



The effects of environment, hosts and space on compositional, phylogenetic and functional beta-diversity in two taxa of arthropod ectoparasites

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Abstract

We studied the effects of variation in environmental, host-associated and spatial factors on variation in compositional, phylogenetic/taxonomic and functional facets of beta-diversity in fleas and gamasid mites parasitic on small mammals and asked whether (a) the importance of these factors as drivers of beta-diversity differs among its multiple facets and (b) the effects of variation in environment, hosts and space on beta-diversity variation differ between the two ectoparasite taxa. To understand the relative effects of each group of predictors, we used a distance-based redundancy analysis and variation partitioning. The greatest portions of variation in the compositional beta-diversity of fleas were equally explained by host-associated and spatial predictors, whereas variation in host species composition contributed the most to variation in the compositional beta-diversity of mites. Variation in the phylogenetic (i.e. based on phylogenetic tree) beta-diversity of fleas was mainly due to variation in the phylogenetic composition of host communities, while the taxonomic (i.e. based on Linnean taxonomy) beta-diversity of mites was influenced by environmental variation. Unique contributions of spatial and environmental variation explained most of the variation in functional beta-diversity and its species replacement (= turnover) component (i.e. beta-diversity explained by replacement of species alone) in fleas and mites, respectively. Variation in the richness difference component (i.e. beta-diversity explained by species loss/gain alone) of functional beta-diversity was mainly affected by either variation in the functional composition of host assemblages (fleas) or its joint action with environmental variables (mites). We conclude that the pattern of the relative effects of environmental, host-associated and spatial factors on beta-diversity is context-dependent and may differ among different facets of beta-diversity, among different beta-diversity components and also among taxa dependent on biological affinities.

Keywords Beta-diversity · Fleas · Mites · Species composition · Phylogeny · Traits · Variation

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Introduction

Understanding the evolution of biological communities is impossible without studying the variation in the composition and structure of these communities across space and/or over time. This variation is commonly defined as beta-diversity (Whittaker 1960, 1972) and represents one of the most important concepts in modern ecology. Examining patterns of beta-diversity in various communities is crucial not only from a purely theoretical perspective but also for application to subjects such as biological conservation and public health. Among these studies, investigations of beta-diversity drivers take a central place because they allow us to understand the mechanisms behind patterns of similarity or dissimilarity in species assemblages between locations and times and thus give insights into the processes shaping these assemblages.

Originally, patterns of biological diversity, including beta-diversity, were considered based on the number and identities of species (e.g., Whittaker 1960; Wilson and Shmida 1984). Biological diversity has only been recognized somewhat recently as not limited to the mere number and composition of species but as also encompassing the diversity of phylogenetic and functional entities (Tilman et al. 1997; Webb et al. 2002; Ackerly 2003; Cavender-Bares et al. 2009; De Bello et al. 2010). Indeed, species assemblages can be envisaged as assemblages of sets of certain traits. Some of these traits are inherited from common ancestors, whereas other traits arise *de novo* in the individual species. Compositional, phylogenetic and functional aspects (= facets) of diversity are interconnected but not equal. Consider, for example, two communities with the same number of species, but one community is mainly composed of closely related species, while the other community is mainly composed of distantly related species. Obviously, these communities will be similar in their compositional diversity but substantially different in their phylogenetic (and likely functional) diversity.

Few would deny the role of environment in shaping biological communities and species interactions therein. From the pioneering work of MacArthur and Levins (1967) onward, a plethora of studies have demonstrated environmental effects on species diversity. Furthermore, given that environment represents a combination of multiple factors including local environmental variables, as well as climate and spatial gradients, the importance of various environmental drivers may differ between compositional, phylogenetic and functional facets of diversity. However, recent studies testing the effect of environment on different biodiversity facets produced contrasting results. For example, Soininen et al. (2016) demonstrated that while the compositional diversity of stream diatoms was best explained by spatial variables, their functional diversity (in terms of guild richness) responded most strongly to environmental gradients. In contrast, Heino and Tolonen (2017) and Rocha et al. (2018) reported a similar response

of the compositional, taxonomic (as a proxy for phylogenetic) and functional diversity of freshwater macroinvertebrates to local environmental and spatial variables. This suggests that the pattern of the relationships between various environmental aspects and multiple facets of diversity may manifest differently in different taxa. In particular, the effects of environment on beta-diversity may differ between free-living and parasitic species.

Similarly to free-living species, parasite communities are affected by local environmental and spatial factors (Poulin 2007; Krasnov 2008; Krasnov et al. 2019a). However, the environment for a parasite includes not only its surrounding abiotic and biotic factors but also the most important component of its environment—its host. Hosts provide parasites not only with food but also with places to live and reproduce and often serve as tools for parasite dispersal (Poulin 2007). As a result, parasite diversity has been repeatedly shown to respond to host diversity (Poulin 2007; Krasnov et al. 2007; Kamiya et al. 2014), although environmental effects on parasite diversity may also be strong (e.g. Poulin 2007; Adlard et al. 2015). Furthermore, strong associations between host and parasite phylogenies, as well as between host and parasite traits, have also been reported (Hadfield et al. 2014; Krasnov et al. 2016). Consequently, the phylogenetic and functional facets of parasite diversity can be affected by variables describing the phylogenetic and functional aspects of host species composition. In particular, this may be the case for parasite beta-diversity. Indeed, the association between host and parasite phylogenetic turnovers has been recently reported by Clark et al. (2018).

Here, we studied the effects of variation in off-host and host-associated environmental factors (the former will henceforth be referred to as environmental factors) on variation in the compositional, phylogenetic/taxonomic and functional beta-diversity of two taxa of ectoparasitic arthropods (fleas and gamasid mites) exploiting small mammalian hosts in the Palearctic, while accounting for spatial structure in all these beta-diversity facets by introducing spatial variables into the analyses. Fleas are holometabolous insects with obligatory haematophagous imagoes and non-parasitic larvae. All Palearctic species alternate between periods spent on the bodies and the nests/burrows of their hosts, although the proportion of time spent on the hosts' bodies and in their burrows differs among flea species (see below). Pre-imaginal stages develop off-host (see Krasnov 2008). Gamasid mites demonstrate a vast range of lifestyles and feeding strategies, from endoparasitism via obligate and facultative haematophagy to predation on small invertebrates and phoresy (Radovsky 1985). Here, we focused on mites collected from host bodies that were either obligatory or facultative haematophagous. The latter spend most of their life off-host, whereas the former either are nidicolous and attack the host only to obtain a bloodmeal or prefer to stay and even to reproduce on host bodies. We asked whether (a) the roles of environmental,

host-associated and spatial variables as drivers of beta-diversity differ among its multiple facets and (b) the effects of environment, hosts and space on beta-diversity differ between the two ectoparasite taxa.

Differences between biological communities (i.e. beta-diversity) can be partitioned into components that result from contrasting underlying processes, namely species replacement and species losses or gains (Harrison et al. 1992; Williams 1996; Lennon et al. 2001; Baselga 2007, 2010; Cardoso et al. 2014, Legendre 2014). Furthermore, the processes of replacement and loss/gain can be applied not only to species but also to phylogenetic lineages or traits. In other words, the partitioning of beta-diversity into additive components portraying different processes can be applied not only to separate species but also to separate phylogenetic lineages (for phylogenetic beta-diversity) or traits (functional beta-diversity). In this study, we used the approach of Cardoso et al. (2014) and partitioned the total beta-diversity (β_{total}) into its species replacement (= turnover, β_{repl}) and richness difference (β_{rich}) components. Then, we tested for the effects of environmental, host-associated and spatial variables on each of these components for each beta-diversity facet and each ectoparasite taxon.

Materials and methods

Ectoparasite and host distribution

The data on flea and gamasid mite distribution across the Palearctic were extracted from published surveys and unpublished data (for mites) that reported a given flea or mite species recorded on a given host species. It is well known that estimation of parasite species composition can be inaccurate for small samples (Poulin 2007). To avoid this inaccuracy, we considered data from surveys that aimed to study the entire flea or mite community harboured by the entire community of small mammals in a given region. Then, we selected surveys in which (a) 10 or more individuals of each host species were examined and (b) at least 500 individuals belonging to all small mammal species were captured. Parasitological examination of 10 conspecific individuals has been proved to allow reliable estimation of ectoparasite species richness and composition (Krasnov et al. 2005). In total, we used data on 202 flea and 69 mite species collected from 135 and 68, respectively, small mammal species (rodents, shrews, moles and pikas) across 45 and 30 regions, respectively (see map in Fig. S1 of Supplementary Material). For fleas, these regions were distributed from 69.80° in the North to 38.14° in the South and from 16.94° in the West to 161.21° in the East. For mites, the sampled regions were distributed from 97.74° in the North to 39.61° in the South and from 11.48° in the West to 161.21° in the East. Details on sampling methods and

respective references can be found elsewhere (Krasnov et al. 2015 for fleas and Krasnov et al. 2010a for mites). In addition to 28 regional surveys referenced in Krasnov et al. (2010a), we used data reported for Norway (Edler and Mehl 1972), while the data for Tomsk region (Davydova and Belova 1972) were divided into two datasets (the middle and the southern boreal forests).

Flea phylogeny and mite taxonomy

As the backbone of flea phylogeny, we used the most recent molecular phylogeny of the order Siphonaptera (Zhu et al. 2015). This tree comprised almost all genera (but not all species) from our dataset. To determine the positions of species from our dataset that were not represented in Zhu et al. (2015), we used either their morphologically derived taxonomic affinities or additional molecular and/or morphological phylogenetic studies (see Krasnov et al. 2019b for references).

No phylogenetic tree is available for gamasid mites except for the tree of Dowling and OConnor (2010). However, this tree is poorly resolved and does not comprise the majority of the species from our dataset. Consequently, we used the Linnean taxonomic tree with four above-species hierarchical levels (subgenus, genus, subfamily, family) as a proxy for phylogeny. Mite taxonomy was taken from various taxonomic sources (Bregotova 1956; Vinarski and Korralo-Vinarskaya 2016, 2017). Sixty-nine mite species considered in this study were represented by four families, five subfamilies, eight genera and nine subgenera.

Flea and mite traits

Traits for both ectoparasite taxa included (a) mean abundance on the principal host; (b) the degree of host specificity in terms of the numbers of hosts exploited in a region (corrected for the confounding effect of the sampling effort); (c) phylogenetic diversity of a host spectrum within a region or (d) across all regions where a given ectoparasite species was recorded; (e) body size; and (f) the degree of sexual dimorphism. The rationale and details of the calculations of the mean abundance and variables describing the degree of host specificity can be found elsewhere (Poulin et al. 2011; Krasnov et al. 2013, 2015; Surkova et al. 2018b). In brief, we substituted the original values of the number of hosts exploited by a flea or a mite in a region with the residuals of the regression of their log-transformed values against the log-transformed number of hosts examined within this region. We then averaged these values across regions for each flea or mite species. Phylogenetic host specificity was measured as the $\Delta+$ index of Clarke and Warwick (1999) and Warwick and Clarke (2001) modified to take into account phylogenetic rather than taxonomic distances and calculated using the function “taxondive” of the package “vegan” (Oksanen et al. 2018)

implemented in the R 3.5.1 Statistical Environment (R Core Team 2018). The construction of the phylogenetic tree of hosts used to calculate phylogenetic host specificity is described below. The body size of an ectoparasite species was estimated via either maximal body length (fleas) or the mid-line length of the dorsal shield (mites). Details of body size measurements are described in Krasnov et al. (2013) and Surkova et al. (2018a, b). Due to substantial sexual size dimorphism in both fleas and mites, we used the median of the average male and average female body size as a characteristic of the body size of each ectoparasite species. The degree of sexual dimorphism was estimated as the logarithmic female-to-male size ratio (see Smith 1999 for rationale and explanations).

In addition, we characterized each flea species by (a) seasonality (whether the main reproductive period was during the warm season or the cold season or year round) and (b) micro-habitat preferences. The latter trait is associated with the proportion of time a flea spends on either the body of its host (“body species”) or in its burrow (“nest species”) or equally (“both body and nest species”). Detailed explanations and references for both traits can be found elsewhere (see Krasnov 2008 and references therein). In gamasid mites, a particular feeding mode is a characteristic species trait (e.g. Radovsky 1985). We designated each mite species as (a) an obligate exclusive haematophage (feeds solely on the host’s blood), (b) an obligate non-exclusive haematophage (feeds on both the host’s blood and small nidicolous arthropods) or (c) a facultative haematophage based on information from Bregetova (1956) and Zemskaya (1973).

Environmental variables

We determined the latitudinal and longitudinal positions of the centre of each region with ArcGIS 10.6. Environmental variables for each region included altitude (mean, maximal and minimal), amount of green vegetation [normalized difference vegetation indices (NDVI)], four variables describing air temperature (mean, maximum, annual and monthly ranges) and precipitation. NDVI and precipitation were calculated separately for autumn, winter, spring and summer. The sampling area of each region was calculated using data from an original source. Environmental variables for a region were averaged within this area across 30 arc-second grids (ca. 1 km resolution). Data on altitude were obtained using ArcGIS 10.6; data on NDVI were obtained from the VEGETATION Programme (<http://free.vgt.vito.be>), whereas data on air temperature and precipitation were obtained from the WORLDCLIM (BIOCLIM) 2.0 package (Fick and Hijmans 2017). The majority of environmental variables correlated with one another ($r = 0.33–0.92$, $p < 0.05$ for all). To avoid multicollinearity, we applied principal component analyses (PCA) of environmental variables separately for flea and mite data and substituted

the original values with the scores of the three (for fleas) or four (for mites) first principal components, which were then used as environmental variables (E1–E3 or E1–E4, respectively). These principal components explained 76.02% and 85.76% of environmental variation for flea and mite data, respectively. For flea data, E1 represented mainly an increase in summer precipitation and summer and autumn NDVI, and E2 correlated negatively with altitude, whereas E3 reflected an increase in mean and maximal air temperatures and spring and winter NDVI (see Table S1 in Supplementary Material). For mite data, E1 was associated mainly with an increase in maximal air temperature and E2 with an increase in mean air temperature, precipitation (fall, spring and summer) and a decrease in the annual range of air temperature, while E3 reflected an increase in mean and maximal altitude, and E4 correlated positively with NDVI (see Table S2 in Supplementary Material).

Host-associated variables

The host-associated environment was characterized from the perspective of host species composition, host phylogenetic diversity and host trait diversity (see data analyses) separately for flea and mite data. We took the data on host species composition from the original sources on ectoparasite species composition. In other words, we considered only those host species on which fleas or mites were recorded because hosts that do not support ectoparasite communities are unlikely to affect their diversity. We transformed host species composition into continuous predictors for further analyses as follows. First, we constructed distance matrices (separately for flea and mite hosts) of pairwise community dissimilarity between regional host assemblages using the Raup-Crick dissimilarity index (Raup and Crick 1979) with the function “vegdist” of the R package “vegan”. Then, we applied principal coordinate analyses on these distance matrices using the function “cmdscale” of the R base package “stats” and extracted five (Hc1–Hc5) vectors for the composition of host species harbouring either fleas or mites. These vectors explained 71.25% and 71.22% of the variation and were thus continuous variables representing differences in host species composition for fleas and mites, respectively, among regions.

To characterize the host-associated environment from the perspective of host phylogenetic diversity, we used the global phylogenetic supertree of Bininda-Emonds et al. (2007) and established the topology of branches within orders, families and genera using various sources (see references in Krasnov et al. 2019b) (we also used this tree calculating the degree of phylogenetic host specificity of ectoparasites; see above). The lengths of all branches were set to an equal length of 1, and the tree was arbitrarily ultrametricized using the program Mesquite 3.51 (Maddison and Maddison 2018). Then, we constructed distance matrices (separately for flea and mite

hosts) of pairwise phylogenetic community dissimilarity between regional host assemblages (Ives and Helmus 2010) using the R packages “ape” (Paradis et al. 2004) and “picante” (Kembel et al. 2010). We applied a principal coordinate analysis to these distance matrices as described above (i.e. using function “cmdscale”) and extracted five vectors of host phylogenetic composition (Hp1–Hp5) for either flea or mite hosts. Similarly to host species composition factors, the vectors of host phylogenetic composition represented among-region variation in the phylogenetic composition of hosts exploited by fleas and mites and explained 54.35% and 41.58% of this variation, respectively.

To depict the host-associated environment from the perspective of host traits, we characterized host species by quantitative and ordinal traits that could affect either flea or mite parasitism or the species composition and richness of ectoparasite assemblages, namely body mass, basal metabolic rate, skin thickness, hair density, geographic range, population density, degree of sociality, shelter depth and complexity, and hibernation pattern (see rationale, explanations and details in Krasnov et al. 2016). Trait values were extracted either from the PanTHERIA database (Jones et al. 2009) or from various sources (see references in Krasnov et al. 2016). To obtain variables representing among-region variation in host trait composition, we first constructed among-host trait distance matrices (separately for flea and mite hosts) using the Gower distance coefficient with the function “gowdis” implemented in the R package “FD” (Laliberté and Legendre 2010). From these matrices and host species \times region matrices, we then built matrices of trait dissimilarities among regional host assemblages based on trait dissimilarities between host species using a functional dissimilarity measure based on a generalized Sørensen dissimilarity (Ricotta et al. 2016) with the function “PADDIS” implemented in the R package “adiv” (Pavoine 2018). These trait dissimilarity matrices were transformed into continuous predictors via principal coordinate analyses with the R function “cmdscale” (see above). This resulted in two (Ht1 and Ht2; for flea hosts) and three (Ht1–Ht3; for mite hosts) vectors reflecting among-region variation in the trait composition of host assemblages and explaining 64.45% and 69.32% of this variation.

Spatial variables

To obtain spatial variables for the main analyses (see below), we applied the approach of Moran Eigenvectors Maps (MEM) [= the principal coordinates of neighbouring matrices (PCNMs)] (Dray et al. 2006), which allows the evaluation of spatial structures over a range of scales with the first to the last eigenvectors representing ever-decreasing spatial scales (Borcard and Legendre 2002). We built a truncated Euclidean distance matrix from geographic coordinates of the regions (separately for fleas and mites) and then extracted

eigenvectors with positive eigenvalues (Borcard and Legendre 2002). These spatial variables (further referred to as PCNMs) were extracted using the function “pcnm” implemented in the R package “vegan”. Then, we tested each PCNM for spatial autocorrelation using Moran’s I test implemented in the R package “ape” and retained for further analyses only the PCNMs that were characterized by a significant spatial autocorrelation (13 of 25 PCNMs for flea data and seven of 15 PCNMs for mite data) (Borcard et al. 2018).

Data analyses

We produced three dissimilarity matrices (β_{total} , β_{repl} and β_{rich}) based on each of the following: (a) flea or mite species incidence (compositional beta-diversity), (b) phylogenetic (for fleas) or taxonomic (for mites) information (phylogenetic or taxonomic beta-diversity, respectively) and (c) information on flea or mite species traits (functional beta-diversity) using the function “beta” implemented in the R package “BAT” (Cardoso et al. 2014, 2015, 2018). Average indices of compositional, phylogenetic/taxonomic and functional beta-diversity (β_{total}) and its components (β_{repl} and β_{rich}) were calculated using the function “beta.multi” from the package “BAT” separately for fleas and mites.

To test for the effects of the environment, host-associated factors and space on variation in each component of each of the three facets of flea and mite beta-diversity (compositional, phylogenetic/taxonomic and functional), we applied a distance-based redundancy analysis (db-RDA; Legendre and Legendre 1998; Legendre and Anderson 1999; Borcard et al. 2018). A distance-based redundancy analysis allows one to perform constrained ordinations on data using non-Euclidean dissimilarity measures. Given that our response matrices (pairwise total beta-diversity and its components) consisted of a matrix of distances between “objects” (pairwise between-region differences in species compositions and richness) which may be generated by non-linear measures, application of db-RDA allowed us to determine how well environmental, host-associated and spatial parameters can explain the variation among these “objects” in the matrix. Importantly, db-RDA allows testing for the effect of each separate factor or gradient on the variation in beta-diversity as well as for shared effects of any combination of these factors/gradients. A possibility of estimation of the pure and shared effects of separate explanatory variables represents one of the advantages of db-RDA over other methods of beta-diversity studies such as, for example, multiple regression on distance matrices (MRM; Lichstein 2007). Technically, db-RDA first applies a principal coordinate analysis on the response distance matrix and converts it back to a rectangular table containing rows of objects by columns of “principal coordinates”. This set of “principal coordinates” represent the dissimilarities in a Euclidean space and are then related to additional

environmental parameters using a classical redundancy analysis which, in turn, is a method allowing extraction and summarisation of the variation in a set of response variables (i.e. resulted) principal coordinates as explained by a set of explanatory variables (i.e. environmental, host-associated and spatial gradients). In addition, using db-RDA allowed our results on drivers of beta-diversity of ectoparasitic arthropods being directly comparable with those obtained by Rocha et al. (2018) on drivers of beta-diversity of free-living insects.

In our analyses, variables describing host-associated environment were represented by (a) host species composition for compositional beta-diversity, (b) host phylogenetic composition for phylogenetic (for fleas)/taxonomic (for mites) beta-diversity and (c) host trait composition for functional beta-diversity. The db-RDAs were carried out with the function “capscale” from the R package “vegan” with the option “sqrt.dist” set to “TRUE” to correct for negative eigenvalues (Legendre 2014; Rocha et al. 2018). To understand the pure and shared effects of the off-host environment, host-associated environment and space on each of the three measures of compositional, phylogenetic/taxonomic and functional beta-diversity, we used variation partitioning via the function “varpart” from the R package “vegan”. This function partitions the variation in the response table (in our case pairwise dissimilarity matrix of beta-diversity) into components accounted for explanatory variables and their combined effects. Then we tested for the significance of the pure effects using the function “anova” of the “vegan” package. The latter function was also used to test the significance of separate explanatory variables (Oksanen et al. 2018). Prior to running db-RDAs, we selected

the final sets of predictors using the function “ordistep” of the package “vegan” with 499 permutations. This function allows variable selection for constrained ordination using permutation p values (Borcard et al. 2018; Oksanen et al. 2018). The selection using “ordistep” resulted in the retention, for the main analyses, of only those variables which did not show collinearity, namely all principal components of environmental variables and all predictors associated with composition, phylogeny and traits of hosts, but only five (S1–S5) of 13 PCNMs for flea data and two (S1–S2) of seven PCNMs for mite data.

Results

In fleas, the β_{repl} component was higher than β_{rich} independently of whether beta-diversity was determined by compositional, phylogenetic or functional dissimilarities (Table 1). In mites, indices of all facets of beta-diversity (including β_{total}) were lower than those of fleas with the contribution of the β_{repl} component to the β_{total} of either beta-diversity facet being approximately the same as that of β_{rich} (Table 1).

The distance-based redundancy analyses of flea beta-diversity demonstrated that variation in compositional, phylogenetic and functional β_{total} , as well as the respective β_{repl} components, was significantly associated with variation in all three groups of factors (Table 2, Fig. 1). The same was true for functional β_{rich} . Nevertheless, environmental variables taken separately from other predictors produced significant axes for phylogenetic β_{rich} (Table 2).

Table 1 Indices of compositional, phylogenetic and functional beta-diversity and its fractions (i.e. species replacement and richness difference) of flea and gamasid mite communities harboured by small mammalian hosts in the Palearctic

Ectoparasite taxon	Beta-diversity	Fraction	Average	Variance
Fleas	Compositional	Total	0.88	0.02
		Species replacement	0.63	0.02
		Richness difference	0.25	0.01
	Phylogenetic	Total	0.67	0.02
		Species replacement	0.48	0.01
		Richness difference	0.19	0.00
	Functional	Total	0.63	0.02
		Species replacement	0.42	0.01
		Richness difference	0.21	0.01
Mites	Compositional	Total	0.53	0.05
		Species replacement	0.30	0.03
		Richness difference	0.24	0.02
	Taxonomic	Total	0.39	0.04
		Species replacement	0.21	0.02
		Richness difference	0.18	0.02
	Functional	Total	0.29	0.03
		Species replacement	0.15	0.01
		Richness difference	0.13	0.01

Table 2 Results of the significance tests of distance-based redundancy analyses of the total compositional (C), phylogenetic/taxonomic (P/T) or functional (F) beta-diversity (β_{total}) of flea and mite communities and its components [species replacement (β_{repl}) and richness difference (β_{rich})]. Constrained inertia (ConstI) is the proportion of total variance uniquely explained by the explanatory variables (Borcard et al. 2018). The significance of all explanatory variables, as well as the pure effects of the off-host environment, host-associated environment (compositional, phylogenetic or trait-bases) and space, was tested using the function “anova” in the R package “vegan” (see text for explanations)

Beta-diversity	Fraction	Set of explanatory variables	Fleas			Mites		
			ConstI	SS	F	ConstI	SS	F
C	β_{total}	Entire	0.47	9.01	2.09*	0.51	5.11	1.77*
		Environment	0.15	2.94	2.46*	0.25	2.47	2.11*
		Host-associated	0.24	4.64	3.75*	0.29	2.81	1.93*
		Space	0.22	4.41	2.32*	0.13	1.31	2.09*
	β_{repl}	Entire	0.44	8.34	2.36*	0.73	4.00	1.94*
		Environment	0.20	2.76	2.69*	0.38	2.08	2.44*
		Host-associated	0.32	4.43	2.80*	0.42	2.31	2.18*
		Space	0.30	4.21	2.61*	0.20	1.12	2.42*
	β_{rich}	Entire	0.16	0.17	2.22	0.45	1.96	1.22
		Environment	0.12	0.65	1.6	0.20	0.88	1.49
		Host-associated	0.17	0.91	1.32	0.20	0.88	1.15
		Space	0.16	0.88	1.28	0.10	0.30	1.93
P/T	β_{total}	Entire	0.29	7.46	2.42*	0.47	3.72	1.44*
		Environment	0.18	2.65	2.98*	0.25	2.03	2.15*
		Host-associated	0.28	4.15	3.03*	0.16	1.28	0.98
		Space	0.23	3.48	2.40*	0.13	1.06	2.09*
	β_{repl}	Entire	0.49	6.83	2.76*	0.65	2.93	1.52*
		Environment	0.23	2.43	3.23*	0.38	1.66	2.46*
		Host-associated	0.37	3.94	3.49*	0.21	0.91	0.88
		Space	0.31	3.24	2.67*	0.21	0.89	2.42*
	β_{rich}	Entire	0.14	1.65	1.31	0.47	1.69	1.35
		Environment	0.14	0.58	1.95*	0.20	0.73	1.52
		Host-associated	0.16	0.65	1.28	0.20	0.71	1.41*
		Space	0.15	0.65	1.27	0.09	0.33	1.30
F	β_{total}	Entire	0.26	5.94	2.54*	0.47	2.95	1.94*
		Environment	0.18	2.51	3.01*	0.27	1.70	2.29*
		Host-associated	0.14	2.03	3.60*	0.18	1.16	1.95*
		Space	0.23	3.22	2.36*	0.14	0.88	2.18*
	β_{repl}	Entire	0.40	4.95	2.59*	0.66	2.26	2.12*
		Environment	0.22	2.04	2.97*	0.39	1.32	2.49*
		Host-associated	0.14	1.27	2.62*	0.22	0.74	1.64*
		Space	0.30	2.84	2.58*	0.19	0.33	2.22*
	β_{rich}	Entire	0.26	2.03	2.29*	0.40	1.18	1.42
		Environment	0.17	0.81	2.61*	0.22	0.65	1.75
		Host-associated	0.27	1.30	7.28*	0.23	0.68	2.54*
		Space	0.16	0.77	1.40	0.13	0.38	1.92

SS sum of squares, F pseudo-F (Borcard et al. 2018)

* $p < 0.001$

Furthermore, correlations between ordination axes for compositional β_{rich} and one host-associated factor (Hc1) and one spatial variable (S1) were significant ($p < 0.05$ for both) (Fig. 1). The results of separate significance tests for each explanatory variable and correlations between individual predictors and the first two ordination axes are presented in the Supplementary Material (Tables S3–S5 and Tables S6–S8, respectively).

The ordination axes of the entire model db-RDAs for the β_{total} of all three facets of beta-diversity of mites and their β_{repl} components were significant (Table 2, Fig. 2). However, this was not the case for the pure fraction of host-associated variables and taxonomic beta-diversity (Table 2). Although the variation in compositional, taxonomic and functional β_{rich} represented by axes of the entire model db-RDAs did not differ from random, the pure fraction of host-associated variables

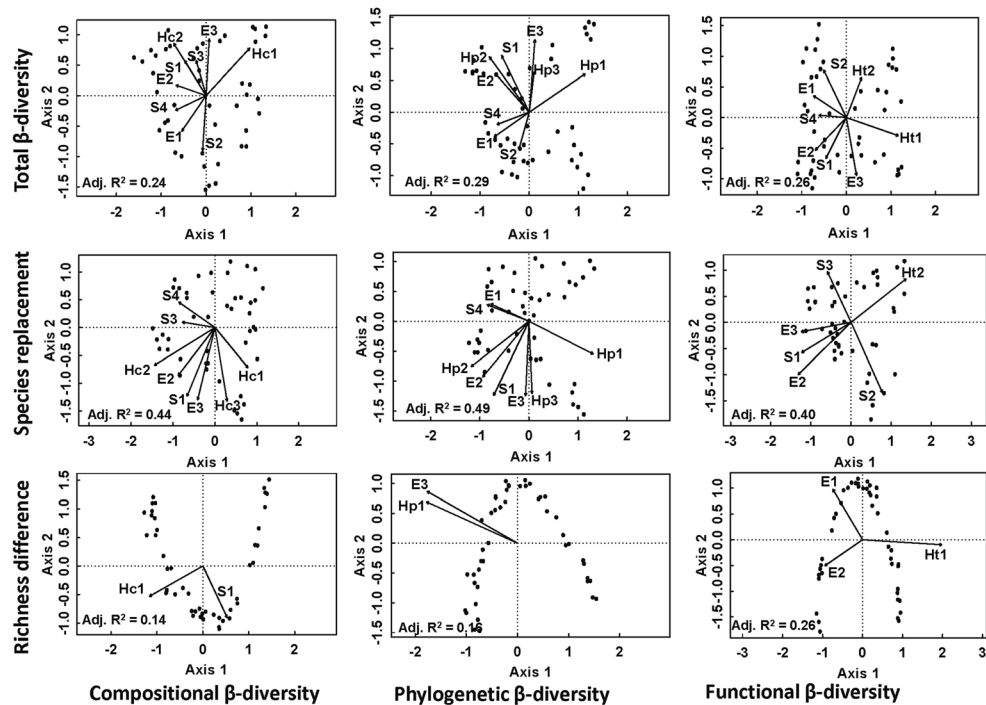


Fig. 1 Biplots of distance-based redundancy analyses of the compositional, phylogenetic and functional beta-diversity (total beta-diversity and its species replacement and richness difference components) of fleas. The length of each arrow is proportional to the correlation between the ordination and the respective variable. E, H (Hc, Hp and Ht) and S are

environmental, host-associated (compositional, phylogenetic and trait-based, respectively) and space variables, respectively. Numbers denote the individual numbers of variables. Only variables significantly correlated with the ordination axes are shown

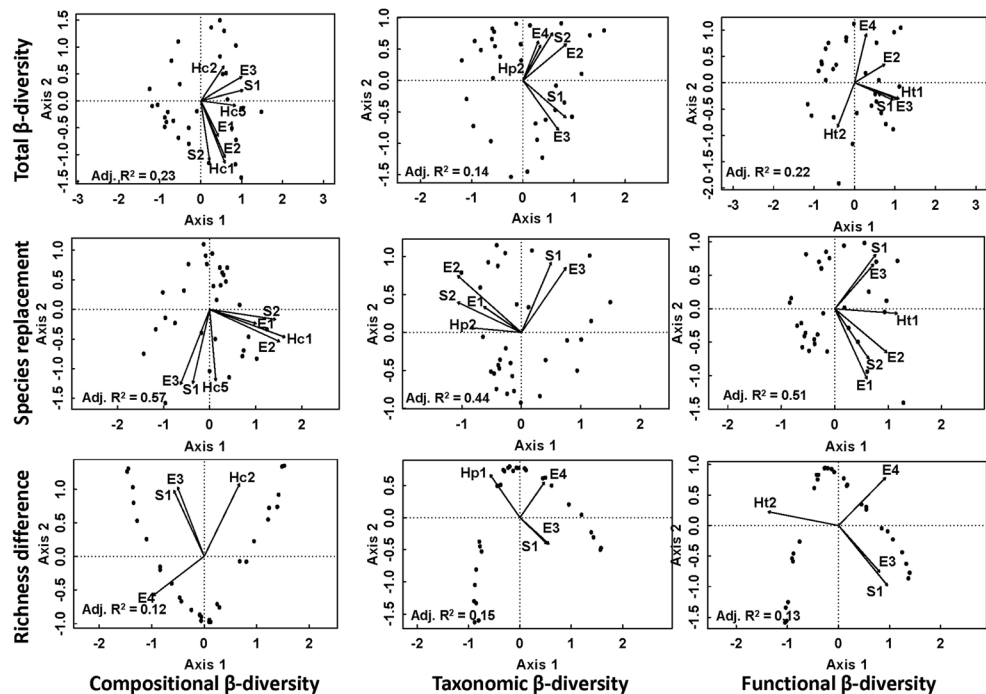


Fig. 2 Biplots of distance-based redundancy analyses of the compositional, taxonomic and functional beta-diversity (total beta-diversity and its species replacement and richness difference components) of gamasid mites. The length of each arrow is proportional to the correlation between the ordination and the respective variable. E, H (Hc, Hp and Ht) and S are

environmental, host-associated (compositional, phylogenetic and trait-based, respectively) and space variables, respectively. Numbers denote the individual numbers of variables. Only variables significantly correlated with the ordination axes are shown

was significant for taxonomic and functional β_{rich} (Table 2, Fig. 2). In addition, some individual environmental, host-associated and/or spatial variables correlated positively with ordination axes for the β_{rich} of all beta-diversity facets (Fig. 2; see also Tables S11–S14 of the Supplementary Material).

Venn diagrams based on variation partitioning and demonstrating variation in flea beta-diversity as explained by unique and shared effects of environmental, host-associated and spatial predictors are presented in Fig. 3. The largest fractions of variation in compositional β_{total} and β_{repl} were almost equally explained by host-associated and spatial predictors. Variation in compositional β_{rich} was jointly explained by all three groups of predictors with the unique effect of environment being important as well. Variation in host phylogenetic composition explained substantially more variation in phylogenetic β_{total} and β_{repl} than other groups of predictors or their joint actions. Similarly to compositional β_{rich} , variation in phylogenetic β_{rich} was best explained by the shared contribution of all groups of predictors followed by the unique contribution of environment. The unique contribution of spatial variables appeared to be the most important in explaining variation in functional β_{total} and β_{repl} , whereas variation in host trait diversity explained the largest fraction of variation in functional β_{rich} .

The variation partitioning of the ordination of mite data is presented in Fig. 4. Host-associated predictors either alone or jointly with environmental predictors explained the largest portion of the variation in compositional β_{total} , β_{repl} and β_{rich} . In contrast, these predictors were the least important in explaining the variation in taxonomic beta-diversity. Instead,

the most important drivers of the latter were environmental predictors, which also acted jointly with spatial variables in explaining most of the variation in taxonomic β_{repl} . The variation in functional β_{total} and β_{repl} was best explained by the unique contributions of environmental predictors followed by host-associated variables, whereas the fractions representing the shared effects of either the two latter or all three groups of explanatory variables significantly explained the variation in the β_{rich} component of this beta-diversity facet.

Discussion

The most important finding of this study is that the pattern of the relative importance of environmental, host-associated and spatial variables is widely variable between beta-diversity facets, their components and the two ectoparasite taxa. This is in contrast to the results of some, but not other, earlier studies of beta-diversity variation (Heino and Tolonen 2017; Rocha et al. 2018 vs Soinen et al. 2016, respectively). Contrasting results of ecological studies dealing with similar questions and carried out on different taxa or even the same taxon can, sometimes, be attributed to differences in analytical approaches (e.g. Poisot et al. 2017 vs. Krasnov et al. 2019a). Here, we intentionally followed the analytical methodology applied by Rocha et al. (2018) for freshwater macroinvertebrates, but the pattern of the relative effect of each group of predictors on each beta-diversity facet was found to be similar in Rocha et al. (2018) and different in our study.

Fig. 3 Venn diagrams based on variation partitioning of the variation in the compositional, phylogenetic and functional beta-diversity of fleas as explained by unique and shared effects of environmental (E), host-associated (Hc, Hp and Ht for species composition, phylogeny and trait composition, respectively) and spatial (S) predictors. Negative fractions and zero (see Legendre 2008) are not shown

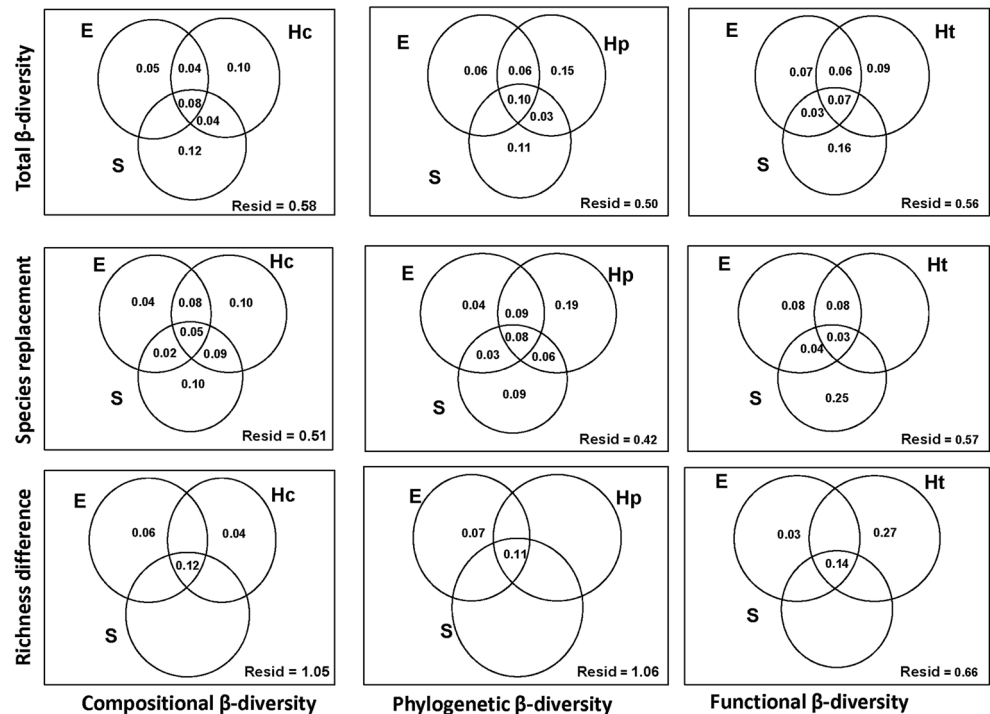
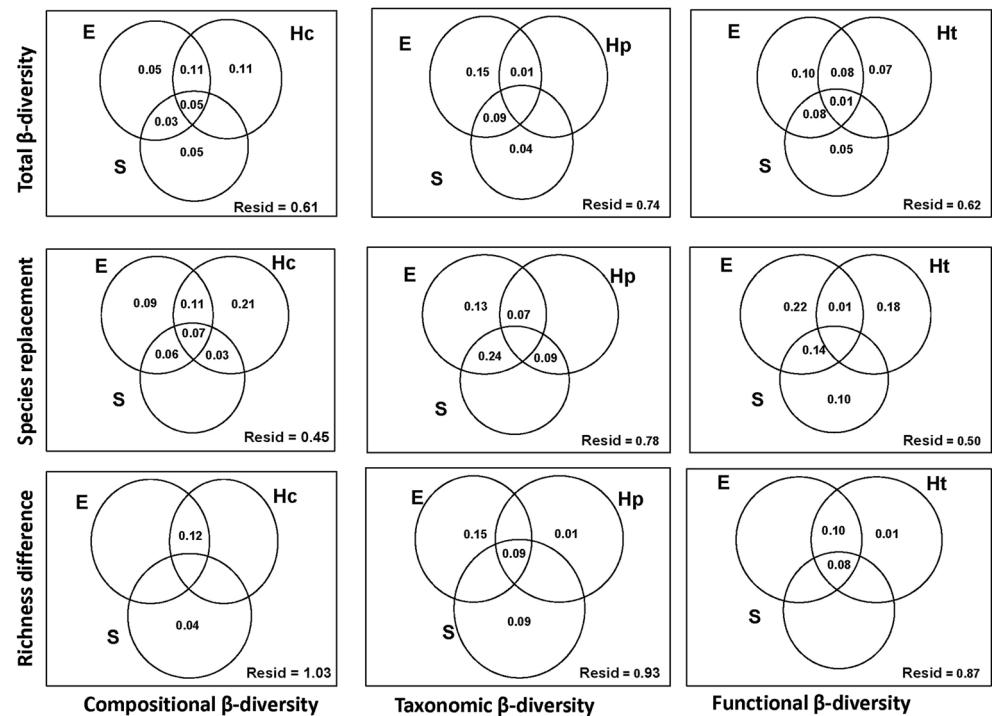


Fig. 4 Venn diagrams based on variation partitioning of the variation in the compositional, taxonomic and functional beta-diversity of gamasid mites as explained by unique and shared effects of environmental (E), host-associated (Hc, Hp and Ht for species composition, phylogeny and trait composition, respectively) and spatial (S) predictors. Negative and zero fractions (see Legendre 2008) are not shown



Environmental effects

We found that environmental variation contributed mostly to variation in (a) the compositional and phylogenetic β_{rich} of fleas and (b) the taxonomic β_{total} , β_{repl} and β_{rich} and functional β_{total} and β_{repl} of mites. The effect of external environment (especially air temperature and moisture) on ectoparasite communities (species richness, species composition, relative abundances) has been repeatedly documented (e.g. Krasnov et al. 2010a, b for fleas; Vinarski et al. 2007 for gamasid mites). Obviously, this effect is realized via responses of individual species (Marshall 1981; Krasnov 2008; Walter and Proctor 2013) and thus is reflected by the species composition of an assemblage. However, the species composition of flea communities was earlier found to be, to a great extent, the result of filtering by host species composition, whereas the abiotic environment played a secondary role (Krasnov et al. 2015). Nevertheless, environmental variation did not adequately explain the variation in the compositional and phylogenetic β_{total} of fleas, but did explain their β_{rich} components quite well, thus reflecting the losses/gains of species or phylogenetic lineages. The effect of environment on compositional β_{rich} can be explained by, for example, species loss due to harsh conditions in northern regions, whereas this effect on phylogenetic β_{rich} can be associated with evolutionary/historical patterns of dispersal in different phylogenetic lineages (e.g. Medvedev 2014).

In contrast to flea communities that are strongly influenced by host-associated variables (Krasnov et al. 2015), ectoparasitic gamasid mites are highly sensitive to both environmental

conditions and host species composition (Vinarski et al. 2007). For example, the similarity in mite assemblages has been found to decrease with both increasing environmental dissimilarity and increasing dissimilarity in host species composition (Vinarski et al. 2007). This is the most likely reason for the variation in the compositional beta-diversity of mites being linked with the variation in both environment and hosts. However, the variation in the taxonomic and functional beta-diversity of mites was almost solely explained by the variation in environmental, rather than host-associated, predictors (except for functional β_{rich}). On one hand, a strong effect of environment on the taxonomic and functional beta-diversity of mites may arise because of the differential responses of mites belonging to different taxonomic groups or possessing different traits due to environmental factors. For example, the relationship between body size and environmental tolerance has been shown in some arthropod taxa (e.g. Kaspari et al. 2015), although this has never been experimentally tested in mites. Nevertheless, indirect observations implied that the linkage between body size and a certain degree of environmental tolerance may be the case for gamasids (Krasnov et al. 2013). On the other hand, the general lack of effect of the variation in the phylogenetic or trait composition of host communities on the variation in the taxonomic or functional, respectively, beta-diversity of mites can be explained by an extremely broad host generalism (both from the phylogenetic and trait-based perspective) of many mites either belonging to the same taxonomic group or possessing the same trait. For example, all *Androlaelaps* mites are obligate non-exclusive haematophages and are found on host species belonging to

different genera, families, orders and even classes and differing in a variety of their ecological, morphological and physiological traits (Vinarski and Korralo-Vinarskaya 2017). Similarly, many (albeit not all) species of *Haemogamasus* are facultative haematophages recorded on multiple rodent and shrew hosts (Vinarski and Korralo-Vinarskaya 2017).

Host effects

Variation in the compositional, phylogenetic or trait structure of host communities was an important factor responsible for variation in (a) the compositional and phylogenetic β_{total} and β_{repl} of fleas and the compositional β_{total} and β_{repl} of mites and (b) the functional β_{rich} of both taxa. Strong links between host and parasite species or phylogenetic lineage composition have often been reported (Krasnov et al. 2012; Dallas and Presley 2014; Maestri et al. 2017). This is not surprising because, from an ecological perspective, the species composition and phylogenetic structure of any community are determined by the availability of resources utilized by the species composing this community, while from an evolutionary perspective, the species of a given community either originated locally or immigrated. In parasite communities, the availability of resources is represented by host availability, as parasites cannot exist without exploiting their hosts, which has itself an important evolutionary component. As a result, the species composition of a parasite community is partly due to the identities of the host species and partly due to the evolution and historical biogeography of these hosts. Although parasite and host phylogenies are rarely fully congruent because of host switching and other co-evolutionary events (Poulin 2007), strong relationships between host and parasite evolutionary histories cannot be refuted (Hadfield et al. 2014). Therefore, parasite species and lineage turnover, but not species or lineage richness, appeared to be strongly influenced by host species and lineage turnover.

We found an effect of host phylogenetic composition on the phylogenetic beta-diversity of fleas, but not on the taxonomic beta-diversity of mites. One of the reasons behind this may be the availability of the phylogenetic tree for fleas but not for mites. The mite taxonomic tree used in our study was poorly resolved and contained only one superfamily, four families (among them Macronyssidae with one species recorded in one region only), five subfamilies and eight genera. It seems that this did not allow us to distinguish successfully among different mite assemblages by their taxonomic composition, so that mite taxonomic composition varied substantially more weakly along axes that portrayed host phylogenetic composition than along environmental gradients.

Variation in the trait composition of host communities was the main factor explaining the total functional beta-diversity, as well as its richness difference component, in both taxa. In addition, the effect of host traits was important as a driver of functional β_{repl} in mites. The link between the traits of a

consumer species and a consumed species is well known for free-living organisms (Rezende et al. 2007; Spitz et al. 2014). Moreover, the importance of trait complementarity between parasites and their hosts for understanding the ecology and evolution of host-parasite interactions has been recognized (e.g. McQuaid and Britton 2013). Indeed, a study that specifically tested the association between parasite (fleas) and host (small mammals) traits reported that fleas possessing certain traits exploit mostly hosts possessing certain traits (Krasnov et al. 2015 for fleas). The complementarity of parasite and host traits is predominantly related to the resource acquisition by parasites, including both extracting the resource from a host and avoiding or minimizing the effect of its defence efforts. In haematophagous ectoparasites, the extraction of the resource (blood) can be achieved due to morphological complementarity between parasite mouthparts and host skin thickness and/or depth of cutaneous blood vessels. The host's anti-parasitic grooming impairs ectoparasite feeding and causes their mortality (e.g. Hawlena et al. 2007). Consequently, ectoparasites exploiting hosts with higher grooming abilities are usually characterized by developed anti-grooming tools such as combs and setae (Marshall 1982; Krasnov 2008). These examples suggest that the disappearance of a host trait (represented by species possessing this trait) from a location may lead to a loss of a complementary trait represented by ectoparasite species. Similarly, a turnover of host traits may be coupled with a turnover of respective ectoparasite traits. These processes may underlie the effect of variation in the trait composition of host communities on variation in the functional beta-diversity of parasites.

Spatial effects

Spatial variation, jointly with host-associated or environmental factors, was the main driver of the compositional and functional β_{total} and β_{repl} of fleas, while space played a minor (if any) role as a driver of mite beta-diversity. The lack of any substantial effect of space on either facet of mite beta-diversity suggests that, in general, biodiversity of this taxon is scale-invariant. The reason for this can be that mites use their hosts not only as a food source but also as an important tool for dispersal (Radovsky 1985; Walter and Proctor 1999). As a result, and despite their limited abilities for active dispersal, the passive dispersal of mites (i.e. phoresy on various mammals and even birds and insects) allows them to overcome long distances. In other words, mites are broadly spread by their hosts, so that their beta-diversity (= dissimilarity among locations) does not depend on distance between locations (see also Vinarski et al. 2007).

By contrast, the contributions of spatial variables were important in explaining the variation in flea beta-diversity, especially in its species replacement component. This suggests that flea assemblages are spatially structured with this structure

manifested mainly at the large scale (because the PCNMs that correlated significantly with ordination axes were the first three or four; Tables S6–S8 of Supplementary Material). In part, this is because of the great spatial extent of our study (mean and maximal distance between pairs of regions were 2880.5 km and 7939.3 km, respectively). Biologically, this shows substantial differences in species composition but not species richness between flea assemblages situated far away from each other. For example, flea assemblages of both south-eastern Azerbaijan and the Mongolian Central Khangay were composed of the same number of species (21), but there were no shared species between these assemblages. In contrast, although the flea communities of Slovakia and Poland differed slightly in their species richness (24 and 20, respectively), 19 species were present in both regions.

In conclusion, the pattern of the relative effects of environmental, host-associated and spatial factors on beta-diversity is context-dependent and may differ among different facets of beta-diversity and their different components. This suggests that compositional, phylogenetic/taxonomic and functional beta-diversity can be governed by different rules (e.g. Soiminen et al. 2016), similarly to the case of alpha-diversity (Krasnov et al. 2010a, b). In addition, this pattern may also differ among communities of different taxa depending on their biological affinities.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Ackerly DD (2003) Community assembly, niche conservatism and adaptive evolution in changing environments. *Int J Plant Sci* 164:S165–S184. <https://doi.org/10.1086/368401>
- Aldredge RD, Miller TL, Smit NJ (2015) The butterfly effect: parasite diversity, environment, and emerging disease in aquatic wildlife. *Trends Parasitol* 31:160–166. <https://doi.org/10.1016/j.pt.2014.11.001>
- Baselga A (2007) Disentangling distance decay of similarity from richness gradients: response to Soiminen et al. 2007. *Ecography* 30:838–841. <https://doi.org/10.1111/j.2007.0906-7590.05191.x>
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr* 19:134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A (2007) The delayed rise of present-day mammals. *Nature* 446: 507–512. <https://doi.org/10.1038/nature05634>
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Model* 153:51–68. [https://doi.org/10.1016/S0304-3800\(01\)00501-4](https://doi.org/10.1016/S0304-3800(01)00501-4)
- Borcard D, Gillet F, Legendre P (2018) Numerical ecology with R, 2 edn. Springer, New York. <https://doi.org/10.1007/978-3-319-71404-2>
- Bregetova NG (1956) Gamasid mites (Gamasoidea). A short identification key. *Acad Sci USSR. USSR, Moscow (in Russian)*
- Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PAV, Podani J, Schmera D (2014) Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *J Biogeogr* 41:749–761. <https://doi.org/10.1111/jbi.12239>
- Cardoso P, Rigal F, Carvalho JC (2015) BAT – Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods Ecol Evol* 6:232–236. <https://doi.org/10.1111/2041-210X.12310>
- Cardoso P, Rigal F, Carvalho JC (2018) BAT: biodiversity assessment tools. R package version 1.6.0. <https://CRAN.R-project.org/package=BAT>
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecol Lett* 12: 693–715. <https://doi.org/10.1111/j.1461-0248.2009.01314.x>
- Clark NJ, Clegg SM, Sam K, Goulding W, Koane B, Wells K (2018) Climate, host phylogeny and the connectivity of host communities govern regional parasite assembly. *Divers Distrib* 24:13–23. <https://doi.org/10.1111/ddi.12661>
- Clarke KR, Warwick RM (1999) The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Mar Ecol Progr Ser* 184:21–29. <https://doi.org/10.3354/meps184021>
- Dallas T, Presley SJ (2014) Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities. *Oikos* 123:866–874. <https://doi.org/10.1111/oik.00707>
- Davydova MS, Belova OS (1972) Fauna of gamasid mites of the floodplain of the Ob River. In: Maximov AA (ed) Biological resources of the River Ob valley. Nauka, Siberian Branch, Novosibirsk, USSR, pp 306–324 in Russian
- De Bello F, Lavergne S, Meynard CN, Lepš J, Thuiller W (2010) The partitioning of diversity: showing Theseus a way out of the labyrinth. *J Veget Sci* 21:992–1000. <https://doi.org/10.1111/j.1654-1103.2010.01195.x>
- Dowling APG, OConnor BM (2010) Phylogeny of Dermansysoidea (Acari:Parasitiformes) suggests multiple origins of parasitism. *Acarologia* 50:113–129. <https://doi.org/10.1051/acarologia/20101957>
- Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Model* 196:483–493. <https://doi.org/10.1016/j.ecolmodel.2006.02.015>
- Eidler A, Mehl R (1972) Mites (Acari, Gamasina) from small mammals in Norway. *Norsk Entomologisk Tidsskr* 19:133–147
- Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315. <https://doi.org/10.1002/joc.5086>
- Hadfield JD, Krasnov BR, Poulin R, Nakagawa S (2014) A tale of two phylogenies: comparative analyses of ecological interactions. *Am Nat* 183:174–187. <https://doi.org/10.1086/674445>
- Harrison S, Ross SJ, Lawton JH (1992) Beta-diversity on geographic gradients in Britain. *J Anim Ecol* 61:151–158. <https://doi.org/10.2307/5518>
- Hawlena H, Abramsky Z, Krasnov BR, Saltz D (2007) Host defence versus intraspecific competition in the regulation of infrapopulations

- of the flea *Xenopsylla conformis* on its rodent host *Meriones crassus*. *Int J Parasitol* 37:919–925. <https://doi.org/10.1016/j.ijpara.2007.01.015>
- Heino J, Tolonen KT (2017) Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity. *Limnol Oceanogr* 62:2431–2444. <https://doi.org/10.1002/lno.10577>
- Ives AR, Helmus MR (2010) Phylogenetic metrics of community similarity. *Am Nat* 176:E128–E142. <https://doi.org/10.1086/656486>
- Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648. <https://doi.org/10.1890/08-1494.1> (last modified 2014)
- Kamiya T, O'Dwyer K, Nakagawa S, Poulin R (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biol Rev* 89:123–134. <https://doi.org/10.1111/brv.12046>
- Kaspari M, Clay NA, Lucas J, Yanoviak SP, Kay A (2015) Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. *Glob Chang Biol* 21:1092–1102. <https://doi.org/10.1111/gcb.12750>
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Krasnov BR (2008) Functional and evolutionary ecology of fleas. A model for ecological parasitology. Cambridge Univ Press, Cambridge. <https://doi.org/10.1017/CBO9780511542688>
- Krasnov BR, Shenbrot GI, Khokhlova IS, Poulin R (2005) Nested pattern in flea assemblages across the host's geographic range. *Ecography* 28:475–484. <https://doi.org/10.1111/j.0906-7590.2005.04238.x>
- Krasnov BR, Shenbrot GI, Khokhlova IS, Poulin R (2007) Geographical variation in the “bottom-up” control of diversity: fleas and their small mammalian hosts. *Glob Ecol Biogeogr* 16:179–186. <https://doi.org/10.1111/j.1466-8238.2006.00273.x>
- Krasnov BR, Mouillot D, Shenbrot GI, Khokhlova IS, Vinarski MV, Korralo-Vinarskaya NP, Poulin R (2010a) Similarity in ectoparasite faunas of Palaearctic rodents as a function of host phylogenetic, geographic or environmental distances: which matters the most? *Int J Parasitol* 40:807–817. <https://doi.org/10.1016/j.ijpara.2009.12.002>
- Krasnov BR, Mouillot D, Shenbrot GI, Khokhlova IS, Poulin R (2010b) Deconstructing spatial patterns in species composition of ectoparasite communities: the relative contribution of host composition, environmental variables and geography. *Glob Ecol Biogeogr* 19:515–526. <https://doi.org/10.1111/j.1466-8238.2010.00529.x>
- Krasnov BR, Mouillot D, Khokhlova IS, Shenbrot GI, Poulin R (2012) Compositional and phylogenetic dissimilarity of host communities drives dissimilarity of ectoparasite assemblages: geographical variation and scale-dependence. *Parasitology* 139:338–347. <https://doi.org/10.1017/S0031182011002058>
- Krasnov BR, Vinarski MV, Korralo-Vinarskaya NP, Khokhlova IS (2013) Ecological correlates of body size in gamasid mites parasitic on small mammals: abundance and niche breadth. *Ecography* 36:1042–1050. <https://doi.org/10.1111/j.1600-0587.2012.00140.x>
- Krasnov BR, Shenbrot GI, Khokhlova IS, Stanko M, Morand S, 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. <https://doi.org/10.1111/ecog.00915>
- Krasnov BR, Shenbrot GI, Khokhlova IS, 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. <https://doi.org/10.1111/oik.02178>
- Krasnov BR, Shenbrot GI, Warburton EM, van der Mescht L, Surkova EN, Medvedev SG, Pechnikova N, Ermolova N, Kotti BK, Khokhlova IS (2019a) Species and site contributions to β -diversity in fleas parasitic on the Palearctic small mammals: ecology, geography and host species composition matter the most. *Parasitology* 146:653–661. <https://doi.org/10.1017/S0031182018001944>
- Krasnov BR, Shenbrot GI, van der Mescht L, Warburton EM, Khokhlova IS (2019b) Phylogenetic and compositional diversity are governed by different rules: a study of fleas parasitic on small mammals in four biogeographic realms. *Ecography (Early View)* 42:1000–1011. <https://doi.org/10.1111/ecog.04224>
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305. <https://doi.org/10.1890/08-2244.1>
- Legendre P (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J Plant Ecol* 1:3–8. <https://doi.org/10.1093/jpe/rtm001>
- Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. *Glob Ecol Biogeogr* 23:1324–1334. <https://doi.org/10.1111/geb.12207>
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24. [https://doi.org/10.1890/0012-9615\(1999\)069\[0001:DBRATM\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2)
- Legendre P, Legendre L (1998) Numerical ecology, 2nd Engl edn. Elsevier, Amsterdam
- Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *J Anim Ecol* 70:966–979. <https://doi.org/10.1046/j.0021-8790.2001.00563.x>
- Lichstein J (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol* 188:117–131. <https://doi.org/10.1007/s11258-006-9126-3>
- MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *Amer Nat* 101:377–385. <https://doi.org/10.1086/282505>
- Maddison WP, Maddison DR (2018) Mesquite: a modular system for evolutionary analysis, version 3.51. <http://mesquiteproject.org>
- Maestri R, Shenbrot GI, Krasnov BR (2017) Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. *J Biogeogr* 44:1880–1890. <https://doi.org/10.1111/jbi.13025>
- Marshall AG (1981) The ecology of ectoparasitic insects. Acad Press, London
- McQuaid CF, Britton NF (2013) Host-parasite nestedness: a result of co-evolving trait-values. *Ecol Complex* 13:53–59. <https://doi.org/10.1016/j.ecocom.2013.01.001>
- Medvedev SG (2014) The Palearctic centers of taxonomic diversity of fleas (Siphonaptera). *Entomol Rev* 94:345–358. <https://doi.org/10.1134/S0013873814030075>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) Vegan: community ecology package. R package version 2.5–2. <https://CRAN.R-project.org/package=vegan>
- Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290. <https://doi.org/10.1093/bioinformatics/btg412>
- Pavoine S (2018) Adiv: analysis of diversity. R package version 1.2. <https://CRAN.R-project.org/package=adiv>
- Poisot T, Guévevieux-Julien C, Fortin M-J, Gravel D, Legendre P (2017) Hosts, parasites and their interactions respond to different climatic variables. *Glob Ecol Biogeogr* 26:242–251. <https://doi.org/10.1111/geb.12602>

- Poulin R (2007) Evolutionary ecology of parasites: from individuals to communities, 2nd edn. Princeton University Press, Princeton
- Poulin R, Krasnov BR, Moullot D (2011) Host specificity in phylogenetic and geographic space. *Trends Parasitol* 27:355–361. <https://doi.org/10.1016/j.pt.2011.05.003>
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL <https://www.R-project.org/>
- Radovsky FJ (1985) Evolution of mammalian mesostigmatid mites. In: Kim KC (ed) Coevolution of parasitic arthropods and mammals. Wiley, New York, pp 441–504
- Raup DM, Crick RE (1979) Measurement of faunal similarity in paleontology. *J Paleontol* 53:1213–1227. <https://doi.org/10.2307/1304099>
- Rezende EL, Jordano P, Bascompte J (2007) Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos* 116:1919–1929. <https://doi.org/10.1111/j.0030-1299.2007.16029.x>
- Ricotta C, Podani J, Pavoine S (2016) A family of functional dissimilarity measures for presence and absence data. *Ecol Evol* 6:5383–5389. <https://doi.org/10.1002/ece3.2214>
- Rocha M, Bini LM, Domisch S, Tolonen KT, Jyrkänkallio-Mikkola J, Soininen J, Hjort J, Heino J (2018) Local environment and space drive multiple facets of stream macroinvertebrate beta diversity. *J Biogeogr* 45:2744–2754. <https://doi.org/10.1111/jbi.13457>
- Smith RJ (1999) Statistics of sexual size dimorphism. *J Hum Evol* 36:423–459. <https://doi.org/10.1006/jhev.1998.0281>
- Soininen J, Jamoneau A, Rosebery J, Passy SI (2016) Global patterns and drivers of species and trait composition in diatoms. *Glob Ecol Biogeogr* 25:940–950. <https://doi.org/10.1111/geb.12452>
- Spitz J, Ridoux V, Brind'Amour A (2014) Let's go beyond taxonomy in diet description: testing a trait-based approach to prey-predator relationships. *J Anim Ecol* 83:1137–1148. <https://doi.org/10.1111/1365-2656.12218>
- Surkova EN, Warburton EM, van der Mescht L, Khokhlova IS, Krasnov BR (2018a) Body size and ecological traits in fleas parasitic on small mammals in the Palearctic: larger species attain higher abundance. *Oecologia* 188:559–569. <https://doi.org/10.1007/s00442-018-4235-y>
- Surkova EN, Korralo-Vinarskaya NP, Vinarski MV, Stanko M, Warburton EM, van der Mescht L, Khokhlova IS, Krasnov BR (2018b) Sexual size dimorphism and sex ratio in arthropod ectoparasites: contrasting patterns at different hierarchical scales. *Int J Parasitol* 48:969–978. <https://doi.org/10.1016/j.ijpara.2018.05.006>
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302. <https://doi.org/10.1126/science.277.5330.1300>
- Vinarski MV, Korralo-Vinarskaya NP (2016) An annotated catalogue of the gamasid mites associated with small mammals in Asiatic Russia. The family Laelapidae s. str. (Acari: Mesostigmata: Gamasina). *Zootaxa* 4111:223–245. <https://doi.org/10.11646/zootaxa.4111.3.2>
- Vinarski MV, Korralo-Vinarskaya NP (2017) An annotated catalogue of the gamasid mites associated with small mammals in Asiatic Russia. The family Haemogamasidae (Acari: Mesostigmata: Gamasina). *Zootaxa* 4273:001–018. <https://doi.org/10.11646/zootaxa.4273.1.1>
- Vinarski MV, Korralo NP, Krasnov BR, Shenbrot GI, Poulin R (2007) Decay of similarity of gamasid mite assemblages parasitic on Palearctic small mammals: geographic distance, host-species composition or environment. *J Biogeogr* 34:1691–1700. <https://doi.org/10.1111/j.1365-2699.2007.01735.x>
- Walter DE, Proctor HC (1999) Mites: ecology, evolution and behaviour. Springer, Dordrecht, Netherlands
- Walter DI, Proctor HC (2013) Mites: ecology, evolution & behaviour. Life at a microscale, 2nd edn. Springer, Dordrecht. <https://doi.org/10.1007/978-94-007-7164-2>
- Warwick RM, Clarke KR (2001) Practical measures of marine biodiversity based on relatedness of species. *Oceanogr Mar Biol Annu Rev* 39:207–231
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33:475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol Monogr* 30:279–338. <https://doi.org/10.2307/1943563>
- Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* 21:213–251. <https://doi.org/10.2307/1218190>
- Williams PH (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proc R Soc B* 263:579–588. <https://doi.org/10.1098/rspb.1996.0087>
- Wilson MW, Shmida A (1984) Measuring beta diversity with presence-absence data. *J Ecol* 72:1055–1064. <https://doi.org/10.2307/2259551>
- Zemskaya AA (1973) Parasitic gamasid mites and their medical significance. Meditsina, Moscow (in Russian)
- Zhu Q, Hastriter MW, Whiting MF, Dittmar K (2015) Fleas (Siphonaptera) are cretaceous, and evolved with Theria. *Mol Phyl Evol* 90:129–139. <https://doi.org/10.1016/j.ympev.2015.04.027>

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