

Species and site contributions to β -diversity in fleas parasitic on the Palearctic small mammals: ecology, geography and host species composition matter the most

Research Article

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Abstract

The β -diversity of fleas parasitic on small mammals in 45 regions of the Palearctic was partitioned into species [species contributions to β -diversity (SCBD)] and site (= assemblage) contributions [local contributions to β -diversity (LCBD)]. We asked what are the factors affecting SCBD and LCBD and tested whether (a) variation in ecological, morphological, life history and geographic traits of fleas can predict SCBD and (b) variation in flea and host community metrics, off-host environmental factors, host species composition of flea assemblages can predict LCBD. We used spatial variables to describe geographic distribution of flea assemblages with various LCBD values. SCBD significantly increased with an increase in abundance and a decrease in phylogenetic host specificity of a flea as well as with size and latitude of its geographic range, but was not associated with any morphological/life history trait. LCBD of flea assemblages did not depend on either flea or host species richness or environmental predictors, but was significantly affected by compositional uniqueness (= LCBD) of regional host assemblages and variables describing their species composition. In addition, variation in LCBD was also explained by broad-to-moderate-scale spatial variables. We conclude that SCBD of fleas could be predicted *via* their ecological and geographic traits, whereas LCBD of their assemblages could be predicted *via* host composition.

Introduction

One of the central aims of ecology is to understand patterns of biological diversity and processes behind these patterns. It is universally accepted that biological diversity is divided across scales into α diversity (diversity within a site), β -diversity (diversity among localities or time-points) and γ diversity (total diversity within a landscape). The concepts of α and γ diversity can be easily grasped, whereas the concept of β -diversity is more complicated. One of the reasons for this is that spatial and/or temporal β -diversity of a biological community represents a combination of different components. For example, Pavoine and Dolédec (2005) and Pavoine *et al.* (2016) argued that real biological units (e.g. communities) exist in a complex nested hierarchy of spaces such as patches within habitats, habitats within landscapes, landscapes within geographic regions, so that spatial β -diversity can be partitioned into (a) dissimilarity of communities among units of a finer scale within units of a broader scale and (b) dissimilarity of communities among units of a broader scale. Looking at β -diversity from another angle, Baselga (2010) proposed to deconstruct β -diversity into two dissimilarity components, namely dissimilarity due to 'pure' spatial turnover and dissimilarity due to nestedness. Recently, Legendre and De Cáceres (2013) developed a method allowing disentangling between the effects of individual species and the effects of species assemblages (= sites) on total β -diversity. In this approach, total β -diversity is estimated *via* total variance of the community data matrix and then it is partitioned into (a) the degree of relative importance of individual species for β -diversity across area [representing thus species contributions to β -diversity (SCBD)] and (b) indicators of the compositional uniqueness of the assemblages as compared with other sites [that is local contributions to β -diversity (LCBD)]. This partitioning of

β -diversity appears to be helpful in understanding the reasons behind differential roles of species and assemblages in total β -diversity. On the one hand, the contribution of a species to β -diversity (SCBD) may be affected by various species-specific traits such as abundance (Vilmi *et al.*, 2017; da Silva *et al.*, 2018), niche breadth (Heino and Grönroos, 2017) or life history traits affecting the interactions of this species with other species or the environment. On the other hand, the contribution of an assemblage to β -diversity (LCBD) can be related to environmental factors (e.g. Tonkin *et al.*, 2016) as well as to the structure of the target biological community (e.g. da Silva *et al.*, 2018).

Development of the Legendre and De Cáceres' (2013) approach for decomposing β -diversity triggered a burst of recent studies that related SCBD and/or LCBD to species-specific and site-specific characteristics, respectively, in a variety of plant and animal taxa (Tonkin *et al.*, 2016; Heino and Grönroos, 2017; Kong *et al.*, 2017; Vilmi *et al.*, 2017; da Silva *et al.*, 2018; Landeiro *et al.*, 2018; Tolonen *et al.*, 2018). However, only two studies applied partitioning of β -diversity into SCBD and LCBD components to parasitic species. Biguezoton *et al.* (2016) analysed β -diversity of ixodid ticks, whereas Poisot *et al.* (2017) studied β -diversity of fleas. The former study considered both SCBD and LCBD, but did not relate either SCBD to species traits or LCBD to site characteristics. The latter study considered LCBD only (both for parasites and hosts as well as their interactions) and analysed their relationships with climatic variables. Both studies thus missed an important component of parasite biology, namely their utmost dependence on host species. Indeed, contrary to free-living species, parasites have a dual environment including, on the one hand, traditional environmental factors such as climate and vegetation, and, on the other hand, an assemblage of hosts which has supreme importance for parasites because parasites cannot exist without their hosts. Consequently, SCBD and LCBD of parasites cannot be completely understood without testing for the effects of hosts on these metrics. In particular, SCBD of parasites are likely affected by their host specificity (i.e. the size and/or composition of host spectra), whereas LCBD of parasite assemblages are likely affected by host species composition of a site or region.

Here we asked what are the factors affecting SCBD and LCBD of fleas parasitic on small mammals in 45 regions of the Palearctic. We tested (a) whether variation in ecological, morphological, life history and geographic traits can predict SCBD of fleas and (b) if variation in flea and host community metrics, off-host environmental factors and host species composition can predict LCBD of flea assemblages. In addition, and following Tonkin *et al.* (2016) and da Silva *et al.* (2018), we tested whether spatial variables may describe the geographic distribution of regions with various degrees of uniqueness of flea species composition.

Materials and methods

Data on flea and host species composition

We used data on species composition of fleas and their small mammalian hosts (Soricomorpha, Rodentia and ochotonid Lagomorpha) in 45 regions of the northern and temperate Palearctic compiled from published surveys and used in our earlier studies [see map of the regions and references in Krasnov *et al.* (2011, 2015)]. In this study, we used only data from the surveys in which at least 500 host individuals were examined. We omitted from our data host species such as squirrels, flying squirrels, chipmunks and hedgehogs and their specific fleas (e.g. *Tarsopsylla octodecimdentata* and *Archeopsylla erinacei*) because these hosts require special trapping methods and they were either undersampled or not sampled at all. In total, the database

included 202 flea species collected from 136 small mammal species.

Trait variables

Flea species were characterized by 10 traits. Three of these traits represented ecological variation (characteristic abundance, mean size of a host spectrum, phylogenetic distinctness of a global host spectrum). These quantitative traits have been shown to be true attributes of a flea species and vary significantly less among populations of the same species than among species (Krasnov *et al.*, 2004a, 2006; Mouillot *et al.*, 2006; Krasnov and Poulin, 2010). The size and phylogenetic distinctness of a host spectrum essentially represent niche breadth of a flea (Garnick, 1992; Poulin *et al.*, 2011). Two traits represented bionomics (= life history) of fleas: microhabitat preference and seasonal peak of reproduction. Microhabitat preference is determined by the proportion of time fleas spend on either the body of a host or in its burrow/nest. This proportion is a species-specific trait that distinguishes so-called 'body' fleas from 'nest' fleas [see details in Krasnov (2008)]. Seasonal peak of reproduction may occur during either the warm or cold period ('summer' or 'winter', respectively) or else a flea is able to reproduce all year without clear seasonality. Three morphological traits included armament (i.e. occurrence and/or the number of sclerotized combs, an ordinal variable; see Krasnov *et al.*, 2016) as well as body size and the degree of sexual size dimorphism (both quantitative variables). The remaining two traits were biogeographic: size and latitude of the centre of geographic range. See Supplementary Material Appendix 1 for detailed explanations on the selection and measurements of flea traits as well as calculations of characteristic abundance, host specificity indices and sexual size dimorphism.

Following Heino and Grönroos (2017) and da Silva *et al.* (2018), we substituted the original values of bionomic and morphological traits with the 'morphobionomic trait' vectors. The latter were the first two principal coordinate axes extracted from the principal coordinate analysis of distance trait matrix constructed using Gower distance coefficient with the function 'gowdis' using package 'FD' (Laliberté and Legendre, 2010) of the R statistical environment (R Core Team, 2018). Principal coordinate analysis was carried out using function 'cmdscale' of the R base package 'stats'. The two morphobionomic trait vectors (MBV1 and MBV2) explained 91.05% of variation and were continuous variables representing between-species differences in their morphological and life history traits. To guarantee that morphobionomic trait vectors adequately reflected original between-species distances in traits, we ran Mantel's correlation test between the matrix of Euclidean distances based on coordinates along MBV1 and MBV2 and the original matrix of Gower distances and found strong correlation between the two matrices (Mantel $r = 0.84$, $P < 0.001$). The first vector (MBV1) represented a gradient of body size of flea species from large to small, whereas the second vector (MBV2) showed a decrease in the degree of sexual size dimorphism (see details in Supplementary Material Appendix 1, Table S1). The relationships between ordinal (i.e. armament) and nominal (i.e. 'nest' vs 'body' vs 'both' preference) morphobionomic traits and the respective trait vectors are presented in Supplementary Material Appendix 1, Table S2 and Fig. S1. In brief, the negative area of MBV1 was mainly associated with species either preferring to stay on a host's body (i.e. 'body' fleas) or without clear microhabitat preference, demonstrating either summer or non-seasonal reproduction and having only a pronotal comb, whereas coordinates of 'nest' fleas with winter reproduction and either full (a pronotal and a genal) or no comb armament along this vector were mainly positive. 'Nest' species or those without clear microhabitat preferences having summer reproduction and either both combs or no combs at all

were distributed mainly in the positive area of MBV2, whereas the opposite was true for 'body' fleas that reproduce in winter or all year round and have a pronotal comb only. There was no clear relationship between the pattern of flea armament and coordinates along MBV2 (Supplementary Material Appendix 1, Fig. S1).

Environmental (off-host and host-associated) variables

We characterized sampled regions by their off-host and host-associated environment. We calculated the sampling area in a sampled region based on data from an original source. The latitudinal and longitudinal positions of the region centres were determined using ArcGIS 10.6. Regional environmental variables included topography (mean altitude), amount of green vegetation (normalized difference vegetation indices), separately for autumn, winter, spring and summer], air temperature (mean, maximum and minimum as well as annual and monthly ranges) and precipitation (for autumn, winter, spring and summer). Environmental data were averaged over a region across 30 arc-second grids. Elevation data were obtained using ArcGIS 10.6. NDVI data were taken from the VEGETATION Programme (<http://free.vgt.vito.be>), whereas temperature and precipitation variables were extracted from WORLDCLIM (BIOCLIM) 2.0 package (Fick and Hijmans, 2017). We ran principal component analyses of environmental variables and then substituted their original values with the scores of the three first principal components (PC1, PC2 and PC3). These three components explained 79.70% of environmental variation. PC1 represented mainly an increase in annual range of air temperatures and a decrease in the amount of green vegetation, PC2 correlated negatively with the mean, maximal and minimal air temperatures, whereas PC3 reflected an increase in spring and winter precipitation and mean altitude of a region (see details in Supplementary Material Appendix 2, Table S2).

To characterize a region from the perspective of host species composition, we calculated the numbers of host species belonging to one of 19 phylogenetic/ecological clades/groups (see Supplementary Material Appendix 3, Table S3) in each region [see justification in Krasnov *et al.* (2015)]. This allowed us to take into account both numerical and phylogenetic facets of a regional host community composition. These host-associated variables were considered ordinal. To transform these variables into continuous predictors for further analysis, we applied principal coordinate analysis on a distance matrix based on Manhattan distance and then extracted the first three 'host composition' vectors (HCV1, HCV2 and HCV3). This was done using the R packages 'vegan' (Oksanen *et al.*, 2018) and 'labdsv' (Roberts, 2016). Similarly to morphobionomic trait vectors (see above), these host composition vectors were continuous variables describing differences between regions in host composition and explained 82.0% of among-region variation (see details in Supplementary Material Appendix 3, Table S4). HCV1 was responsible for more than half of the explained variation and reflected a compositional gradient from bank voles, moles and soricine shrews (negative area) to gerbils, jerboas and ground squirrels (positive area); HCV2 was associated with a decrease in the number of species of *Microtus* voles; whereas HCV3 correlated negatively with the number of *Ochotona* and *Myodes* species and positively with species richness of crocidurines. The matrix of Euclidean distances based on coordinates on HCV1–HCV3 and the original matrix of Manhattan distances were strongly correlated (Mantel $r = 0.97$, $P < 0.001$) demonstrating that the three vectors of host composition adequately reflected between-region differences in host composition.

Structure of flea and host communities

We used flea and host species richness as well as host compositional uniqueness as metrics of structure of their communities. Estimates of flea and host species richness across regions can be affected by unequal among-region sampling effort (i.e. number of host individuals examined; Morand and Poulin, 1998) and unequal sampled area (Rosenzweig, 1995). Flea species richness was significantly, albeit weakly, affected by sampling effort but was not affected by the area of a region ($r^2 = 0.10$, $F = 4.83$, $P = 0.03$ and $r^2 = 0.03$, $F = 0.52$, $P = 0.23$, respectively), whereas host species richness was affected by the area ($r^2 = 0.23$, $F = 13.03$, $P < 0.001$). To control for the confounding effects of sampling effort and the area of a region, we regressed (a) the number of flea species recorded against the number of host individuals examined and (b) the number of host species against the sampled area in the log–log space. Then, we substituted the original values of flea and host species richness by their residual deviations from these regressions. Compositional uniqueness of host communities was assessed *via* their local contribution to total host β -diversity (=LCBD for hosts; see below for details on calculation of this metric).

Spatial variables

Following da Silva *et al.* (2018), we applied the approach of Moran Eigenvectors Maps (MEM) [also known as the principal coordinates of neighbouring matrices (PCNMs)] (Borcard and Legendre, 2002; Dray *et al.*, 2006) in which spatial variables are calculated from geographic coordinates of each region. We built a truncated Euclidean distance matrix from coordinates and then extracted eigenvectors with positive eigenvalues that were used as predictors in further analysis (Borcard and Legendre, 2002). In general, MEM allows evaluation of spatial structures over a range of scales with the first to the last eigenvectors representing ever-decreasing spatial scales from broad to fine (Borcard and Legendre, 2002), although this is mainly true for a spatially regular sampling design (Dray *et al.*, 2006; Borcard *et al.*, 2018). We extracted 25 spatial variables (= positive eigenvectors further referred to as PCNMs) using the R package 'vegan'. Then, we tested for spatial autocorrelation in these variables using Moran's I test implemented in the R package 'ape' (Paradis *et al.*, 2004). PCNMs that demonstrated significant spatial autocorrelation (13 of 25 PCNMs) were retained for the main analysis (see Borcard *et al.*, 2011 for justification and explanations).

Data analyses

We calculated species and local (=region) contributions to β -diversity of fleas (SCBD and LCBDf, respectively) using the approach of Legendre and De Cáceres (2013). We constructed a presence/absence region-by-species matrix which was subsequently Hellinger-transformed. This transformation takes the square root of the quotient of the value of each cell in a data matrix and its row sum and thus gives low weights to species with low counts and many zeros across regions. Then, we calculated SCBD values for each species and LCBDf values for each region using function 'beta.div' and Hellinger dissimilarity coefficient implemented in the R package 'adespatial' (Dray *et al.*, 2018). Local contributions to β -diversity of hosts (=LCBDh) was calculated in a similar way using a Hellinger-transformed presence/absence region-by-host species matrix.

We modelled the responses of (a) SCBD to trait variables and (b) LCBDf to environmental (both off-host and host-associated) variables, spatial variables and variables describing flea and host community metrics. Because the response variables ranged from

Table 1. Summary of β -regression analyses of the effect of ecological (model ET), morphobionomic (model MBT) and biogeographic traits (model GT) of flea species on their contributions to β -diversity (SCBD)

Model	Predictor	Estimate \pm s.e.	z	Pseudo- r^2 of a model
ET	Intercept	-5.95 \pm 0.15*	-38.87*	
	Abundance	0.61 \pm 0.11*	5.68*	
	Number of host species	0.25 \pm 0.22	1.16	
	Phylogenetic distinctness of host spectrum	0.003 \pm 0.001*	2.65*	
				0.30
MBT	Intercept	-5.30 \pm 0.06*	-87.60*	
	MBV1	-0.27 \pm 0.24	-1.13	
	MBV2	0.20 \pm 0.28	0.74	
				0.01
GT	Intercept	-10.81 \pm 0.49*	-21.87*	
	Geographic range size	0.74 \pm 0.10*	7.38*	
	Geographic range latitude	0.02 \pm 0.008*	3.04*	
				0.54

Morphobionomic traits were represented by two vectors produced by principal coordinate analysis (MBV1, MBV2; see text for explanations).

*- $P < 0.05$.

0 to 1 (without attaining either 0 or 1 values), we applied β -regression with a logit link function. The β -regression approach is the most suitable for models with a response variable of this type because, in particular, it naturally incorporates heteroscedasticity and skewness inherent to these variables [Cribari-Neto and Zeileis, 2010; see also Heino and Grönroos (2017) and da Silva *et al.* (2018)]. The β -regressions were carried out using the R package 'betareg' (Cribari-Neto and Zeileis, 2010).

To better understand the effect of predictors of different nature on either SCBD or LCBDf, we ran three separate models for the former and four separate models for the latter. First, we analysed how SCBD of a flea species varies in response to (a) ecological flea traits (abundance, size of a host spectrum and its phylogenetic distinctness); (b) morphobionomic traits (seasonality, armament, body size, the degree of sexual size dimorphism represented by two morphobionomic trait vectors, see above); and (c) biogeographic traits (size and latitude of geographic range). Second, we tested for the dependence of LCBDf on (a) structure of flea and host communities (flea and host species richness and contribution of regional host communities to total host β -diversity); (b) off-host environment (represented by three principal components of environmental variables, see above); and (c) host-associated environment in terms of the number of host species belonging to the main phylogenetic/ecological clades (represented by three host composition vectors, see above). Finally, (d) we used PCNMs (see above) as explanatory variables to assess the spatial distribution of LCBDf across the Palearctic.

Results

More than one-third of the 202 flea species (71 species) demonstrated a higher than average contribution to total β -diversity (SCBD). These species belonged to different genera and families (see Supplementary Material Appendix 4). The β -regression analyses demonstrated that SCBD significantly increased with an increase in mean abundance of a flea species and a decrease in its phylogenetic host specificity (i.e. an increase in phylogenetic distinctness of a host spectrum) (Table 1, Fig. 1). Fleas with large and more northern geographic ranges contributed to total β -diversity significantly more than fleas with small and more southern geographic ranges (Table 1, Fig. 2). Furthermore,

geographic traits of fleas explained more variation in their SCBD than ecological traits (compare pseudo- R^2 of the models, Table 1). In contrast to ecological and geographic traits, morphological and life history traits had no effect on SCBD (Table 1).

Almost half of 45 regional flea assemblages (21 assemblages) had above-average contributions to total flea β -diversity (see Supplementary Material Appendix 5, Fig. 2S). LCBDf did not depend on either flea or host species richness, but was significantly affected by compositional uniqueness of host assemblages (Table 2, Fig. 3). Variables associated with off-host environment had no effect whatsoever on LCBDf (Table 2), whereas the opposite was true for vectors describing composition of regional host assemblages (Table 2). For example, the contribution of flea assemblages to total β -diversity was higher in regions with a greater number of gerbil, jerboa, ground squirrel and marmot species than in regions with a high diversity of bank voles and *Sorex* shrews (Fig. 4). Among spatial variables, only PCNMs 2 and 4 were significantly associated with LCBDf (Table 2) with the former being positively and the latter being negatively related to LCBDf. Distribution of PCNMs and their values is presented in Fig. 5. Host compositional uniqueness and host composition explained almost equal proportions of variation in LCBDf, whereas the contribution of spatial variables was 1.5 times lower (Table 2).

Discussion

We found that SCBD was affected by ecological and biogeographic, but not morphological and life history traits of flea species. LCBD of flea assemblages was strongly related to LCBD of host assemblages and host species composition, but not to vegetation and climatic variables. In other words, dissimilarity of a given host assemblage from other host assemblages drives dissimilarity of its flea assemblage from other flea assemblages. In addition, LCBD of fleas demonstrated some spatial structure at a broad-to-moderate scale.

Positive relationships between species abundance and SCBD have also been found in stream insect (Heino and Grönroos, 2017), fish (Kong *et al.*, 2017) and dung beetle (da Silva *et al.*, 2018) communities, although this was mainly true when SCBD was calculated using species abundance but not

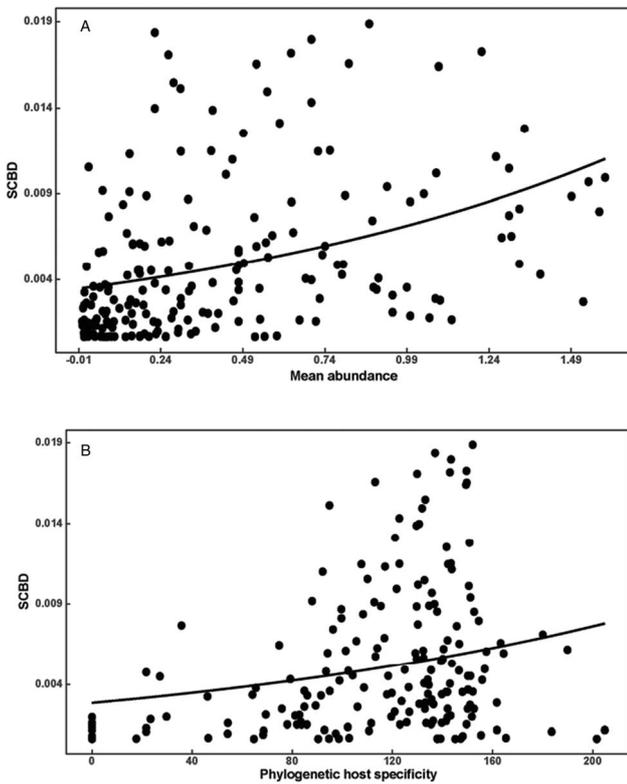


Fig. 1. Relationships between the contribution to total β -diversity of flea species (SCBD) and their characteristic abundances (A) and phylogenetic distinctness of host spectra (B).

presence/absence data. In addition, in both Heino and Grönroos (2017) and da Silva *et al.* (2018), the quadratic term of the abundance variable was found to be significant, whereas no curvilinearity can be envisaged from the relationship between abundance and SCBD in our study (Fig. 1). As mentioned above, flea abundance has been shown to vary only within relatively narrow species-specific boundaries and thus can be considered as a true flea species trait (Krasnov *et al.*, 2006). Our results thus demonstrate that species with inherently high abundance tended to contribute more to total β -diversity than species with low abundance. Heino and Grönroos (2017) suggested that the relationship between abundance and SCBD may result from a positive relationship between abundance and occupancy [see also Legendre and De Cáceres (2013)], so that species with high SCBD values are expected to show high local abundance and high occupancy as well as a large variation in abundance across locations. This is unlikely true for fleas because of low among-location variation in the abundance metric considered in this study (Krasnov *et al.*, 2006). An alternative explanation for the effect of mean abundance on SCBD can be linked to high among-species variation in abundance (coefficient of variation is 0.97) and a small proportion of species with relatively high characteristic abundance (e.g. >1; 24 of 202 species). As a result, assemblages containing highly abundant species might be strongly dissimilar from the remaining assemblages.

The relationship between SCBD and niche breadth in free-living insects has been found to be either very weak (Heino and Grönroos, 2017) or absent (da Silva *et al.*, 2018). On the contrary, this relationship appeared to be significant for fleas. This discrepancy might be a result of different approaches to the definition of niche breadth. In our case, we considered niche breadth as a diversity of host species exploited rather than defining it as a tolerance to environmental variables. Positive association between

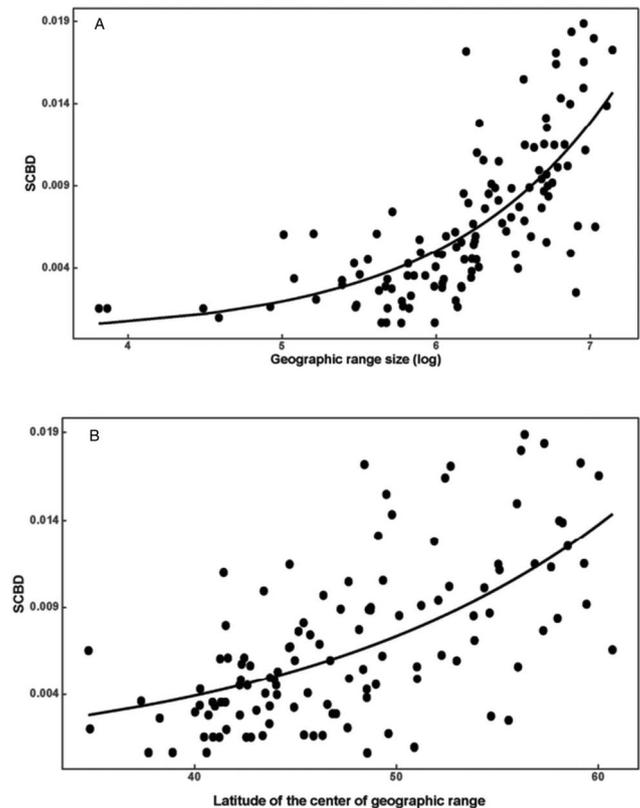


Fig. 2. Relationships between the contribution to total β -diversity of flea species (SCBD) and the sizes (A) and latitudes of the centres (B) of their geographic ranges.

SCBD and flea niche breadth (inversely indicated by phylogenetic host specificity) can, at least in part, result from positive relationships between this trait and abundance. Indeed, host generalist fleas that tend to exploit phylogenetically/taxonomically unrelated species usually attain higher abundances (Krasnov *et al.*, 2004b). Furthermore, our earlier studies demonstrated that phylogenetic/taxonomic distinctness of host spectra in fleas (i) is positively related to their geographic range (Krasnov *et al.*, 2005) and (ii) increases towards higher latitudes (Krasnov *et al.*, 2008). In addition, fleas with more northerly distributions have larger geographic ranges (Krasnov *et al.*, 2008). These complex inter-relationships between characteristic abundance, phylogenetic host specificity and geographic distribution result thus in predictability of flea species contribution to total β -diversity. This is indirectly supported by the associations between SCBD and (a) geographic range position and (b) phylogenetic, but not numerical, host specificity. Our earlier study (Krasnov *et al.*, 2008) demonstrated significant correlation between latitude of the geographic range and the former, but not the latter, measure of host specificity. In other words, highly abundant and broadly distributed host generalists with northern geographic ranges contributed more to total β -diversity than less abundant host-specific fleas with narrow and southern geographic ranges. The effect of geographic range position on SCBD seems to be further translated into spatial pattern of LCBD (see below). In addition, the distribution of data points on Fig. 1B is clearly triangular. This means that fleas exploiting closely related hosts invariably demonstrated low SCBD, while SCBD of fleas recorded on unrelated hosts might be either high or low. This indicates an important role of the composition of a host spectrum.

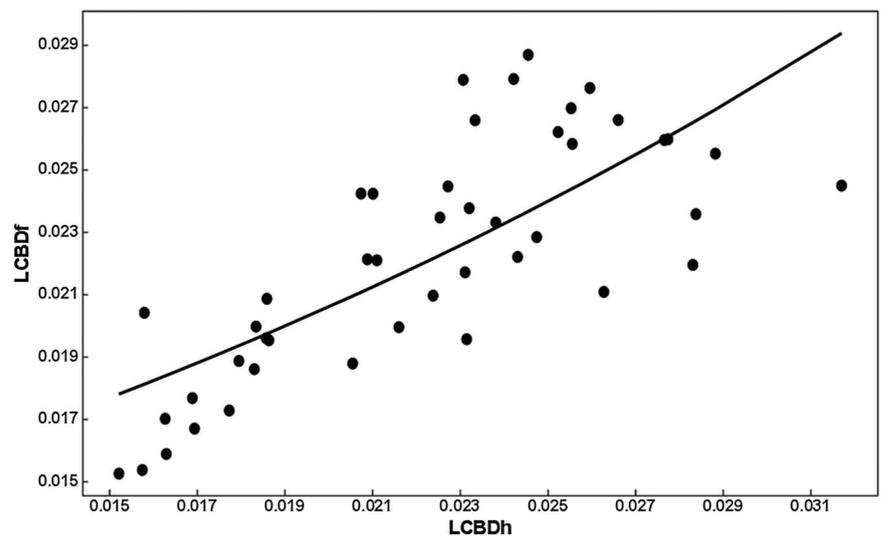
LCBD of regional flea assemblages was found to be determined mainly by composition of regional host assemblages and their LCBD (=LCBDh), but not species richness of either fleas or

Table 2. Summary of β -regression analyses of the effect of regional flea and host community metrics (model CM), off-host environmental variables (model OHE), variables describing host composition (model HCE) and spatial variables (model SP) on contributions of regional flea assemblages to β -diversity (LCBdf)

Model	Predictor	Estimate \pm s.e.	z	Pseudo- r^2 of a model
CM	Intercept	$-4.48 \pm 0.11^*$	-39.82^*	0.62
	Flea species richness	-0.13 ± 0.11	-1.20	
	Host species richness	0.002 ± 0.13	0.01	
	LCBDh	$31.10 \pm 4.94^*$	6.29^*	
OHE	Intercept	$-3.78 \pm 0.02^*$	-151.84^*	0.05
	PC1	0.01 ± 0.02	0.51	
	PC2	-0.02 ± 0.02	-0.88	
	PC3	0.03 ± 0.02	1.29	
HCE	Intercept	$-3.79 \pm 0.01^*$	-261.74^*	0.69
	HCV1	$0.01 \pm 0.001^*$	7.93^*	
	HCV2	$0.01 \pm 0.002^*$	5.18^*	
	HCV3	$0.008 \pm 0.003^*$	2.53^*	
SP	Intercept	$-3.79 \pm 0.02^*$	-190.88^*	0.39
	PCNM2	$0.39 \pm 0.13^*$	3.03^*	
	PCNM4	$-0.47 \pm 0.14^*$	-3.34^*	

LCBDh is contributions of regional host assemblages to total host β diversity. Off-host environment was represented by three principal components (PC1, PC2, PC3); host composition was represented by three vectors produced by principal coordinate analysis (HCV1, HCV2, HCV3); spatial variables were represented by positive eigenvectors (PCNMs) calculated from distances between regions (see text for explanations). For model SP, only predictors with significant coefficients are shown.

*- $P < 0.05$.

**Fig. 3.** Relationship between the contribution of regional flea assemblages to total flea β -diversity (LCBdf) and the contribution of regional host assemblages to total host β -diversity (LCBDh).

hosts and environmental variables. The higher LCBD of a host assemblage is, the higher LCND of the respective flea assemblage is as well. In other studies of free-living species (Tonkin *et al.*, 2016; Heino and Grönroos, 2017; Vilmi *et al.*, 2017; Landeiro *et al.*, 2018; Silva *et al.*, 2018; Tolonen *et al.*, 2018) and parasites (Poisot *et al.*, 2017), the relationships between LCBD and environmental variables were found to be important. Nevertheless, the associations between LCBD and environmental predictors in some of these studies were weak (e.g. Heino and Grönroos, 2017; da Silva *et al.*, 2018). The main reason behind these contradictory results can merely be the differences in life histories of

taxa for which the effect of environment on LCBD was tested. Indeed, Landeiro *et al.* (2018) tested for the effects of environment on LCBD of 14 plant and animal taxa from the same region and found that LCBD of different taxa (or even different ecological groups within the same taxon) were, if at all, associated with different environmental variables. The most surprising discrepancy in the effect of environmental variation on LCBD is between our results and those of Poisot *et al.* (2017) that reported the effect of some climatic predictors on compositional uniqueness of flea assemblages. Although we and Poisot *et al.* (2017) used essentially the same data, the difference in methodological

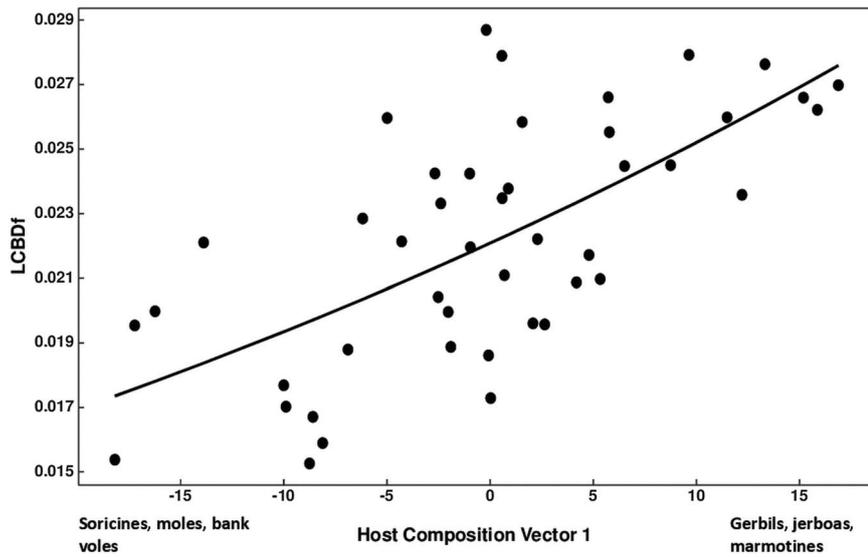


Fig. 4. Relationship between the contribution of regional flea assemblages to total flea β -diversity (LCBDf) and a variable describing host composition of a region (host composition vector 1).

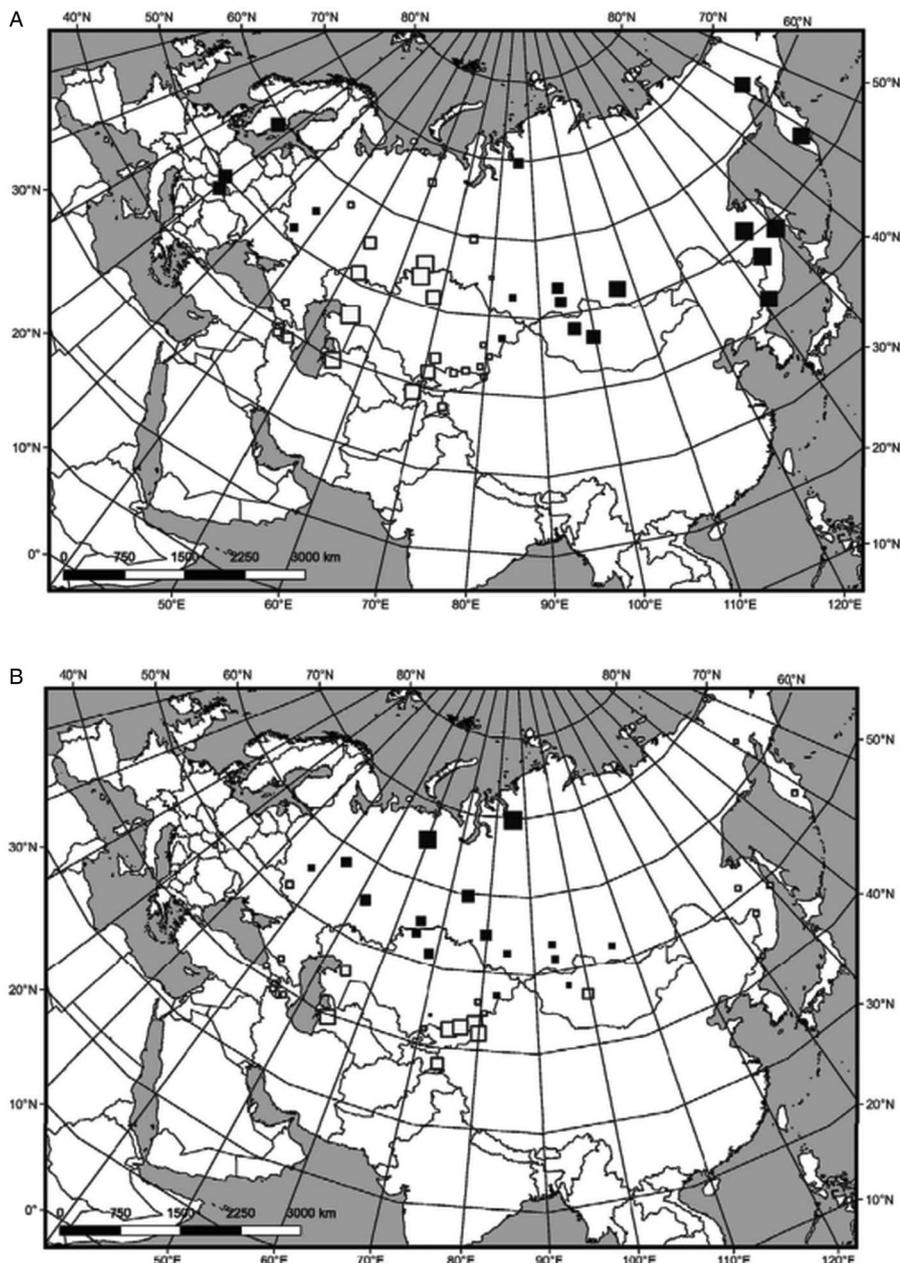


Fig. 5. Map of values of the PCNM variables selected to model LCBD of flea assemblages [(A) PCNM2, (B) PCNM4, see text for explanations]. Sizes of squares are proportional to positive (black) and negative (white) values.

approach is the most likely reason behind this discrepancy between results. First, Poisot *et al.* (2017) related differences in LCBD among flea assemblages to differences in the environment using redundancy analysis, while we applied β -regressions for our analyses. Second and in contrast to Poisot *et al.* (2017), we did not use the data from surveys in which sampling effort was too low (see above). We also did not include in the input matrices those host species that required a special sampling technique, so that these hosts and their fleas were apparently undersampled. Including undersampled regions and species could introduce strong bias in the analysis. For example, it is highly likely that inclusion of hosts and fleas sampled in some regions but not in other regions where they undoubtedly occurred (e.g. squirrels and their fleas) would substantially and spuriously inflate LCBD values of the former. Finally, Poisot *et al.* (2017) measured environmental variables for each region around its centre, whereas we averaged these variables across the entire sampling area within each region. Environmental conditions in the centre of a region do not necessarily represent the entire range of conditions across larger areas.

The lack of the effect of vegetation and climatic variables on LCBD found in this study does not, however, indicate irrelevance of the off-host environment for diversity and/or composition of flea assemblages. In fact, the role of environmental conditions of various aspects of flea communities has been emphasized in our earlier studies (e.g. Krasnov *et al.*, 2010, 2015), including the effect of environment on one of the components of flea β -diversity, namely species turnover along gradients (Maestri *et al.*, 2017). It is possible that the relative importance of the environmental effects varies among different facets of diversity. Moreover, the effect of environment on LCBD may be important or not in dependence of a taxon and/or a region of interest (e.g. Qiao *et al.*, 2015 vs Tonkin *et al.*, 2016).

LCBD of flea assemblages were found to be mainly affected by composition of hosts that these assemblages exploit. As a result, regions with high compositional uniqueness of flea assemblages are also those with high compositional uniqueness of host assemblages. The role of among-region differences in host composition on differences in flea composition can be expected because the tight link between these metrics is well known for a variety of parasite taxa exploiting a variety of host taxa (e.g. Vinarski *et al.*, 2007; Mihaljevic *et al.*, 2018) including fleas parasitic on small mammals (Krasnov *et al.*, 2010). As a result, a particular host composition of a region and its representation across the entire study area determines the extent of contribution of a given parasite assemblage to total β -diversity. For example, higher LCBD values of flea assemblages were associated with host communities composed of gerbils, jerboas and ground squirrels, whereas the opposite was true for communities of bank voles and soricine shrews (see 'Results' section). The former host communities and their fleas are characteristic for arid habitats, whereas the latter host communities and their fleas are predominantly represented in forests. Arid habitats are less represented in the northern and temperate Palearctic than forests, so that communities of arid fleas harboured by arid hosts differ from the majority of other communities and thus contribute more to total β -diversity.

Obviously, host species are unevenly distributed across the continent and a particular host community is associated with a particular landscape. This may, at least partly, explain spatial patterns in LCBD. For example, comparison of model coefficients (Table 2) and geographic distribution of PCNMs (Fig. 5) suggests spatial structure of LCBD. At a relatively broader scale (PCNM2 in Table 2, Fig. 5A), higher LCBD values were mainly found in the predominantly western or predominantly eastern assemblages, whereas lower LCBD values were characteristic for the assemblages in the centre of the continent. At a somewhat

finer scale (PCNM4 in Table 2, Fig. 5B), there was a trend of a south–north gradient in higher-to-lower LCBD values. This suggests that communities in western and eastern regions contained unique species not represented in the major part of the continent (e.g. western *Atyphloceras nuperus* and *Ctenophthalmus bisoctodentatus* and eastern *Amphipsylla marikovskii* and *Ctenophthalmus congeneroides*). The same was likely true for southern assemblages that contained species not distributed across most of the northern and temperate Palearctic (e.g. *Xenopsylla conformis*, *Xenopsylla magdaliniae*, *Mesopsylla hebes*).

Surprisingly, flea species richness had no effect on LCBD values, although this effect has been found in studies of free-living organisms (Heino and Grönroos, 2017; Kong *et al.*, 2017; Vilmi *et al.*, 2017; da Silva *et al.*, 2018). Furthermore, the relationship between LCBD and species richness in different taxa and even in the same taxon in different habitats or sites could be either negative or positive or non-existent (Heino and Grönroos, 2017; Kong *et al.*, 2017; Vilmi *et al.*, 2017; da Silva *et al.*, 2018). Da Silva *et al.* (2018) suggested that the existence or the pronouncedness of the LCBD–species richness relationship may depend on the proportions of rare and common species in the assemblages. This can be the case for fleas. In other words, LCBD of an assemblage can depend on a particular species composition rather than on a mere number of species.

In conclusion, SCBD of fleas was predictably associated with ecological/geographic but not morphological/life history traits. LCBD of flea assemblages was predictably associated with host composition, but not vegetation and climatic variables. Our results suggest that predictors of variation in SCBD and, especially, LCBD of parasites differ from those of free-living taxa due to substantial differences in the life history strategies. More studies on other parasites are required to support this conclusion and determine if parasitic taxa largely follow this general pattern.

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References

- Baselga A (2010) Partitioning the turnover and nestedness components of beta-diversity. *Global Ecology and Biogeography* **19**, 134–143.
- Biguezoton A, Adehan S, Adakal H, Zoungrana S, Farougou S and Chevillon C (2016) Community structure, seasonal variations and interactions between native and invasive cattle tick species in Benin and Burkina Faso. *Parasites & Vectors* **9**, 43.
- Borcard D and Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* **153**, 51–68.

- Borcard D, Gillet F and Legendre P** (2018) *Numerical Ecology with R*, 2 Edn. New York, USA: Springer. doi: 10.1007/978-3-319-71404-2.
- Cribari-Neto F and Zeileis A** (2010) Beta regression in R. *Journal of Statistical Software* **34**, 1–24.
- da Silva PG, Hernández MIM and Heino J** (2018) Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. *Diversity and Distributions* **11**, 1674–1686. doi: 10.1111/ddi.12785.
- Dray S, Legendre P and Peres-Neto PR** (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* **196**, 483–493.
- Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guenard G, Jombart T, Larocque G, Legendre P, Madi N and Wagner HH** (2018) *adespatial: Multivariate Multiscale Spatial Analysis*. R package version 0.2-0. Available at <https://CRAN.R-project.org/package=adespatial>.
- Fick SE and Hijmans RJ** (2017) Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315.
- Garnick E** (1992) Niche breadth in parasites: an evolutionarily stable strategy model, with special reference to the protozoan parasite *Leishmania*. *Theoretical Population Biology* **42**, 62–103.
- Heino J and Grönroos M** (2017) Exploring species and site contributions to beta diversity in stream insect assemblages. *Oecologia* **183**, 151–160.
- Kong H, Chevalier M, Laffaille P and Lek S** (2017) Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system. *PLoS ONE* **12**, e0174582.
- Krasnov BR** (2008) *Functional and Evolutionary Ecology of Fleas. A Model for Ecological Parasitology*. Cambridge, UK: Cambridge University Press.
- Krasnov BR and Poulin R** (2010) Ecological properties of a parasite: species-specific stability and geographical variation. In Morand S and Krasnov BR (eds), *The Biogeography of Host-Parasite Interactions*. Oxford, UK: Oxford University Press, pp. 99–114.
- Krasnov BR, Mouillot D, Shenbrot GI, Khokhlova IS and Poulin R** (2004a) Geographical variation in host specificity of fleas (Siphonaptera): the influence of phylogeny and local environmental conditions. *Ecography* **27**, 787–797.
- Krasnov BR, Poulin R, Shenbrot GI, Mouillot D and Khokhlova IS** (2004b) Ectoparasitic ‘jacks-of-all-trades’: relationship between abundance and host specificity in fleas (Siphonaptera) parasitic on small mammals. *American Naturalist* **164**, 506–516.
- Krasnov BR, Poulin R, Shenbrot GI, Mouillot D and Khokhlova IS** (2005) Host specificity and geographic range in haematophagous ectoparasites. *Oikos* **108**, 449–456.
- Krasnov BR, Shenbrot GI, Khokhlova IS and Poulin R** (2006) Is abundance a species attribute? An example with haematophagous ectoparasites. *Oecologia* **150**, 132–140.
- Krasnov BR, Shenbrot GI, Mouillot D, Khokhlova IS and Poulin R** (2008) Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites. *Journal of Biogeography* **35**, 592–601.
- Krasnov BR, Mouillot D, Shenbrot GI, Khokhlova IS and Poulin R** (2010) Deconstructing spatial patterns in species composition of ectoparasite communities: the relative contribution of host composition, environmental variables and geography. *Global Ecology and Biogeography* **19**, 515–526.
- Krasnov BR, Stanko M, Khokhlova IS, Shenbrot GI, Morand S, Korralo-Vinarskaya NP and Vinarski MV** (2011) Nestedness and β -diversity in ectoparasite assemblages of small mammalian hosts: effects of parasite affinity, host biology and scale. *Oikos* **120**, 630–639.
- Krasnov BR, Shenbrot GI, Khokhlova IS, Stanko M, Morand S and Mouillot D** (2015) Assembly rules of ectoparasite communities across scales: combining patterns of abiotic factors, host composition, geographic space, phylogeny and traits. *Ecography* **38**, 184–197.
- Krasnov BR, Shenbrot GI, Khokhlova IS and Degen AA** (2016) Trait-based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. *Oikos* **125**, 29–38.
- Laliberté E and Legendre P** (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305.
- Landeiro VI, Franz B, Heino J, Siqueira T and Bini LM** (2018) Species-poor and low-lying sites are more ecologically unique in a hyperdiverse Amazon region: evidence from multiple taxonomic groups. *Diversity and Distributions* **24**, 966–977.
- Legendre P and De Cáceres M** (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters* **16**, 951–963.
- Maestri R, Shenbrot GI and Krasnov BR** (2017) Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. *Journal of Biogeography* **44**, 1880–1890.
- Mihaljevic JR, Hoye BJ and Johnson PTJ** (2018) Parasite metacommunities: evaluating the roles of host community composition and environmental gradients in structuring symbiotic communities within amphibians. *Journal of Animal Ecology* **87**, 354–368.
- Morand S and Poulin R** (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* **12**, 717–727.
- Mouillot D, Krasnov BR, Shenbrot GI, Gaston KJ and Poulin R** (2006) Conservatism of host specificity in parasites. *Ecography* **29**, 596–602.
- Oksanen J, Blanchet G, Friendly M, Kindt P, Legendre P, McGlinn D, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E and Wagner H** (2018) *vegan: Community Ecology Package*. R package version 2.5-2. Available at <https://CRAN.R-project.org/package=vegan>.
- Paradis E, Claude J and Strimmer K** (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics (Oxford, England)* **20**, 289–290.
- Pavoine S and Dolédec S** (2005) The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. *Environmental and Ecological Statistics* **12**, 125–138.
- Pavoine S, Marcon E and Ricotta C** (2016) ‘Equivalent numbers’ for species, phylogenetic or functional diversity in a nested hierarchy of multiple scales. *Methods in Ecology and Evolution* **7**, 1152–1163.
- Poisot T, Guéveaux-Julien C, Fortin M-J, Gravel D and Legendre P** (2017) Hosts, parasites and their interactions respond to different climatic variables. *Global Ecology and Biogeography* **26**, 242–251.
- Poulin R, Krasnov BR and Mouillot D** (2011) Host specificity in phylogenetic and geographic space. *Trends in Parasitology* **27**, 355–361.
- Qiao X, Li Q, Jiang Q, Lu J, Franklin S, Tang Z and Jiang M** (2015) Beta diversity determinants in Badagongshan, a subtropical forest in central China. *Scientific Reports* **5**, 17043.
- R Core Team** (2018) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.
- Roberts DW** (2016) *labdsv: Ordination and Multivariate Analysis for Ecology*. R package version 1.8-0. Available at <https://CRAN.R-project.org/package=labdsv>.
- Rosenzweig ML** (1995) *Species Diversity in Space and Time*. Cambridge, UK: Cambridge University Press.
- Tolonen KE, Leinonen K, Erkinaro J and Heino J** (2018) Ecological uniqueness of macroinvertebrate communities in high-latitude streams is a consequence of deterministic environmental filtering processes. *Aquatic Ecology* **52**, 17–33.
- Tonkin JD, Heino J, Sundermann A, Haase P and Jähnig SC** (2016) Context dependency in biodiversity patterns of central German stream metacommunities. *Freshwater Biology* **61**, 607–620.
- Vilmi A, Karjalainen SM and Heino J** (2017) Ecological uniqueness of stream and lake diatom communities shows different macroecological patterns. *Diversity and Distributions* **23**, 1042–1053.
- Vinarski MV, Korralo NP, Krasnov BR, Shenbrot GI and Poulin R** (2007) Decay of similarity of gamasid mite assemblages parasitic on Palearctic small mammals: geographic distance, host-species composition or environment. *Journal of Biogeography* **34**, 1691–1700.