12	−1.44	0.17
	SEF	−0.02 ± 0.06	−0.25	0.80
β_{SPFR}	α-NHS	−0.39 ± 0.25	−1.60	0.15
	α-S_{TD}	0.09 ± 0.25	0.36	0.72
	γ-NHS	0.03 ± 0.18	0.18	0.85
	γ-S_{TD}	0.21 ± 0.14	0.19	0.85
	GRS	−0.12 ± 0.07	−1.99	0.08
	SEF	−0.11 ± 0.06	−2.00	0.09

S.E., standard error.

4. Discussion

A parasite may differ in the degree of its host specificity considered at different scales. Indeed, a hypothetical parasite may be (i) a local and regional specialist, (ii) a local and regional generalist, (iii) a local specialist but regional generalist, and (iv) a local generalist but regional specialist (Gaston et al., 1997; Krasnov et al., 2008). Furthermore, the relationships between the local and regional specificity of a parasite may determine the degree of its gamma-specificity, although not always in a straightforward way (see below). For example, a local and regional specialist uses a few hosts and/or phylogenetically closely-related hosts locally (high alpha-specificity) whose identities or taxonomic affinities do not change from locality to locality (high beta-specificity), so that the number and/or taxonomic diversity of all host species used by this parasite across its entire geographic range are low (high gamma-specificity) and it can be classified as an all-around specialist. A local and regional generalist uses many hosts and/or phylogenetically-distant hosts locally (low alpha-specificity), while the species composition of its host spectra varies substantially among localities (low beta-specificity), so its gamma-specificity is obviously low and it can be categorized as an all-round generalist. Similarly, a local specialist/regional generalist is expected to demonstrate high alpha-specificity and low beta-specificity, whereas a local generalist/regional specialist is characterized by low alpha-specificity and high beta-specificity. In both these cases, gamma-specificity is expected to be moderate. The comparison of alpha-, beta- and gamma-specificity of fleas used in our study has demonstrated that the majority of combinations of these traits are observed in nature, albeit with different frequencies of occurrence.

Given that all metrics of host specificity presented here are inverse indicators of host specificity, the scatter of species points in Fig. 3 suggest that all-around generalists (low alpha- and low beta-specificity; upper right quadrant of the bivariate space) and local specialists/regional generalists (high alpha-specificity and low beta-specificity; upper left quadrant) were equally represented. For example, *C. assimilis* not only exploited many hosts locally (on average, 9.7 species belonging to different higher taxa; e.g., in the Altai mountains these hosts belonged to two orders and four families), but the species composition of its local host spectra varied greatly among regions, resulting in a high (0.83) spatial turnover of host species. As a result, the total number of hosts used by this species was high (Fig. 4A), that is, it demonstrated low gamma-specificity. In contrast, *O. ilovaiskii* exploited locally, on average, 2.0 host species only. However, across locations

these hosts belonged to three families and five genera, so that the spatial turnover of host species reached 0.85. High spatial turnover of only a few hosts resulted in moderate values of gamma-specificity for this flea, especially in terms of S_{TD} (Fig. 4B). This example contradicts the earlier view that the colonization abilities of specialist taxa, capable of using only a narrow range of resources, are limited (Krasnov et al., 2008).

Two species from our dataset, namely *M. hebes* and *C. indages*, demonstrated low spatial turnover of hosts (0.46 and 0.57, respectively). *M. hebes* behaved as an all-round specialist (high alpha-specificity, high beta-specificity and high gamma-specificity) independently of whether its alpha- and gamma-specificity were measured as the number of host species or their taxonomic diversity (Figs. 3 and 4). Similarly to *O. ilovaiskii*, the local number of hosts exploited by *M. hebes* was 2.0. However, it was recorded on jerboas in all 10 regions where it occurred, on a hamster or a ground squirrel in one region, and on a gerbil in two regions. In contrast, the assignation of *C. indages* to either all-round specialists or local generalists/ regional specialists depended on whether the size or the taxonomic diversity of the local host spectra was considered. On the one hand, it exploited 2.6 hosts locally on average (high alpha-specificity; Fig. 3A) but, on the other hand, within any location these hosts often belonged to different subfamilies and sometimes even to different orders (low alpha-specificity; Fig. 3B). However, the degree of its beta- and gamma-specificity was low (Fig. 4). The example of *C. indages* suggests two important points, namely (i) assignation of a parasite to local/regional/global specialists or generalists is not always straightforward but rather context-dependent, and (ii) the facet of host specificity captured by beta-specificity differs from those obtained from other measures of host specificity.

As defined in this paper, beta-specificity is a derivative of one of the components of beta-diversity. In general, beta-diversity is a measure of the difference in species composition between sites (Koleff et al., 2003) with its turnover component being a consequence of processes such as environmental sorting or spatial and historical constraints (Nekola and White, 1999; Qian et al., 2005; Baselga, 2010) that result in structured assemblages of species along gradients (Qian et al., 2005). The biological interpretation of beta-specificity is thus that it is the difference between the species composition of local host spectra due to stochastic losses and acquisitions of hosts. The simplest scenario for the loss of one host and the acquisition of another host is the dispersal of a parasite to an area where (i) the original host is absent or becomes extinct shortly after dispersal and (ii) the parasite encounters a local host suitable for exploitation. This new host may not necessarily be related to the original host. This scenario can be considered as an instance of ecological fitting; that is, a situation in which a parasite mainly tracks the resource provided by a host rather than the host per se (Brooks et al., 2006). In addition, ecological fitting may explain incongruities between parasite and host phylogenies (Brooks et al., 2006). High values of β_{SPF} in the majority of fleas coupled with high values of taxonomic diversity of their local host spectra suggest that ecological fitting may indeed be a reason behind the spatial turnover of hosts among localities. Furthermore, the value of beta-specificity may indicate whether ecological fitting has influenced a given flea species and what is the dispersal ability of this species. The latter can be important from a medical or veterinary point of view as fleas are vectors of many diseases (see Krasnov, 2008 for review). The main pre-requisite of ecological fitting, that is, tracking by a parasite of the resource rather than the host per se, applies well to fleas (see Krasnov et al., 2010a for detailed explanation). Moreover, in the only two studies where the phylogeny of fleas and that of their hosts were compared, they were found incongruent and host switches seemed to predominate during the history of flea-host associations (Krasnov and Shenbrot, 2002; Lu and Wu, 2005).
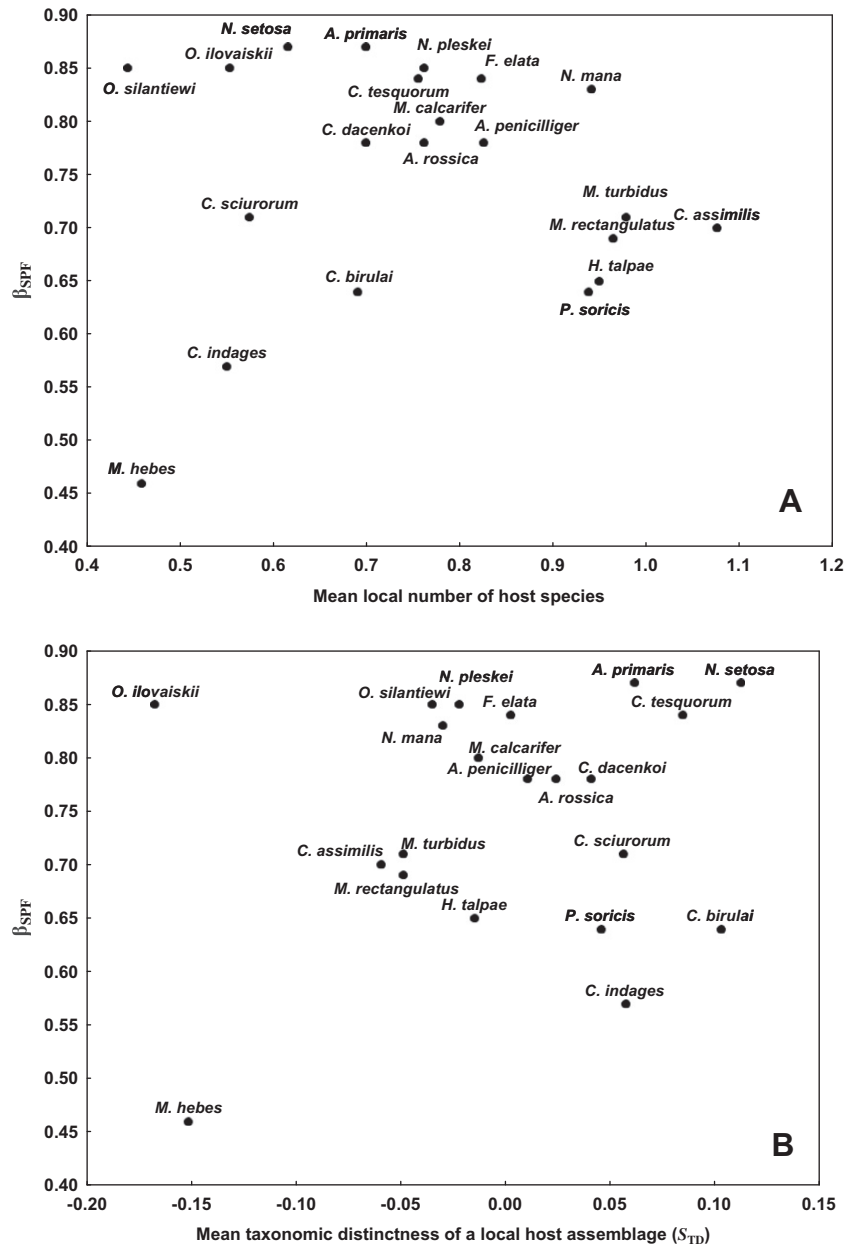
Fig. 3. Scatterplots of beta-specificity calculated as β_{SPF} (see Section 2.2) against log mean local number of exploited hosts (A) or their taxonomic diversity controlled for the size of the host spectrum (B) across 21 flea species.

The strong phylogenetic signal detected in beta-specificity supports earlier results showing that the resemblance of closely-related species with respect to their ecological traits is more easily detectable on a large than a small scale (Silvertown et al., 2006; Krasnov et al., 2010b). The phylogenetic dependence of beta-specificity in flea species may arise if (i) there are some life history features that place limits on the ability of fleas to use either many or a few hosts which are either closely or distantly related, and (ii) these features are subjected to natural selection. The former is supported by the fact that host specificity in fleas (in terms of both number of hosts exploited and their taxonomic diversity) varies within some species-specific boundaries (Krasnov et al., 2004b). The latter appears likely from the similarity among closely-related flea species in the number of hosts they exploit (Mouillot et al., 2006), suggesting that these features might be inherited from common ancestors.

Beta-specificity not only represents a new aspect of host specificity, it is also characterized by a number of useful features. First, this measure is not correlated with traditional measures of host specificity but instead captures an additional facet of a parasite's ecological niche that reflects niche position rather than niche breadth. Second, beta-specificity appeared to be independent from sampling effort (that is, the number of host individuals examined). This is important because data from different regions usually come from different studies with unequal sampling effort, and analyses involving beta-specificity should not require control for uneven sampling. Third, the calculation of beta-specificity relies on presence–absence data which are not only readily available, but also often more appropriate for analyses of parasite ecology because (i) measurements of occurrences are generally more reliable than measurements of abundances (Gotelli and McCabe, 2002; Gotelli and Rohde, 2002) and (ii) presence/absence data are often the only data available from many localities and many parasites. Otherwise, if it is essential to include species abundances in the calculation of beta-specificity, we suggest the use of appropriate tools based on the Shannon entropy (Jost, 2007) or on Jaccard-type or Sørensen-type indices (Chao et al., 2005). Such indices equal zero when
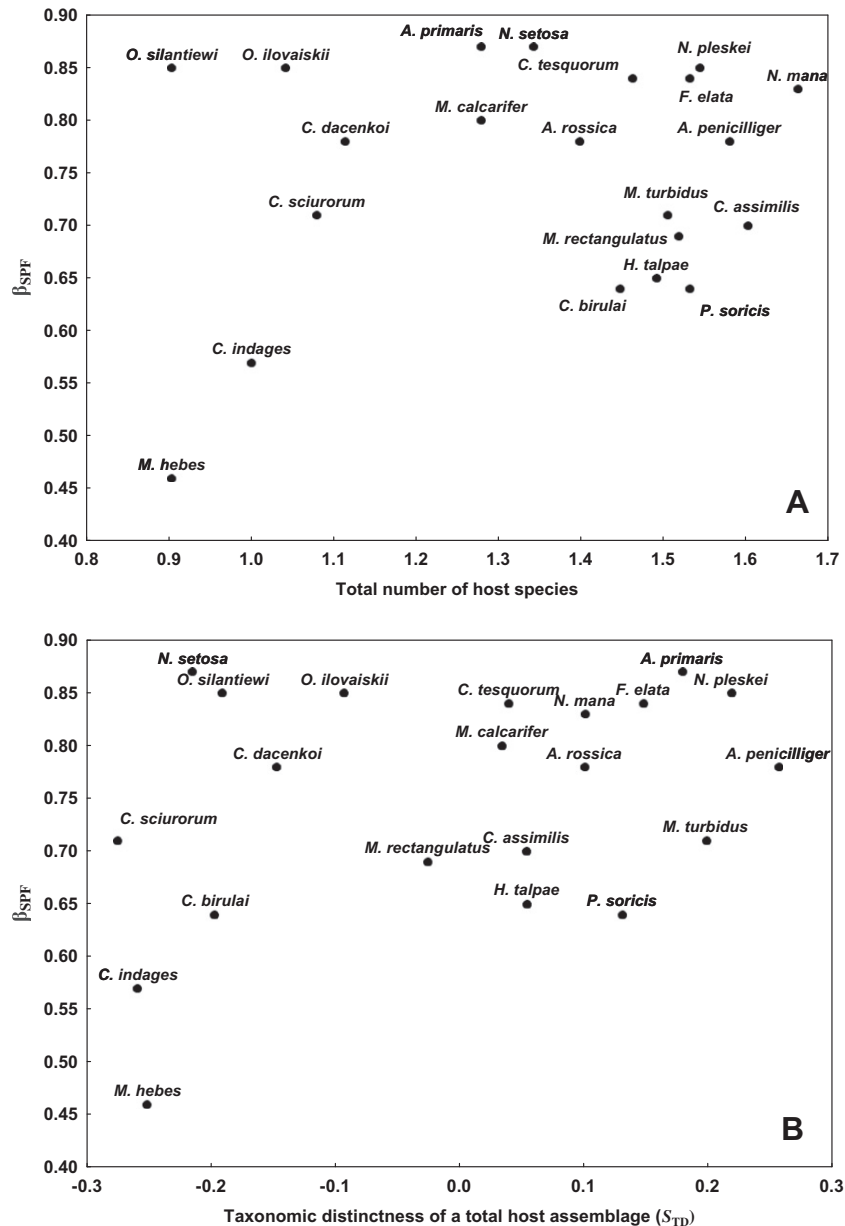
Fig. 4. Scatterplots of beta-specificity calculated as β_{SPF} (see Section 2.2) against log total number of exploited hosts across all regions (A) or their taxonomic diversity controlled for the size of the host spectrum (B) across 21 flea species.

communities share the same species and when species have the same relative abundances in all communities. In summary, beta-specificity provides a new perspective of host use on a scale relevant to studies on topics ranging from biogeography to evolution. However, in our study we measured beta-specificity for only one type of parasite-host association in only one, albeit large, geographic region. The behavior and applicability of this measure should be further tested with other parasite and host taxa in other geographic realms.

Acknowledgements

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