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Research article

Latitudinal distributions of the species richness, phylogenetic diversity, and functional diversity of fleas and their small mammalian hosts in four geographic quadrants

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We studied latitudinal patterns in the species richness (SR), the phylogenetic diversity (PD), and the functional diversity (FD) of fleas and their mammalian hosts. We asked whether these patterns in either fleas, hosts, or both 1) conform to a classical latitudinal gradient; 2) vary geographically; and 3) differ between fleas and hosts. We also asked whether the patterns of PD and FD follow those of SR. We collected data on the latitudinal distribution of 1022 flea and 900 mammal species from literature sources and calculated the SR, PD, and FD of both groups in 1° latitude bands. Then, we used broken-stick regression models to analyse separately the latitudinal variation of 1) each diversity facet and 2) fleas and hosts in each geographic quadrant. The classical latitudinal gradient pattern was not found in either fleas or hosts across any facet of diversity or geographic quadrant, except for the PD of fleas in the southeastern quadrant and the FD of hosts in the southwestern quadrant. Latitudinal patterns of the SR, PD and FD of fleas and hosts differed substantially between geographic quadrants. Furthermore, the latitudinal distributions of flea and host SR were similar in three of four quadrants (except the northeastern quadrant), whereas the latitudinal distributions of flea and host PD were similar in the southwestern quadrant only. No similarity in flea versus host FD was revealed. The latitudinal patterns of flea and host PD and FD mostly did not follow those of their SR. We conclude that latitudinal gradients of species richness and phylogenetic and functional diversity appeared not to be universal phenomena. Instead, the latitudinal distributions of these diversity facets represent an

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interplay of ecological (current and past) and historical processes. For parasites, the processes acting on hosts add another layer of complexity underlying their latitudinal diversity patterns.

Keywords: diversity, fleas, global scale, hosts, latitude, species richness

Introduction

A latitudinal gradient in species richness is one of the most pervasive and popular biogeographic patterns. It represents a within-taxon increase in species richness towards the equator and could arise due to various mechanisms, such as climatic restrictions on the life cycles of various organisms; higher productivity in the tropics and subtropics as compared with arid, temperate, and arctic zones; gradients in the landmass areas; solar radiation; unequal rates and times of diversification in the tropics; and climatic changes caused by periodic changes in the orbit of the Earth (i.e. Milankovitch oscillations) (Dobzhansky 1950, Pianka 1966, Rohde 1992, 1998, Rosenzweig 1995, Chown and Gaston 2000, Gaston 2000, Dynesius and Jansson 2000, Colwell and Lees 2000, Willig et al. 2003, Hillebrand 2004, Mittelbach et al. 2007, Brown 2014, Preisser 2019). If latitudinal patterns are produced by global processes, then these patterns are expected to be universal (Hillebrand 2004, Mittelbach et al. 2007). However, although latitudinal gradients in species diversity have been shown for a very large variety of taxa, including animals, plants, and bacteria (Kaufman 1995, Weiser et al. 2007, Andam et al. 2016, Hanly et al. 2017), many exceptions have also been reported. Some taxa demonstrated a reverse latitudinal gradient in species richness (higher richness at higher latitudes; e.g. Kouki et al. 1994, Mateo et al. 2016), whereas other taxa showed either no latitudinal pattern at all (Colesie et al. 2014) or a non-linear shape of the latitude–species richness relationship (Lin et al. 2021). Furthermore, Rohde (1996, 1999) questioned the generality of a latitudinal gradient in species diversity and suggested that it largely represents a ‘local’ phenomenon restricted to the Holarctic above the latitudes of 40–50°N.

Parasites constitute a great (if not the greatest) fraction of global biodiversity (Poulin and Morand 2004, Dobson et al. 2008), and many parasites cause diseases in humans, livestock, wildlife, and crops. Nevertheless, studies of latitudinal patterns in parasite species richness have lagged behind those of free-living species. This could be due to the fact that 1) parasites are ultimately dependent on their hosts, and thus, latitudinal patterns in parasite diversity should be considered together with those of hosts (Poulin 2014) and/or that 2) parasites are represented by a huge variety of phyla, life cycles, and patterns of parasitism. During the last three decades, searches for latitudinal patterns in parasite species richness have been carried out on many parasite taxa (including micro-, endo-, and ectoparasites) (Poulin 1995, Rohde and Heap 1998, Calvete et al. 2003, Krasnov et al. 2004a, Nunn et al. 2005, Poulin and Leung 2011, Preisser 2019, Johnson and Haas 2021). Similar to the relationship between latitude and

species richness in free-living organisms, a variety of patterns have been reported, ranging from the classical (Preisser 2019) to the reversed latitudinal gradient (Krasnov et al. 2004a) to no latitudinal gradient whatsoever (Poulin and Leung 2011, Kamiya et al. 2014) (reviewed by Preisser 2019). One of the reasons for this diversity of patterns is that parasite assemblages are fragmented among host individuals, populations, species, and communities (Poulin 2007). Therefore, patterns of the latitudinal gradient of parasite species richness could be scale-dependent in relation to the hierarchical host unit considered. For example, when flea species richness was considered within a host species, significantly higher richness was found at higher latitudes (Krasnov et al. 2004a). However, when flea species richness was considered at the scale of separate regional host communities, no relationship with latitude was found (Guilhaumon et al. 2012). Poulin (2014) argued that studies of latitudinal gradient in parasite species richness within a host species would be more appropriate than those considering parasite species richness within host assemblages. However, we believe that pooling data on parasites from multiple host species and considering these pools as units for testing latitudinal patterns is no less appropriate. Such an approach is similar to the method generally used in studies of latitudinal gradient in species richness for free-living organisms, which will make the results of studies on both sides of the parasite–host association comparable.

Studies of latitudinal gradient in the species richness of the same or closely related parasites, carried out in different locations, can also produce contrasting patterns (Thieltges et al. 2009, Bordes et al. 2010, Torchin et al. 2015). In addition, the probability of finding a strong latitudinal gradient in species richness would likely increase with an increase in the study's latitudinal span. To the best of our knowledge, only a few studies have considered latitudinal gradients in parasite species richness at the global scale. Guernier et al. (2004) studied a variety of microparasites infesting humans worldwide and found significant negative relationship between latitude and pathogens and parasite species richness. However, given that humans exist in a largely artificial environment, the latitudinal patterns of human parasites were likely confounded by a variety of sociocultural factors (Poulin 2014, Preisser 2019). Nevertheless, humans (i.e. a single host species) have been studied as hosts for pathogens and parasites more than any other species. Guilhaumon et al. (2012) looked at fleas parasitic on small mammals in six continents, but their data were limited to only 16 regions. Preisser (2019) investigated latitudinal patterns of nematodes, trematodes, and cestodes, but considered the helminth diversity of cricetid rodent hosts only. Recently, Maestri et al. (2023) compared diversity of coronaviruses and their mammalian hosts across the

world and reported that hotspots of coronavirus diversity concentrated in east Asia and Europe. However, their database included only 116 mammalian species. In other words, latitudinal gradients in parasite species diversity at the global scale remain to be further investigated.

It is commonly accepted that species richness is only one of the facets of biodiversity. Other facets, such as phylogenetic and functional diversity, are no less important from both theoretical and applicative perspectives (Faith 1992, Pavoine 2012, Miller et al. 2018, Mammola et al. 2021). In contrast to species diversity, fewer studies have investigated latitudinal gradients in phylogenetic and functional diversity, and these studies have produced conflicting results for both free-living and parasitic species. For example, a classical latitudinal gradient in phylogenetic diversity was found in New World woody plants; however, it was found only in the Northern Hemisphere, despite the fact that a classical latitudinal gradient in species richness was recorded in this group in both hemispheres (Kerkhoff et al. 2014). This was later supported for woody, but not herbaceous, plants at the global scale (Massante et al. 2019). Regarding parasites, Clark (2018) did not find support for a latitudinal gradient in the worldwide phylogenetic diversity of avian blood parasites. The same was true for fleas parasitic on small mammals within four biogeographic realms (Krasnov et al. 2019), although the latter study considered a restricted latitudinal span. In contrast, Villalobos-Segura et al. (2020) reported a positive correlation between latitude and the taxonomic distinctness (a substitute for phylogenetic diversity) of helminths in Mexico.

The relationship between functional diversity and latitude is also unclear, even for the same taxonomic group. For example, Stuart-Smith et al. (2013) reported that fish assemblages in temperate regions demonstrated higher functional diversity than those in the tropics. On the contrary, Diamond and Roy (2023) found that functional diversity in nine of 11 studied fish families was relatively stable from the equator through the tropics and then sharply decreased. To the best of our knowledge, no study has specifically investigated latitudinal patterns in the functional diversity of parasites, although studies of the relationships between latitude and separate functional traits have been carried out (Poulin and Hamilton 2000, Krasnov et al. 2008, van der Mescht et al. 2018, Poulin 2021). To date, no general latitudinal trend of parasite functional diversity can be elucidated.

Given the tight relationships between parasites and their hosts, it is not surprising that a positive relationship between parasite and host species diversity has been reported (Krasnov et al. 2004b, Kamiya et al. 2014, Poulin 2014), although this relationship may exist in some, but not other, parts of the world (Krasnov et al. 2007). This, however, did not always result in the latitudinal gradient of parasite diversity automatically mirroring that of their hosts (Guilhaumon et al. 2012). The same can be true for phylogenetic and functional diversity, although links between the phylogenetic diversity of parasites and hosts has been found in some, but not other, biogeographic realms (Krasnov et al. 2019).

Here, we investigated latitudinal patterns in species richness and phylogenetic and functional diversity in fleas and their small mammalian hosts across (almost) the entire world. Fleas are obligate haematophagous parasites, mainly characteristic of small mammals. Their imagoes alternate between periods when they occur on host bodies and periods when they occur in their burrows/nests; non-parasitic flea larvae develop entirely off-host (Krasnov 2008). The aims of this study were threefold. First, we asked whether latitudinal patterns in the species richness and the phylogenetic and functional diversity of fleas and their hosts conform to a latitudinal gradient (= a decrease in diversity with an increase in latitude). Second, we asked whether these patterns 1) vary geographically and 2) differ between fleas and hosts. Third, we asked whether latitudinal patterns of phylogenetic and functional diversity follow those of species richness.

Material and methods

Data on the latitudinal distribution of fleas and their hosts

We collected data on fleas and their small mammalian hosts (Didelphimorphia, Macroscelidea, Eulipotyphla, Rodentia, and the ochotonid Lagomorpha) from published regional surveys (including 'grey' sources) in 15 different regions in the Afrotropics, 23 regions in the Nearctic, 17 regions in the Neotropics, and 36 regions in the Palearctic (maps and references in Krasnov et al. 2022a). We did not include in the analyses data on fleas from Australia, Wallacea and Indomalaya, or China because 1) Australia is isolated from other land masses, 2) the flea fauna in Wallacea and Indomalaya is poorly investigated and 3) data on fleas from China are largely unavailable, and most species descriptions in the regional monographs are not informative enough for our aims. We focused on mammal species on which at least one flea species was recorded. We collected data on the latitudinal distribution of flea species and their hosts. The ubiquitous rodents (*Rattus norvegicus*, *Rattus rattus* and *Mus musculus*) and fleas (*Xenopsylla cheopis*, *Xenopsylla brasiliensis*, *Nosopsyllus fasciatus* and *Nosopsyllus londiniensis*) were excluded from the analyses. For fleas, we used various sources, including original species descriptions (Krasnov et al. 2018a, b, 2022a, b), as well as the Global Biodiversity Information Facility (GBIF 2023) database. The latitudinal distribution of each flea species was determined according to the coordinates of the northernmost and southernmost records of this species. We included a flea species in the analysis even if there was only one occurrence point for this species because ultimately we were interested in the presence of a flea species in a latitudinal band (below). The latitudinal distribution of each mammal species was determined from a map of its geographic range. Maps of mammal geographic ranges were taken from databases of the International Union of Nature Conservation (IUCN 2022). We assumed the continuous range of each species between its northernmost and southernmost records.

Following [Diamond and Roy \(2023\)](#), we allocated each flea or mammal species to latitude bands of 1° separately for each of the four geographic quadrants (northeastern, southeastern, northwestern, and southwestern) from the equator to the northernmost or the southernmost 1° latitude band in which at least one species of flea or host harbouring fleas was found. In total, we used data on 1022 flea and 900 mammal species. We analysed latitudinal distributions of the tree facets of diversity separately for each geographic quadrant because 1) we were interested in general latitudinal trend of each diversity facet, whereas consideration of latitude–diversity patterns across the entire globe or a separate hemisphere would mask the real pattern; 2) eastern and western quadrants within a Northern or Southern Hemisphere are divided by ocean(s) which makes consideration of diversity within an entire hemisphere unreliable; and 3) flea and host species compositions are substantially different between geographic quadrants.

Phylogenies

Phylogenetic trees for fleas and hosts were constructed separately for each geographic quadrant. For fleas, we used the most recent and comprehensive molecular phylogenetic tree of [Zhu et al. \(2015\)](#) that comprised most flea genera, albeit no species, from our dataset. The topology of the remaining genera and species was established based on either their morphologically derived taxonomic positions ([Hadfield et al. 2014](#)) or molecular and morphological phylogenetic studies of several taxa ([Krasnov et al. 2022b](#)). Because no information on branch lengths was available, we assigned all branch lengths to 1 and arbitrarily ultrametrized the resultant tree using the option ‘Arbitrarily ultrametrize’ in the Mesquite modular system for evolutionary analysis ([Maddison and Maddison 2021](#)). Mammal phylogenies (topologies and branch lengths) were taken as subsets from the 10 000 species-level birth–death tip-dated completed trees for 5911 mammal species (DNA-only trees did not include many species from our dataset) of [Upham et al. \(2019\)](#). We took 1000 random trees for each quadrant and constructed a consensus quadrant-specific tree using the function *consensus.edge* of the package ‘phytools’ ([Revell 2012](#)) implemented in the R Statistical Environment (www.r-project.org). Subsequently, the resultant tree was ultrametrized using the function *force.ultrametric* (with option *method = ‘extend’*) of ‘phytools’, and polytomies were resolved using the function *fix.poly* of the R package ‘RRphylo’ ([Castiglione et al. 2018](#)).

Functional traits

We characterized each flea by four ecological and two morphological traits. Ecological traits included 1) the total number of host species exploited across a flea’s geographic range (taken from collected data; [Krasnov et al. 2022a](#)); 2) phylogenetic diversity of these hosts (= host spectrum); 3) the latitudinal span of geographic range (difference between the coordinates of the northernmost and the southernmost

record); and 4) microhabitat preference, defined as the relative time spent either in the hair of the host(s) or in its/their nest(s)/burrow(s) (preference for hair, preference for nest, or no clear preference). The two former traits reflected the degree of a flea’s host specificity. Phylogenetic diversity of a host spectrum was calculated as Faith’s ([Faith 1992](#)) phylogenetic diversity (= PD). Because PD is not independent of species richness, we calculated it using the function *ses.pd* of the R package ‘picante’ ([Kembel et al. 2010](#)). This function compares observed PD to the values expected under randomization [in our case, using the algorithm ‘independent swap’ ([Gotelli 2000](#))], which resulted in standardized values of PD, independent of the number of species in a sample. Data on microhabitat preferences were taken from species descriptions and the various above-mentioned sources, as well as from [Ioff et al. \(1965\)](#), [Krasnov \(2008\)](#) and [Krasnov et al. \(2016\)](#). Morphological traits included 1) the occurrence and number of sclerotized ctenidia (no ctenidia, only a pronotal ctenidium, both pronotal and genal ctenidia) and 2) body length [ranked variable based on female body lengths: small (1–2 mm), medium (2–3 mm), and large (> 3 mm)]. Sclerotized ctenidia allow a flea to anchor itself in the host’s hair and withstand host grooming efforts ([Krasnov 2008](#)). Data on body length were taken from species descriptions and [Surkova et al. \(2018\)](#). If the data on a flea species’ body length were unavailable, we assigned ranked body length for this species according to the ranked body length of the majority of its congeners, as values of flea body length have been shown to be phylogenetically conserved ([Surkova et al. 2018](#)).

Each mammalian host was characterised by two morphological (average body mass and relative brain mass), one geographic (geographic range size), and eight ecological traits that may presumably be associated with patterns of flea parasitism. The ecological traits were 1) location of a nest (ground level, above ground, or below ground); 2) life style (ground-dwelling, fossorial, or arboreal, or else a combination of styles); 3) diel activity (diurnal, nocturnal, or around the clock); 4) feeding habits (omnivorous, folivorous, granivorous, or insectivorous or else a combination of feeding habits); 5) hibernation/torpor pattern (hibernating/torporing or not); 6) population density (individuals per km²); 7) home range size (km²); 8) dispersal range (the distance travelled by a species between the birth location and the breeding location); 9) social group size (the number of individuals that spend most of their time together); and 10) habitat breadth (the number of distinct level 1 IUCN habitats). Data on morphological and ecological traits were taken from the PanTHERIA database ([Jones et al. 2009](#)), the EltonTraits database ([Wilman et al. 2014](#)), the COMBINE database ([Soria et al. 2021](#)), and volumes 5–8 of the Handbook of the Mammals of the World ([Mittermeier and Wilson 2015, 2018, Wilson et al. 2016, 2017](#)). Further descriptions and rationales for using the functional traits for fleas and their hosts described above can be found in [Krasnov et al. \(2016\)](#). Geographic range sizes for hosts were calculated from their range maps ([IUCN 2022](#)).

Measurements of species richness, functional diversity, and phylogenetic diversity

For each geographic quadrant, we constructed two incidence matrices of either flea or host species. To calculate species richness (SR), we first counted the number of species in each 1° latitude band. Then, given the commonly known positive relationship between species richness and area (Preston 1960, Rosenzweig 1995), we regressed the log-transformed number of species in a band against the log-transformed land area of this band (separately for each quadrant and excluding regions in the Eastern Hemisphere as described above) and substituted the original values of SR with their residual deviations from these regressions. Land areas were calculated using ArcGIS Pro 3.1.0.

To calculate phylogenetic diversity (PD) and functional diversity (FD), we used the above-mentioned Faith's PD as a measure of either phylogenetic or functional diversity, due to this metric's ubiquity (Petchey et al. 2009), implemented as the standardized effect sizes of either PD or FD using the 'independent swap' algorithm of the null models in the R package 'picante' (above). To calculate PD, we used the incidence matrices of flea or host distribution across latitude bands and quadrant-specific phylogenetic trees (above). To calculate FD, we first constructed distance trait matrices, using the Gower distance coefficient with the function *gowdis* implemented in the R package 'FD' (Laliberté and Legendre 2010), and we then built functional dendrograms from these matrices using the function *hclust* (method='average') of R. Functional dendrograms and incidence matrices were then used to calculate FD.

Data analyses

Following Diamond and Roy (2023), we modelled the distribution of SR, PD and FD along latitudes with a broken-stick

(= piecewise) regression, separately for each quadrant and using absolute values of latitude as explanatory variables. In a broken-stick regression, the explanatory variable is partitioned into intervals with a separate line segment being fitted to each interval. This method allows one to determine points of sharp changes in the response variable's distribution and has the advantage of linearity (Mugge 2003, 2008).

Broken-stick regressions, for each response variable and each geographic quadrant, were fitted using the R package 'segmented' (Mugge 2020). First, we ran each model with zero to five break-points and selected the best model based on the Bayesian Information Criterion using the function *segmented* of the package 'segmented'. This procedure returns information on the model with the 'optimal' number of break-points that best fit the data and identifies these break-points. Then, we ran the final model for each quadrant, each diversity facet, and either fleas or hosts, using the function 'segmented' and specifying the number and approximate latitudinal locations according to the results of the previous step.

Results

Latitude and species richness

Summaries of the broken-stick models of the latitudinal patterns in flea and host SR are presented in Table 1 (heat maps in Supporting information). In both the northern and southern quadrants of the Eastern Hemisphere, flea SR first decreased from the equator to an approximate absolute latitude of 10–15°, then sharply increased to an absolute latitude of about 30–40°, and then decreased again (Fig. 1). In addition, there was also an increase in flea SR after 70°N of latitude in the northeastern quadrant. Latitudinal patterns of flea SR in the Western Hemisphere were somewhat similar between the northern and the southern quadrants,

Table 1. Summary of the broken-stick regressions of flea (F) or host (H) species richness against the absolute value of latitude (1° latitude bands) in four geographic quadrants (NE: northeastern, SE: southeastern, NW: northwestern, SW: southwestern). MC: model (species richness~latitude) coefficient \pm SE, n: number of break-points, BP: break-point \pm SE; CDS: coefficient difference-in-slopes (difference in slopes between two consecutive segments). *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: non-significant.

Quadrant	F/H	MC	R ²	n	BP	CDS
NE	F	-0.28 \pm 0.04***	0.89	3	10.46 \pm 0.65	0.42 \pm 0.04*
					40.22 \pm 0.85	-0.23 \pm 0.01***
72.95 \pm 0.80					0.40 \pm 0.09***	
SE	H	0.003 \pm 0.001*	0.53	3	8.00 \pm 2.11	-0.003 \pm 0.001*
					38.64 \pm 2.04	0.003 \pm 0.001 ^{ns}
	51.36 \pm 1.60				-0.004 \pm 0.001***	
NW	F	-0.04 \pm 0.01***	0.74	3	14.60 \pm 1.19	0.10 \pm 0.01***
					31.82 \pm 0.51	-0.32 \pm 0.07***
	35.15 \pm 0.76				0.48 \pm 0.24**	
SW	H	-0.03 \pm 0.01*	0.33	2	10.00 \pm 1.43	0.09 \pm 0.04 ^{ns}
					15.08 \pm 1.62	-0.07 \pm 0.03***
	22.00 \pm 3.14				-0.04 \pm 0.01***	
NW	F	0.05 \pm 0.007***	0.91	3	42.08 \pm 1.84	-0.07 \pm 0.01***
					65.72 \pm 0.82	-0.24 \pm 0.5***
	21.13 \pm 1.62				-0.04 \pm 0.01***	
SW	F	0.02 \pm 0.002***	0.86	1	41.55 \pm 0.64	-0.10 \pm 0.01***
	H	0.06 \pm 0.007***	0.63	1	24.40 \pm 1.70	-0.09 \pm 0.01***

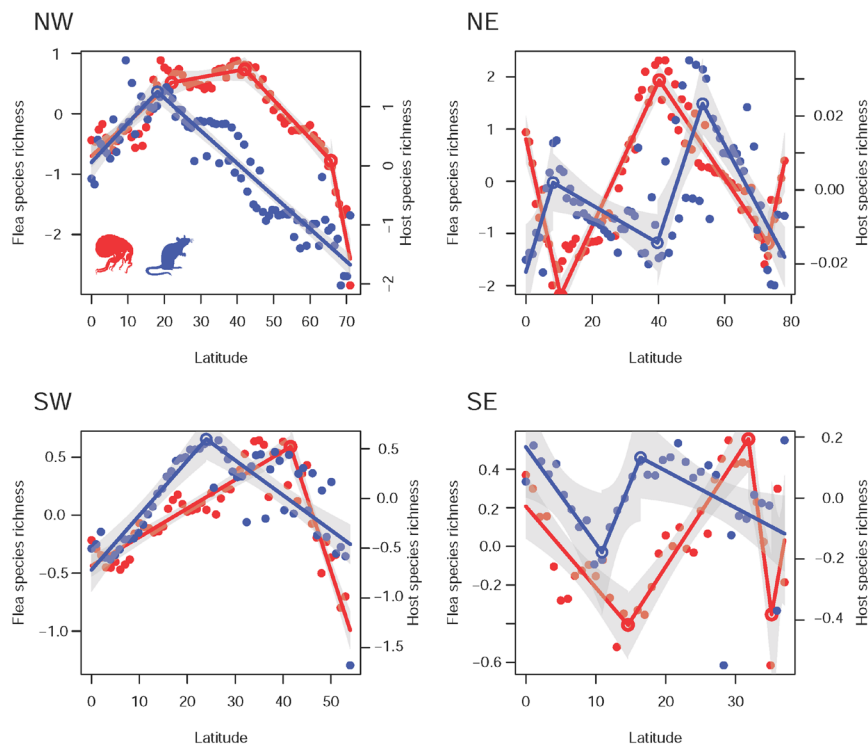


Figure 1. Broken-stick regressions of species richness (corrected for land area) of fleas (red) and hosts (blue) along 1° latitude bands. Dots: species richness values, open circles: break-points, shaded area: 95% confidence interval. NW: the northwestern geographic quadrant, NE: the northeastern geographic quadrant, SW: the southwestern geographic quadrant, SE: the southeastern geographic quadrant.

being unimodal with break-points around 40° of an absolute latitude (Fig. 1). Coefficients of the models indicated that the general latitudinal trends of flea SR were negative in the Eastern Hemisphere and positive in the Western Hemisphere (Table 1).

The pattern of host SR distribution along latitudes in the northern quadrant of the Eastern Hemisphere was opposite to that of flea SR, namely, SR increased from the equator to 10°N latitude, then decreased to 40°N, again increased to 60°N, and then dropped to 70°N (Fig. 1). This was also supported by the signs of the model coefficients (Table 1). In contrast, host SR distribution in the southern quadrant of the Eastern Hemisphere was similar to that of flea SR, although

the difference between the slopes of the second and the third segments was not significant (Table 1). Furthermore, the break-points of host SR were shifted, relative to those of flea SR, to lower latitudes (Fig. 1). The same was true in both quadrants of the Western Hemisphere where distributional patterns of host and flea SR were similar.

Latitude and phylogenetic diversity

The latitudinal distribution patterns of flea PD differed between geographic quadrants (Table 2, Fig. 2). In the northeastern quadrant, flea PD sharply increased from the equator to 4°N latitude, then sharply decreased to 12°N, and then

Table 2. Summary of the broken-stick regressions of flea (F) or host (H) phylogenetic diversity against the absolute value of latitude (1° latitude bands) in four geographic quadrants (NE: northeastern, SE: southeastern, NW: northwestern, SW: southwestern). MC: model (phylogenetic diversity ~ latitude) coefficient \pm SE, n: number of break-points, BP: break-point \pm SE; CDS: coefficient difference-in-slopes (difference in slopes between two consecutive segments). *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Quadrant	F/H	MC	R ²	n	BP	CDS
NE	F	0.93 \pm 0.17***	0.57	2	4.43 \pm 0.49	-1.24 \pm 0.19***
	H	0.02 \pm 0.008*	0.71	2	12.00 \pm 1.13 34.30 \pm 1.02 39.67 \pm 0.94	0.32 \pm 0.08*** -0.50 \pm 0.16** 0.54 \pm 0.16***
SE	F	-0.22 \pm 0.03***	0.79	1	16.00 \pm 3.33	0.16 \pm 0.05***
	H	0.06 \pm 0.02*	0.20	1	16.00 \pm 3.70	-0.10 \pm 0.04**
NW	F	0.13 \pm 0.05*	0.24	1	9.52 \pm 2.45	-0.14 \pm 0.05***
	H	-0.06 \pm 0.008***	0.71	1	35.40 \pm 1.76	0.12 \pm 0.01***
SW	F	-0.09 \pm 0.01***	0.82	2	31.74 \pm 1.59 36.41 \pm 0.97	-0.38 \pm 0.21*** 0.68 \pm 0.21***
	H	-0.05 \pm 0.006***	0.51	1	50.62 \pm 1.21	0.52 \pm 0.22***

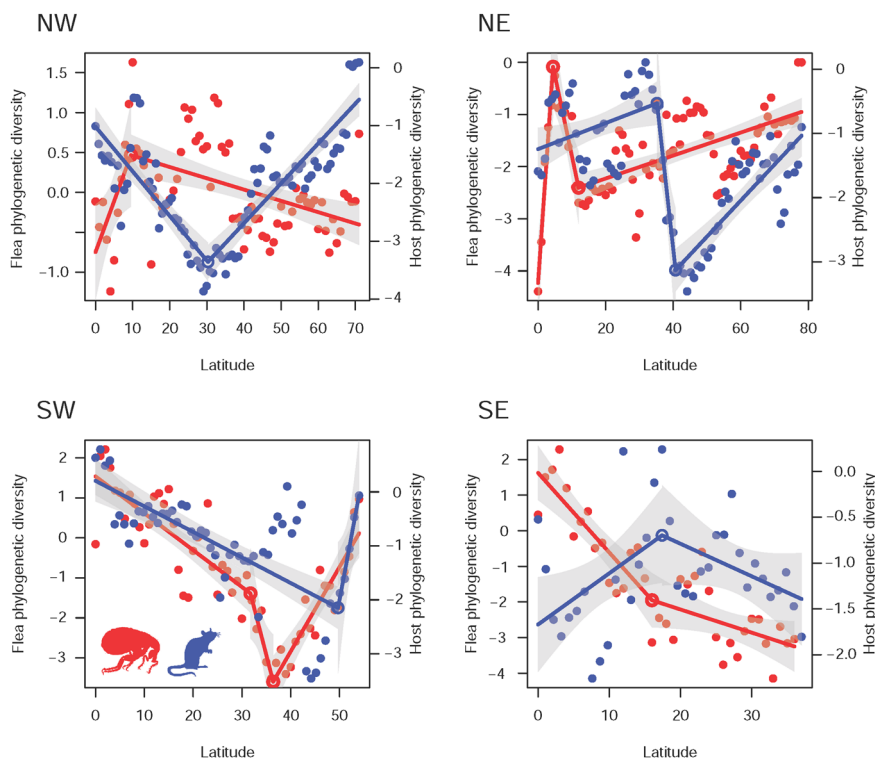


Figure 2. Broken-stick regressions of the phylogenetic diversity (standardized effect size calculated using the ‘independent swap’ null model) of fleas (red) and hosts (blue) along 1° latitude bands. Dots: species richness values, open circles: break-points, shaded area: 95% confidence interval. NW: the northwestern geographic quadrant, NE: the northeastern geographic quadrant, SW: the southwestern geographic quadrant, SE: the southeastern geographic quadrant.

grew steadily (Fig. 2). In the southeastern quadrant, flea PD steadily decreased, although the slope of this decrease became shallower after 15°S latitude. The behaviour of flea PD along latitude, in the northern and southern quadrants of the Western Hemisphere, demonstrated opposite trends, namely hump-shaped in the former, but concave in the latter. The general latitudinal trend of flea PD, as indicated by the signs of the model coefficients, was positive in the Northern Hemisphere and negative in the Southern Hemisphere (Table 2).

Latitudinal trends of host PD were similar to those of flea PD in the northeastern and the southwestern quadrants, but with break-points shifted to higher absolute latitudes (Fig. 2). In contrast, latitudinal trends of host PD differed substantially from those of flea PD in the southeastern and northwestern quadrants. In the former, flea PD decreased from the equator to the south, whereas in the latter, it sharply declined from the equator to 35°N and then increased to the extreme north (Fig. 2). See also the heat maps of latitudinal distributions of flea and host PD in Supporting information.

Latitude and functional diversity

The general trend of flea FD in the Northern and the Southern Hemisphere was opposite to that found for PD, namely, negative in the north and positive in the south (Table 3). Furthermore, in the northeastern quadrant, flea FD sharply

decreased from the equator to approximately 50°N latitude and then sharply increased, whereas in the southeastern quadrant, it increased from the equator to approximately 20°N latitude and then sharply decreased (Fig. 3). Patterns of flea FD in the Western Hemisphere were more complicated. In the northwestern quadrant, FD substantially varied across latitudes, decreasing from the equator to 20°N latitude and from 30 to 40°N latitude, while increasing from 20 to 30°N latitude and from 40°N latitude (Fig. 3), although differences between the slopes of the first and the second segments, as well as between the second and the third segments were not significant (Table 3). In the southwestern quadrant, flea FD increased along the first six 1° latitude bands, then decreased till 40°S latitude, and then increased again.

Latitudinal distributions of host FD varied between geographic quadrants and differed from those of flea FD in the same quadrant. In the northeastern quadrant, host FD attained the lowest values at approx. 17°N, 43°N and 78°N, and the highest values at approx. 35°N and 58°N (Fig. 3). In the southeastern quadrant, host FD drastically decreased from the equator to 4°S, then increased to about 20°S, and then slowly decreased to the south (Fig. 3). In the northwestern quadrant, host FD steadily decreased with an increase in latitude until it reached a latitude of about 64°N and then increased to the extreme north (Fig. 3). In the southwestern quadrant, host FD demonstrated a classic latitudinal gradient, decreasing from the equator to the south (Fig. 3). See

Table 3. Summary of the broken-stick regressions of flea (F) or host (H) functional diversity (standardized effect size calculated using the 'independent swap' null model) against the absolute value of latitude (1° latitude bands) in four geographic quadrants (NE: northeastern, SE: southeastern, NW: northwestern, SW: southwestern). MC: model (functional diversity ~ latitude) coefficient ± SE, n: number of break-points, BP: break-point ± SE; CDS: coefficient difference-in-slopes (difference in slopes between two consecutive segments). *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: not significant.

Quadrant	F/H	MC	R ²	n	BP	CDS
NE	F	-0.08 ± 0.006***	0.73	1	50.40 ± 1.84	0.20 ± 0.02***
	H	-0.07 ± 0.02***	0.85	4	17.64 ± 1.01	0.30 ± 0.03*
					34.80 ± 0.64	-0.59 ± 0.07***
					42.73 ± 0.79	0.51 ± 0.07***
					58.25 ± 1.16	-0.27 ± 0.03***
SE	F	0.16 ± 0.02***	0.62	1	22.55 ± 1.53	-0.35 ± 0.05***
	H	-0.41 ± 0.11**	0.73	2	4.80 ± 0.74	0.53 ± 0.11***
NW	F	-0.06 ± 0.02*	0.56	3	19.04 ± 1.69	-0.15 ± 0.03***
					19.45 ± 2.82	0.14 ± 0.05 ^{ns}
					32.12 ± 1.67	-0.28 ± 0.07 ^{ns}
					43.02 ± 1.65	0.23 ± 0.05***
SW	H	-0.03 ± 0.003***	0.58	1	74.21 ± 1.20	0.43 ± 0.09***
	F	0.54 ± 0.11***	0.85	3	6.55 ± 0.94	-0.58 ± 0.11***
					21.68 ± 2.45	-0.17 ± 0.04***
					39.22 ± 0.84	0.49 ± 0.04***
					27.00 ± 0.01	-0.06 ± 0.01***

also the heat maps of the latitudinal distributions of flea and host FD in Supporting information.

Discussion

Overall, we did not find the classical latitudinal gradient pattern in either facet of diversity, in any geographic quadrant, for either fleas or hosts. Exceptions to this were flea PD in the southeastern quadrant (Fig. 2) and host FD in the southwestern quadrant (Fig. 3). The latitudinal patterns of both flea and host SR, PD and FD differed substantially between geographic quadrants. Furthermore, the latitudinal distributions of flea and host SR were similar in three of four quadrants (except the northeastern one), whereas the latitudinal distributions of flea and host PD were similar in the southwestern quadrant only. No similarities in flea versus host FD were revealed. Finally, the latitudinal patterns of both the PD and FD of both fleas and hosts mostly did not follow those of their species richness except the PD of fleas in the northwestern quadrant and the FD of hosts in the southeastern quadrant (re-arranged Fig. 1–3 for easier comparison in Supporting information).

Species richness

The latitudinal patterns of both flea and host SR in all geographic quadrants were characterized by peaks and dips, similar to what was reported in, for example, swallowtail butterflies, albeit for the Northern Hemisphere only (Condamine et al. 2012). However, in contrast to the results of the latter study, flea and host SR were not necessarily the highest at the equator. One of the reasons for this could be that the climate in the equatorial zones is highly humid, and many small mammals inhabit tree crowns. These conditions are unfavourable for fleas, especially in their pre-imaginal

stages (Krasnov 2008). In addition, our knowledge on fleas in the equatorial zones is more limited compared to other regions. As a result, fleas in the equatorial zones 1) are represented by a relatively small number of species and 2) cannot utilize the majority of small mammalian hosts. Consequently, a pool of mammalian hosts harbouring fleas represent only a relatively minor subset of all small mammals inhabiting these zones and are represented by species possessing certain traits that make them suitable hosts for fleas (e.g. shelters and nests appropriate for the development of pre-imaginal fleas; Krasnov et al. 2004a). When the majority of small mammal species are taken into account, the latitudinal pattern of their SR conforms to a classical latitudinal gradient (Maestri and Patterson 2016).

The occurrence of break-points in the latitudinal distribution of flea SR suggests sharp changes in the number of species at certain latitudes. The most likely mechanisms behind this could be changes in flea faunas at the borders of biogeographical realms or major biomes/ecoregions (Olson et al. 2001), associated with changes in environmental factors or otherwise at mountain ridges that could be barriers for flea dispersal. For example, the break-point at 10°N latitude in the northeastern quadrant corresponded to the border between the Afrotropical and the Palearctic realms, which also represents the transition from the Sahel's tropical grasslands to Saharan desert habitats. SR thus decreases from the equator to this boundary and then starts to increase. The break-point at 40°N latitude occurred at approximately the major mountain ridges of Eurasia (Pyrenees, Caucasus, Tian Shan). The break-point of flea SR at 10–15°S in the southeastern quadrant could be associated with the transition from Zambezi woodlands to xeric savannas. In the southwestern quadrant, the break-point at about 30–40°S could reflect the border between tropical/subtropical savannas and temperate grasslands. Previously, we reported that regional flea assemblages form biogeographic, but not ecological, clusters, so that the differences in flea

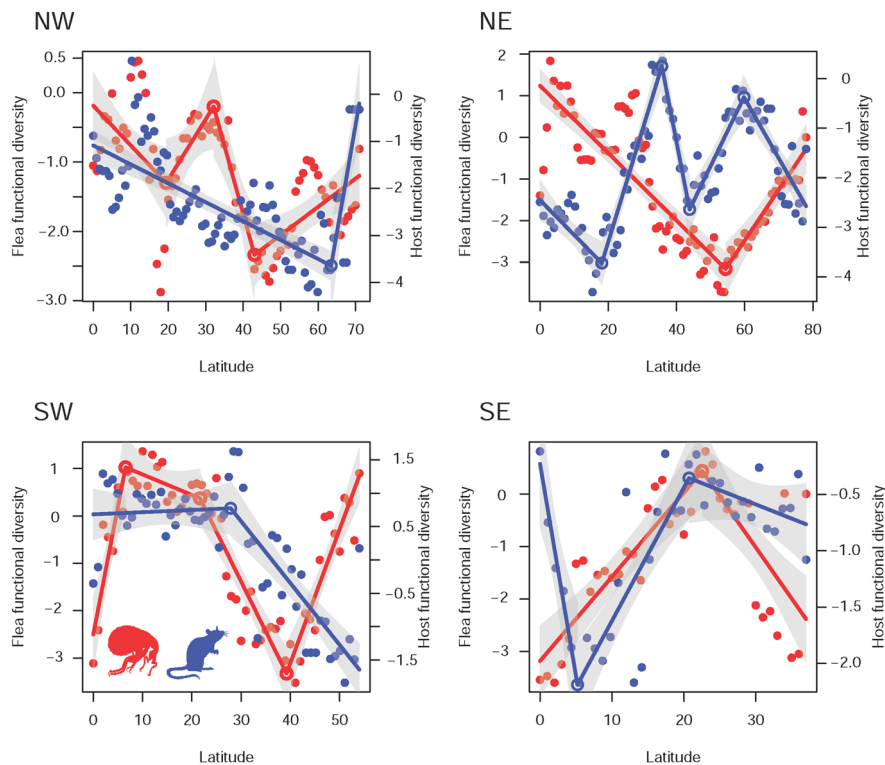


Figure 3. Broken-stick regressions of the functional diversity (standardized effect size calculated using the ‘independent swap’ null model) of fleas (red) and hosts (blue) along 1° latitude bands. Dots: species richness values, open circles: break-points, shaded area: 95% confidence interval. NW: the northwestern geographic quadrant, NE: the northeastern geographic quadrant, SW: the southwestern geographic quadrant, SE: the southeastern geographic quadrant.

species composition between biomes within a biogeographic realm could not be distinguished (Krasnov et al. 2022a). The contradiction between the results of this study and those of Krasnov et al. (2022a) could be associated with the fact that the differences between flea assemblages of different ecoregions may or may not be substantial enough to be revealed by some analyses [step-down factor analysis (Alroy 2019) in Krasnov et al. (2022a)]. This may depend on biome/ecoregion identities (Gibert et al. 2021).

The break-points in flea SR either followed (the southeastern quadrant) or were followed by (the southwestern quadrant) or almost coincided with (the northeastern quadrant) the break-points in the SR of the hosts they exploited, thus reflecting an association between parasite and host SR (Krasnov et al. 2004b, Kamiya et al. 2014). Moreover, the directions of change in the latitudinal pattern of flea SR mirrored those of host SR in three of the four geographic quadrants. These directions in the northeastern quadrant were the opposite of each other, which contrasted with the pattern in the other three geographic quadrants. On the one hand, this supports the results of Krasnov et al. (2007) in that the relationship between flea and host diversity varies geographically. On the other hand, this contradicts the results of Krasnov et al. (2007) because they found a link between flea and host SR in the Palearctic but not in the Nearctic. This contradiction could be caused by the methodological differences between this study and Krasnov et al. (2007)

because the latter 1) considered mainly the northern and central Palearctic and 2) calculated SR in separate regions rather than along latitude bands. The reason for the opposite directions of latitudinal changes between flea and host SR in the northeastern quadrants could be the sheer land area of the northwestern quadrant in which the same latitude band can cover several biomes/ecoregions. As a result, different latitudinal distributions of fleas and hosts within and between regions may be realized in mixed patterns. In addition, the responses to biome/ecoregion subdivisions in terms of SR may differ between fleas and hosts. We recognize that these explanations are highly speculative and warrant further investigations.

Other studies on a latitudinal gradient in SR demonstrated differential latitudinal patterns between different taxonomic units (e.g. classes of helminths in Preisser 2019 or families of fish in Diamond and Roy 2023). In our case, this could not be the reason behind the substantial variation of SR along latitudes because this variation has been found even when the analyses were restricted to separate families (Supporting information for three flea families in the northeastern quadrant).

Phylogenetic diversity

The lack of congruence between the latitudinal patterns of PD and SR supports our earlier finding that the compositional

and phylogenetic diversity of fleas are governed by different rules (Krasnov et al. 2019). Our explanation was that compositional diversity was mainly associated with current ecological conditions, whereas PD was driven mainly by evolutionary/historical processes. The same explanation can be applied to the SR and PD of both fleas and hosts in the current study. Furthermore, variation in the latitudinal pattern of flea PD between geographic quadrants can arise due to differences in the predominant phylogenetic lineages, which are characterised by differential speciation rates and dispersal patterns. The latter, in turn, are strongly influenced by plate tectonics (Condamine et al. 2012). In particular, fleas originated in Gondwana, and the main diversification events took place after the Cretaceous–Tertiary boundary (Medvedev 2000a, b, Zhu et al. 2015). The ancestral geographic state of fleas was most likely Australia and South America, connected via Antarctica, until the upper Eocene. Then, host dispersal from South to North America likely resulted in flea dispersal there (these continents were likely to have been temporarily connected during the upper Cretaceous; see details and references in Zhu et al. 2015). The route of flea dispersal to the Old World (from North America to Europe or Asia or from South America to Africa and then to Eurasia) is still debated (Zhu et al. 2015). As a result of multiple waves of host and subsequent flea migrations, different parts of the world are characterised by the predominance of certain flea genera and families. These genera and families differ in the number of species and their geographic ranges, which likely reflects the between-genus/family differences in the rate of speciation. For example, the largest families/subfamilies (Hysrichopsyllidae, Leptopsyllidae, Ceratophyllidae) are characteristic of the Palearctic, whereas the smaller families and subfamilies (Chimaeropsyllidae, Xiphiopsyllidae, Craneopsyllinae) are distributed in the Afrotropics and the Neotropics (Traub 1980, Medvedev 2005). This results in the proportion of endemic genera being the highest in the Afrotropics and the Neotropics and much lower in the Palearctic and the Nearctic (Medvedev 2005). In addition, the dynamics of glaciation/interglaciation events that are more characteristic of the Northern than the Southern Hemisphere could affect the latitudinal distribution of phylogenetic lineages, leading to multiple peaks of latitudinal PD distribution, although it is unclear why multiple peaks were found in the northeastern, but not the north–western, quadrant. Perhaps, this is due to the higher number and variety of mountain systems in Eurasia than in North America. These systems could represent barriers to dispersal for certain flea and host lineages.

The reason behind the difference in the latitudinal pattern of PD between fleas and hosts in some geographic quadrants could be that the diversification of parasites is not necessarily a response to the diversification of hosts. In fact, co-speciation of parasites and their hosts is rare (Poulin 2007) because their common evolutionary history is often complicated by a variety of evolutionary events (Page 2003). Furthermore, co-speciation could occur in some, but not other, phylogenetic lineages of fleas and hosts (Krasnov and Shenbrot 2002).

Functional diversity

As mentioned above, the latitudinal distributions of the SR, PD and FD of fleas and their hosts demonstrate different patterns. The lack of a strong correlation between SR and FD has been found in other taxa (Fonseca and Ganade 2001, Diamond and Roy 2023). This suggests that either some species occurring at a latitude band are functionally redundant (Rosenfeld 2002) or that the functional traits selected for the calculation of FD were not informative enough (Llopis-Belinguier et al. 2019). We believe that the former explanation is more relevant for the results of this study, especially for latitude bands with a similar homogeneous environment. Indeed, flea species that co-occur in a region appeared to be more similar in their traits than expected by chance, although this has been studied only in the Palearctic (Krasnov et al. 2015). Furthermore, intensive speciation can result in multiple closely related species that are similar in their traits. However, rapid speciation accompanied with strong divergent selection can shape phenotypic diversification (Pressoir and Berthaud 2004). The highest speciation rates of fleas are thought to be characteristic of temperate regions in the Palearctic, because this region contains many mountain ranges spanning east–west (in contrast to other realms where mountain ranges predominantly span north–south). These ranges could promote reproductive isolation and thus facilitate speciation. As a result, the highest flea SR and the lowest flea FD were found at about 50° in the northeastern quadrant, although flea PD at these latitudes had moderate values. Different latitudinal patterns of PD and FD could arise because some functional traits are phylogenetically conserved (e.g. body size of fleas and hosts; Surkova et al. 2018, Fourcade and Alhajeri 2023; respectively), whereas others are not (e.g. host specificity for fleas and geographic range size for hosts; Krasnov et al. 2011, Guy et al. 2019; respectively).

In conclusion, latitudinal gradients of SR, PD and FD did not appear to be universal phenomena. Instead, the latitudinal distributions of these diversity facets likely represent an interplay of ecological (current and past) and historical processes. For parasites, the processes acting on their hosts add another dimension that could influence the latitudinal patterns of their diversity, which makes these patterns more complicated. However, a caveat should be mentioned. A negative latitude–diversity pattern for human pathogens and parasites highlighted by Grenier et al. (2004) suggests that the results of studies of the latitude–diversity relationships in other species that reported no or reversed pattern should be taken with caution because, as mentioned above, human parasites are known much better than parasites of any other host species. In other words, the likelihood of highlighting real latitude–diversity patterns may strongly depend on sampling effort and geographical gaps. Nevertheless, we believe that the results of our study are based on one of the most exhaustive and detailed databases of parasites and their hosts.

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Author contributions

Boris R. Krasnov: Conceptualization (lead); Formal analysis (lead); Methodology (lead); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Vasily I. Grabovsky:** Formal analysis (equal). **Irina S. Khokhlova:** Data curation (equal); Formal analysis (equal); Writing – original draft (equal); Writing – review and editing (equal). **Maria Fernanda López Berrizbeitia:** Data curation (equal); Writing – review and editing (equal). **Sonja Matthee:** Conceptualization (equal); Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Uri Roll:** Conceptualization (equal); Formal analysis (equal); Software (equal); Writing – original draft (equal); Writing – review and editing (equal). **Juliana P. Sanchez:** Conceptualization (equal); Data curation (equal); Writing – review and editing (equal). **Georgy I. Shenbrot:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Luther van der Mescht:** Data curation (equal); Writing – review and editing (equal).

Data availability statement

Data on flea and host latitudinal distributions are available from the Mendeley Data repository: <https://doi.org/10.17632/fv7h3cfs47.2> (Krasnov et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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