Research Article

Author for correspondence:
Boris R. Krasnov, E-mail: krasnov@bgu.ac.il

CAMBRIDGE
UNIVERSITY PRESS

Phylogenetic patterns in regional flea assemblages from 6 biogeographic realms: strong links between flea and host phylogenetic turnovers and weak effects of phylogenetic originality on host specificity

Boris R. Krasnov[1] ⬤ , Georgy I. Shenbrot[1] and Irina S. Khokhlova[2]

[1]Mitrani Department of Desert Ecology, Swiss Institute for Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Midreshet Ben-Gurion, Israel and [2]French Associates Institute for Agriculture and Biotechnology of Drylands, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Midreshet Ben-Gurion, Israel

Abstract

We investigated phylogenetic patterns in flea assemblages from 80 regions in 6 biogeographic realms and asked whether (a) flea phylogenetic turnover is driven by host phylogenetic turnover, environmental dissimilarity or geographic distance; (b) the relative importance of these drivers differs between realms; and (c) the environmental drivers of flea phylogenetic turnover are similar to those of host phylogenetic turnover. We also asked whether the phylogenetic originality of a flea species correlates with the degree of its host specificity and whether the phylogenetic originality of a host species correlates with the diversity of its flea assemblages. We found that host phylogenetic turnover was the best predictor of flea phylogenetic turnover in all realms, whereas the effect of the environment was weaker. Environmental predictors of flea phylogenetic turnover differed between realms. The importance of spatial distances as a predictor of the phylogenetic dissimilarity between regional assemblages varied between realms. The responses of host turnover differed from those of fleas. In 4 of the 6 realms, geographic distances were substantially better predictors of host phylogenetic turnover than environmental gradients. We also found no general relationship between flea phylogenetic originality and its host specificity in terms of either host species richness or host phylogenetic diversity. We conclude that flea phylogenetic turnover is determined mainly by the phylogenetic turnover of their hosts rather than by environmental gradients. Phylogenetic patterns in fleas are manifested at the level of regional assemblages rather than at the level of individual species.

Introduction

A link between species diversity and habitat diversity was first reported more than a half-century ago (MacArthur, 1958, 1964) and was further supported for a variety of plant and animal species (Lawton, 1983; Rosenzweig, 1995; Tews *et al.*, 2004). Given that hosts represent the ultimate habitats for a majority of parasite taxa, it is thus not surprising that studies of the effects of host diversity on parasite diversity have reported strong positive associations between them (Watters, 1992; Krasnov *et al.*, 2004*a*; Thieltges *et al.*, 2011; Kamiya *et al.*, 2014). However, parasite diversity is determined not only by host diversity, but also by environmental factors (e.g. Adlard *et al.*, 2015). In other words, parasite species composition results from an interplay between host species composition and environment. This is especially true for ecto-parasites because they are affected by both hosts and the external off-host environment (Marshall, 1981). Obviously, compositional diversity is not the only component of species diversity. Phylogenetic diversity is no less important because it represents an evolutionary measure of biodiversity that may or may not be reflected by compositional diversity (Miller *et al.*, 2018). Although phylogenetic methods are now broadly applied in parasitological studies (Bass *et al.*, 2015; Selbach *et al.*, 2019), investigations of the patterns of phylogenetic diversity in parasites are still more scarce than those of free-living taxa (but see Clark, 2018; Krasnov *et al.*, 2019*a*, 2019*b*; Llopis-Belenguer *et al.*, 2020).

One of the main questions asked in studies on parasite diversity is whether it is mainly driven by host diversity or environmental factors. The majority of studies on compositional parasite diversity have suggested that the effect of host diversity was more important than that of environmental variation. For example, the diversity of helminth parasites of amphibians, at the global scale, was found to be affected by both precipitation seasonality and host richness, with the effect of the latter being stronger (Martins *et al.*, 2021). The meta-analysis of Kamiya *et al.* (2014) convincingly demonstrated that parasite species richness is strongly correlated with that of their hosts. A study on fleas in northern and central Eurasia suggested that the drivers of flea community composition were scale-dependent, with host

composition playing the main role on the continental scale, whereas the effect of environment was more important on the regional scale (Krasnov et al., 2015). In contrast to compositional diversity, the drivers of parasites' phylogenetic diversity have been poorly studied. Nevertheless, it appeared that the relative effects of host phylogenetic diversity and environment on parasite diversity could vary between geographic regions, even in the same parasite taxon. Among the drivers of the phylogenetic diversity of regional flea assemblages within each of 4 biogeographic realms (the Afrotropics, the Nearctic, the Neotropics and the Palaearctic), host phylogenetic diversity played the most important role in the Palaearctic only, whereas the effect of environment was weak, although the opposite was true for the Afrotropics and the Nearctic (Krasnov et al., 2019a). The latter study dealt with phylogenetic alpha-diversity. Phylogenetic beta-diversity (i.e. dissimilarity in phylogenetic composition between communities) may respond to factors other than compositional beta-diversity. Furthermore, it is unknown whether the drivers of phylogenetic beta-diversity of the same parasite taxon vary between geographic regions or whether these drivers are geographically invariant, as is the case with parasite compositional beta-diversity. In fact, dissimilarity in host species composition, across regions in all 4 aforementioned biogeographic realms, was the most important factor affecting the compositional dissimilarity of flea assemblages, whereas environmental effects were weaker (Krasnov et al., 2020). A similar pattern has been reported for chiropterans and their bat fly parasites (Eriksson et al., 2019). The results of 2 studies on the phylogenetic beta-diversity of fleas were obtained at a relatively small scale (Krasnov et al., 2019b; Maestri et al., 2020) and do not allow answering the question about the geographic variation of predictors of parasite phylogenetic turnover at a large scale.

Elucidating the relationships between the beta-diversities (whether compositional or phylogenetic) of 2 different taxa or between beta-diversity and environment is essentially a test of the relationships between either species (or phylogenetic lineages) turnover of taxon A (e.g. parasites) and taxon B (e.g. hosts) or species (or phylogenetic lineages) turnover and environmental dissimilarity. The drivers of community compositional/phylogenetic turnover should be analysed with an appropriate, non-linear analytical method represented, for example, by generalized dissimilarity modelling (GDM) (Ferrier et al., 2007; Mokany et al., 2022). This is because of 2 main problems associated with any linear analysis of pairwise metrics of dissimilarity/turnover, namely that (a) the range of any dissimilarity index varies from 0 to 1 only, and (b) the rate of species (or phylogenetic lineages) compositional change along a gradient is not necessarily constant, so the model has to take into account the curvilinear relationship between dissimilarity in species/phylogenetic composition and environmental dissimilarity or geographic distance. The GDM resolves both these problems and, moreover, can incorporate various biotic and abiotic predictors into a single model. The GDM has been successfully, albeit rarely, applied in studies of parasite species turnover and has proven to be a promising tool for revealing drivers of parasite diversity (Maestri et al., 2017, 2020; Eriksson et al., 2019; Krasnov et al., 2020; McNew et al., 2021). Phylogenetic generalized dissimilarity modelling (phyloGDM) (Ferrier et al., 2007) represents an extension of the traditional GDM aimed at modelling spatial patterns of phylogenetic, rather than compositional, turnover (Ferrier et al., 2007; Rosauer et al., 2013).

Another phylogenetic pattern in parasite–host associations is related to the phylogenetic originality of either a parasite or a host. A species is considered original if it has only a few close relatives and/or if its branch in the phylogenetic tree is long (i.e. it supposedly evolved quickly) (May, 1990; Vane-Wright et al., 1991; Faith, 1992; Pavoine et al., 2005; Pavoine and Izsak,

2014). Phylogenetically original species are highly interesting from the conservation point of view because of their important roles within communities and ecosystems and increased probability of extinction (e.g. Isaac et al., 2007, 2012; but see Pavoine et al., 2017). Relationships between a species' degree of phylogenetic originality and its ecological features are poorly known. Nevertheless, the results of the few available studies suggest that phylogenetically original species tend to have restricted geographic ranges (Cadotte and Davies, 2010; Veron et al., 2021). Taking into account one of the most persistent macroecological patterns, namely the negative relationship between geographic range size and niche breadth (Brown, 1984), it can be hypothesized that phylogenetic originals are likely ecological specialists. This has never been specifically tested either in free-living species or in parasites. From a parasite perspective, niche specialization can be reflected in a high degree of host specificity, both structural and phylogenetic (sensu Poulin et al., 2011; see Krasnov et al., 2005 for fleas). From a host perspective, if phylogenetically original hosts are also those with a restricted geographic range, then a decrease in the diversity of the parasite assemblages they harbour with an increase in the degree of their phylogenetic originality can be expected because of the negative relationships between a host's geographic range size and the diversity of its parasite assemblage (Feliu et al., 1997; Krasnov et al., 2004b).

Here, we studied phylogenetic patterns of regional flea assemblages in 6 biogeographic realms (the Afrotropics, the Australasia, the Indomalaya, the Nearctic, the Neotropics and the Palaearctic). The aims of this study were 2-fold. First and similar to earlier studies of flea compositional dissimilarity (e.g. Krasnov et al., 2019b), we asked (a) whether flea phylogenetic turnover is mainly driven by host phylogenetic turnover or environmental dissimilarity or alternatively by the geographic distance between flea/host assemblages and (b) whether the patterns of the relationships between flea phylogenetic turnover, host phylogenetic turnover, environmental dissimilarity and geographic distance differ between biogeographic realms due to differences in flea and host evolutionary histories in these realms (Traub, 1980; Medvedev, 2005). To assess the relationships between flea and host phylogenetic turnover, environmental dissimilarity and geographic distances, we applied phyloGDMs. In addition, to understand whether spatial patterns and environmental drivers of flea phylogenetic turnover are similar to those of host phylogenetic turnover (Maestri et al., 2017), we applied phyloGDMs to host phylogenetic turnover as affected by environmental dissimilarity and geographic distances. Second, we asked whether the phylogenetic originality of a flea species correlated with the degree of its host specificity in terms of either size (i.e. the number of host species) or the phylogenetic diversity of its host spectrum. We also asked whether the phylogenetic originality of a host species correlated with the number of flea species it harbours or their phylogenetic diversity.

Materials and methods

Data on fleas, hosts and their interactions

Data on fleas parasitic on small mammalian hosts were taken from a variety of published surveys that reported identities of flea species collected from a given host species [Monotremata, Dasyuromorphia, Didelphimorphia (except large opossums), Paramelemorphia, Notoryctemorphia, Diprotodontia (except Vombatiformes), Macropodiformes (except large kangaroos), Paucituberculata, Macroscelidea, Eulipotyphla, Rodentia and ochotonid Lagomorpha] from 15 regions of the Afrotropics, 8 regions of the Australasia, 10 regions of the Indomalaya, 23 regions of the Nearctic, 17 regions of the Neotropics and 36

regions of the Palaearctic (see lists of regions, maps and references in Krasnov et al., 2022a). Similarly to our earlier study (Krasnov et al., 2022b), whenever possible, we relied on the information in the original sources and did not include in the analyses those findings of certain fleas on certain hosts that the author(s) of the original publications considered to be accidental. Ubiquitous host (*Rattus rattus*, *Rattus norvegicus* and *Mus musculus*) and flea (*Xenopsylla cheopis*, *Xenopsylla brasiliensis*, *Nosopsyllus fasciatus*, *Nosopsyllus londoniensis* and *Leptopsylla segnis*) species, as well as introduced host species (e.g. *Ondatra zibethicus* in the Palaearctic), were also excluded from the analyses. In total, we used data on 213 flea and 196 host species in the Afrotropics, 147 flea and 140 host species in the Australasia, 236 flea and 147 host species in the Indomalaya, 254 flea and 217 host species in the Nearctic, 200 flea and 160 host species in the Neotropics and 338 flea and 209 host species in the Palaearctic.

Phylogenies

Phylogenetic trees for fleas and hosts were constructed for each realm separately because flea faunas, as well as the faunas of flea-harbouring hosts, have been shown to form clear clusters according to the biogeographic realms in which they occur (Krasnov et al., 2022a). For fleas, we used, as a backbone, the most recent and comprehensive (and 1 of only 2 available) molecular phylogenetic tree (Zhu et al., 2015). This tree comprised the majority of flea genera from our datasets, whereas this was not the case for the majority of species. The topology of the remaining genera and species was established based on either their morphologically derived taxonomic positions (Hadfield et al., 2014) or the molecular/morphological phylogenies carried out for some genera (see references in Krasnov et al., 2022b). No information on branch length for ca. 80% of species was available. Consequently, we arbitrarily assigned all branch lengths to a length of 1 and arbitrarily ultrametrized the resultant tree using the option 'arbitrarily ultrametrize' in the Mesquite modular system for evolutionary analysis (Maddison and Maddison, 2021). Polytomies (9 clades in the Indomalaya, 3 clades in the Nearctic and 11 clades in the Palaearctic) were resolved using the function 'fix.poly' of the package 'RRphylo' (Castiglione et al., 2020) of the R programming language for statistical computing (R Core Team, 2022).

Host phylogenetic trees were taken as subsets from the 10 000 species-level birth–death tip-dated completed trees for 5911 mammal species of Upham et al. (2019). We built a consensus tree for each realm from 1000 random trees of Upham et al. (2019) using the function 'consensus.edge' of the R package 'phytools' (Revell, 2012), ultrametrized this tree using the function 'force.ultrametric' (with option method = 'extend') of the 'phytools', and resolved the polytomies using the function 'fix.poly' of the 'RRphylo'.

Environmental data

The latitudinal and longitudinal positions of the centres of the regions were determined using ArcGIS 10.6 based on the information from the original source. Environmental variables for each region included (a) seasonal normalized difference vegetation indices (NDVI) (reflecting the amount of green vegetation in boreal/austral spring, summer, autumn and winter); (b) mean, maximum and minimum air temperature; and (c) seasonal precipitation (for boreal/austral spring, summer, autumn and winter). Environmental data were averaged over a region across 30 arc-second grids. NDVI data were obtained from the database PROBA-V S10 TOC NDVI 1KM (http://www.eovoc.spacebel.be). Air temperature and precipitation variables were extracted from the WORLDCLIM (BIOCLIM) 2.0 package (Fick and Hijmans,

2017). Then, we ran principal component analyses of each category of environmental variables and substituted their original values with the scores of the first principal component. This resulted in 3 composite environmental variables, namely (a) a vegetation variable (based on the NDVI) that reflected the amount of green vegetation, (b) an air temperature variable and (c) a precipitation variable. In each realm, these new variables explained from 72 to 97% of the variation in NDVI, from 74 to 97% of the variation in air temperature and from 71 to 92% of the variation in precipitation (see Supplementary Table S1). In all realms, the vegetation, air temperature and precipitation variables reflected an increase in the respective raw variables, except in the Indomalaya, where the principal component of precipitation variables corresponded to a decrease in the amount of summer rainfall and an increase in rainfall in the remaining seasons (Supplementary Table S1).

Data analyses: phyloGDM

Measures of phylogenetic dissimilarities among sites represent traditional dissimilarity indices where species are replaced by evolutionary units (Ferrier et al., 2007; Nipperess et al., 2010; Pavoine, 2016). For each realm, we constructed a presence/absence matrix for either flea or host species per each region. Then, we calculated flea or host phylogenetic dissimilarity matrices for each realm using the command 'evodiss_family' of the R package 'adiv' (Pavoine, 2020) with option 'method = 7', that is, using coefficient S12 of Gower and Legendre (1986) based on Ochiai (1957). We chose to use this coefficient because it is calculated for incidence rather than abundance data, whereas the abundances of either flea or host species were not available in the majority of data sources. PhyloGDMs were carried out separately for each realm using the R package 'gdm' (Fitzpatrick et al., 2022). First, we ran phyloGDMs to reveal how between-region phylogenetic dissimilarity in flea assemblages was affected by host phylogenetic dissimilarity, environmental dissimilarity and geographic distances. Then, we ran phyloGDMs on host phylogenetic dissimilarity as affected by environmental dissimilarity and geographic distances.

Data analyses: phylogenetic originality and phylogenetic diversity

To test (a) whether the phylogenetic originality of a flea species affected its level of host specificity in terms of the size and phylogenetic diversity of a host spectrum and (b) whether the phylogenetic originality of a host species affected the species richness and phylogenetic diversity of its flea assemblages, we calculated the measures of the phylogenetic originality of a flea or a host species and the phylogenetic diversity of a host spectrum or a flea assemblage separately for each realm. The phylogenetic originality of a flea or a host was calculated as 2Hb index (a vector that maximizes the ^2H index of Pavoine and Izsak, 2014) using the function 'distinctUltra' with the option 'method = 2Hb' of the 'adiv' package. ^2H represents an application of the quadratic entropy (QE) of Rao (1982) modified by Ricotta and Szeidl (2009) and developed by Pavoine et al. (2005) and Pavoine and Izsak (2014), where the QE is equal to the expected dissimilarity between 2 entities randomly selected using a replacement (see mathematical details in Pavoine and Izsak, 2014). Pavoine and Izsak (2014) demonstrated that a maximizing vector for ^2H can be used as a measure of a given species' phylogenetic originality.

The sizes of a flea's host spectrum and the species richness of a host's flea assemblage were calculated as mere numbers of species. Mean pairwise distance (MPD) and mean nearest-taxon distance (MNTD) (Tucker et al., 2017) were used as metrics of the

phylogenetic diversity of either a flea's host spectrum or a host's flea assemblage. Both metrics measure the phylogenetic dispersion of a community. MPD is the average phylogenetic distance between all species, whereas MNTD measures the average phylogenetic distance between the nearest-neighbouring species. The standardized effect sizes of the MPD and MNTD (SES_{MPD} and SES_{MNTD}, respectively) for either host spectra or flea assemblages were obtained by comparing observed phylogenetic relatedness to phylogenetic relatedness expected under the null model of randomization of either a host spectrum or a flea assemblage constructed using the 'independent swap' algorithm (Gotelli and Entsminger, 2001). This algorithm maintains species occurrence frequency and species richness in either a host spectrum or a flea assemblage. Calculations were done using the functions 'ses.mpd' and 'ses.mntd', respectively, of the R package 'picante' (Kembel *et al.*, 2010).

The relationships between a flea species' or a host species' originality (an independent variable) and either the size/species richness of a host spectrum or a flea assemblage or its phylogenetic diversity (a dependent variable) were analysed using generalized linear models. Prior to the analyses, all variables were normalized from 0 to 1.

Results

Phylogenetic turnover

The results of the phyloGDMs that aimed to test (a) how flea phylogenetic turnover was affected by host phylogenetic turnover, environmental dissimilarity and geographic distance and (b) how host phylogenetic turnover was affected by environmental dissimilarity and geographic distance are presented in Tables 1 and 2, respectively. All models explained substantial proportions of deviance. I-splines produced by the phyloGDMs for fleas are presented in Figs 1–3, whereas those for hosts are in Supplementary Figs S1–S3. In all realms, flea phylogenetic turnover was affected first and foremost by host phylogenetic turnover, whereas the effect of environment on flea phylogenetic turnover within a realm was weaker. The shape of the I-spline for host turnover as a predictor of flea turnover was similar in all realms and steeply increased with an increase in host phylogenetic dissimilarity. Furthermore, different environmental variables played different roles in their effect on flea phylogenetic turnover. For example, the most important environmental predictor of flea phylogenetic turnover in the Afrotropics, the Indomalaya and the Palaearctic was temperature gradient (Figs 1–3), whereas this factor did not play any role whatsoever in the Australasia and exerted the weakest impact of all the environmental gradients on flea turnover in the Nearctic and the Neotropics (Figs 2 and 3). Similarly, flea phylogenetic turnover strongly responded to the amount of green vegetation gradient in the Neotropics, but the effect of vegetation in the Palaearctic was extremely weak. The precipitation gradient was associated with flea turnover in the Afrotropics, the Australasia and the Nearctic, whereas it did not have any influence in the remaining realms. In addition, dissimilarity in the phylogenetic composition of flea assemblages between regions increased with an increase of spatial distance between regions in all realms, although this increase was manifested differently in different realms, being strong in the Australasia, moderate in the Nearctic and the Neotropics and weak in the Afrotropics, the Indomalaya and the Palaearctic (Figs 1–3).

Within the same realm, dissimilarity in host and flea phylogenetic composition was differently affected by environmental gradients. For example, the effect of precipitation on dissimilarity in phylogenetic composition in the Afrotropics was strong for hosts and weak for fleas (Fig. 1 and Supplementary Fig. S1). In

the Australasia, the amount of vegetation was a strong predictor of host, but not flea, phylogenetic turnover (Fig. 1 and Supplementary Fig. S1). In 4 of 6 realms (the Australasia, the Nearctic, the Neotropics and the Palaearctic) (Figs 1–3 and Supplementary Figs S1–S3), geographic distances were substantially better predictors of host phylogenetic turnover than environmental gradients.

Phylogenetic originality, host specificity and phylogenetic diversity of flea assemblages

No significant relationships between a flea species' phylogenetic originality (FPO) and either its host spectrum's size (HSR) or phylogenetic diversity were found except in the Palaearctic ($P > 0.05$ for all), where the number of host species exploited by a flea decreased with an increase in a flea's originality (HSR = 0.15–$0.20 \times$ FPO, $R^2 = 0.02$, $F = 4.89$, $P = 0.03$; Fig. 4A). However, the coefficient of determination of this relationship was rather low, and the point scatter in Fig. 4A was clearly triangular, suggesting that fleas with a low degree of originality could exploit either many or only a few host species, whereas highly original fleas were highly host specific. In addition, the negative relationship between the FPO and the phylogenetic diversity of its host spectrum, in terms of MPD, was marginally significant in the Nearctic ($F = 3.10$, $P = 0.08$).

A host's phylogenetic originality (HPO) affected the species richness of its flea assemblage in the Afrotropics and the Palaearctic, both metrics of phylogenetic diversity in the Nearctic, and phylogenetic diversity measured as MNTD in the Australasia (Table 3), whereas no relationships whatsoever were found in the Neotropics and the Indomalaya. In the Afrotropics, the Palaearctic and the Australasia, these relationships were negative, and similar to the effect of FPO on host diversity, point scatters were clearly triangular (Fig. 4B–D). This suggested that phylogenetically non-original host species could harbour either highly diverse or less diverse flea assemblages, whereas flea assemblages of highly phylogenetically original hosts were either species-poor or phylogenetically similar. However, in the Nearctic, both the MPD and MNTD of flea assemblages increased with an increase in HPO (Fig. 4E, F). In other words, flea assemblages of highly phylogenetically original North American hosts were highly phylogenetically diverse. A significantly negative relationship between MNTD and HPO in the Australasia arose mainly due to 2 monotreme hosts (which obviously were highly phylogenetically original) (Fig. 4D). After these hosts were removed from the analysis, the relationship still appeared to be negative, albeit only marginally significant (MNTD = 0.55–$1.77 \times$ HFO, $F = 3.56$, $P = 0.06$). Additionally, negative relationships between HPO and (i) species richness or (ii) phylogenetic dissimilarity, measured as the MPD of its flea assemblage, were marginally significant in the Nearctic ($F = 3.10$, $P = 0.08$) and the Australasia ($F = 3.80$, $P = 0.06$), respectively.

Discussion

The strong link between flea and host phylogenetic turnover found in this study reflects the common evolutionary history of fleas and their hosts. This common history does not, however, necessarily imply co-speciation as advocated in the earliest studies that compared parasite and host phylogenies (e.g. Hafner and Nadler, 1988, 1990; Hafner and Page, 1995). Instead, the common history of parasites and their hosts is often (indeed, almost always) characterized by a variety of other coevolutionary events, such as host switching, lineage sorting and duplications [see definitions in, e.g. Paterson *et al.* (1993); Beveridge and Chilton (2001); Roy (2001)]. As a result, phylogenetic trees of parasites and

Table 1. Flea phylogenetic turnover as explained by host phylogenetic turnover (HPT), environmental variables (Veg, T, P) and geographic distance (GD) between regions in 6 biogeographic realms

Realm	%Deviance explained	Predictor	I-spline 1	I-spline 2	I-spline 3	$\Sigma_{\text{I-splines}}$
Afrotropics	81.28	HPT	0.00	0.16	0.97	1.97
		Veg	0.00	0.00	0.00	0.00
		T	0.17	0.04	0.03	0.24
		P	0.05	0.07	0.005	0.12
		GD	0.11	0.00	0.00	0.11
Australasia	58.72	HPT	0.00	0.00	1.56	1.56
		Veg	0.00	0.00	0.00	0.00
		T	0.00	0.00	0.00	0.00
		P	0.12	0.00	0.00	0.12
		GD	0.00	0.15	0.55	0.70
Indomalaya	77.71	HPT	0.00	0.00	0.70	0.70
		Veg	0.00	0.00	0.32	0.32
		T	0.32	0.00	0.00	0.32
		P	0.00	0.00	0.00	0.00
		GD	0.00	0.12	0.00	0.12
Nearctic	81.55	HPT	0.00	0.00	1.13	1.13
		Veg	0.00	0.00	0.00	0.00
		T	0.00	0.03	0.08	0.11
		P	0.02	0.00	0.16	0.18
		GD	0.00	0.25	0.00	0.25
Neotropics	75.74	HPT	0.00	0.00	0.81	0.81
		Veg	0.00	0.54	0.00	0.54
		T	0.27	0.11	0.00	0.38
		P	0.00	0.00	0.00	0.00
		GD	0.20	0.13	0.00	0.33
Palaearctic	74.47	HPT	0.00	0.00	1.65	1.65
		Veg	0.05	0.03	0.00	0.08
		T	0.00	0.00	0.42	0.42
		P	0.00	0.00	0.00	0.00
		GD	0.15	0.02	0.00	0.17

Veg, T and P composite environmental variables reflecting the amount of green vegetation, air temperature and precipitation, respectively (see text for explanations); I-splines 1, 2 and 3: coefficients of the first, second or third I-spline, respectively; $\Sigma_{\text{I-splines}}$: sum of 3 I-splines (demonstrates the amplitude of an I-spline).

hosts are most often incongruent (e.g. Caira and Jensen, 2001). Our results indicated a pattern of parasite–host coevolution resembling co-speciation but taking place at a phylogenetic level deeper than species and genera. This supports the conclusions of Traub (1980), Whiting *et al.* (2008) and Zhu *et al.* (2015) that flea history and dispersal are strongly tied to those of their mammalian hosts and that flea diversification started when their ancestors became an ectoparasite on mammals. Moreover, flea diversification is undoubtedly a response to the diversification of their hosts (e.g. Morrone and Gutiérrez, 2005) exemplifying the so-called phylogenetic tracking (Russo *et al.*, 2017). Although strict co-speciation has not been proven, repeated episodes of co-speciation might be masked because they are mediated by, for example, vicariant events. Clear clustering of flea assemblages, according to the biogeographic realms to which they belong (Krasnov *et al.*, 2022a), indicated independent (to some extent) flea evolution in different realms. Tight relationships of certain phylogenetic lineages of fleas with certain phylogenetic lineages

of their hosts (e.g. Krasnov *et al.*, 2016) have resulted in patterns of flea geographic distribution that often mirror those of their host (Traub, 1980; Medvedev, 2005; Morrone and Gutiérrez, 2005; López-Berrizbeitia *et al.*, 2020). Recently, Gibert *et al.* (2021) demonstrated that the species composition of fleas and their small mammalian hosts on several continents predominantly depended on historical processes (dispersal). This is because fleas most likely rely on their hosts, using them as dispersal vehicles due to their own limited (if any) dispersal abilities.

Environmental predictors of flea phylogenetic turnover played a less important, albeit substantial, role than host phylogenetic turnover. This indicates the dependence of a flea's ecological requirements on both host identity and environmental factors (Krasnov *et al.*, 1998, 2015) and could be a reasonable explanation for the effect of environment on flea compositional turnover. The environmental effect on phylogenetic turnover suggests that some physiological flea traits determining their environmental requirements and/or preferences might be phylogenetically conserved.

Table 2. Host phylogenetic turnover as explained by environmental variables (Veg, T, P) and geographic distance (GD) between regions in 6 biogeographic realms

Realm	Deviance explained	Predictor	I-spline 1	I-spline 2	I-spline 3	$\Sigma_{\text{I-splines}}$
Afrotropics	19.08	Veg	0.00	0.00	0.00	0.00
		T	0.00	0.00	0.13	0.13
		P	0.00	0.91	0.00	0.91
		GD	0.00	0.00	0.00	0.00
Australasia	38.61	Veg	0.06	0.17	0.00	0.23
		T	0.00	0.00	0.09	0.09
		P	0.00	0.00	0.00	0.00
		GD	0.37	0.00	0.21	0.58
Indomalaya	53.81	Veg	0.08	0.00	0.00	0.08
		T	0.00	0.60	0.00	0.60
		P	0.03	0.00	0.00	0.03
		GD	0.00	0.22	0.00	0.22
Nearctic	52.57	Veg	0.00	0.00	0.00	0.00
		T	0.00	0.00	0.35	0.35
		P	0.07	0.00	0.12	0.19
		GD	0.47	0.32	0.00	0.79
Neotropics	67.31	Veg	0.02	0.06	0.00	0.08
		T	0.08	0.24	0.00	0.32
		P	0.00	0.00	0.04	0.04
		GD	0.15	0.40	0.04	0.58
Palaearctic		Veg	0.04	0.00	0.00	0.04
		T	0.15	0.00	0.26	0.41
		P	0.54	0.00	0.11	0.65
		GD	0.33	0.41	0.26	1.00

Veg, T and P composite environmental variables reflecting the amount of green vegetation, air temperature and precipitation, respectively (see text for explanations); I-splines 1, 2 and 3: coefficients of the first, second or third I-spline, respectively; $\Sigma_{\text{I-splines}}$: sum of 3 I-splines (demonstrates the amplitude of an I-spline).

This, however, has never been studied and, thus, is completely unknown. Nevertheless, some observations have indicated that this might well be the case. For example, a significant phylogenetic signal was found in flea body size (Surkova *et al.*, 2018). Given that body size and many physiological variables are highly correlated in many taxa, including insects (Peters, 1983; Schmidt-Nielsen, 1984; Chown and Gaston, 1997; Chown *et al.*, 2002), a phylogenetic signal in flea physiological traits is expected, which, in turn, might be translated into the relationships between flea phylogenetic turnover and environmental gradients. Furthermore, environmental predictors of flea phylogenetic turnover differed between biogeographic realms. There might be at least 2, not mutually exclusive, reasons behind this. First, the length of an environmental gradient, that is, variation in an environmental variable, can differ between realms, so that environmental variation might be too low for a turnover to respond to. For example, the coefficients of variation of the NDVI variables in the Australasia ranged from 0.47 to 0.52, whereas the coefficients of variation of the precipitation variables were higher and ranged from 0.93 to 1.11. As a result, flea phylogenetic turnover responded to precipitation but not to the amount of green vegetation. Second, different flea lineages might have different environmental requirements/preferences in dependence on the environmental conditions they evolved under, so that lineages in different realms differ in their sensitivity to the same environmental factors. Admittedly, we do not have any information supporting the latter explanation. We

recognize that it is highly speculative and requires special investigation.

As mentioned above, host phylogenetic turnover appeared to be a better predictor of flea phylogenetic turnover than environment. A similar pattern was reported by Krasnov *et al.* (2020) for flea compositional turnover in 4 biogeographic realms. However, the best predictor of dissimilarity in flea species composition in Mongolia was found to be the air temperature gradient, whereas the effect of dissimilarity in host species composition was weaker (Maestri *et al.*, 2017). In other words, the identity of the best predictor of flea compositional turnover might be scale dependent. Comparison of this study's results with those of Krasnov *et al.* (2019*b*) and Maestri *et al.* (2020), however, suggests that predictors of flea phylogenetic turnover are scale invariant. Nevertheless, both studies at the local scale were carried out in the Palaearctic. It remains to be further studied whether predictors of flea phylogenetic turnover are scale-dependent in other biogeographic realms.

Phylogenetic turnovers of fleas and hosts were predicted by different environmental gradients in the same realm. Maestri *et al.* (2017, 2020) reported the same pattern for the compositional beta-diversity of fleas and hosts and concluded that flea species composition responds directly to environmental variables rather than being mediated by host responses. The same appears to be true for the phylogenetic beta-diversity of fleas. The simplest explanation for this may be the sharp differences in ecological requirements, possibilities and constraints between insects (i.e. fleas) and mammals.
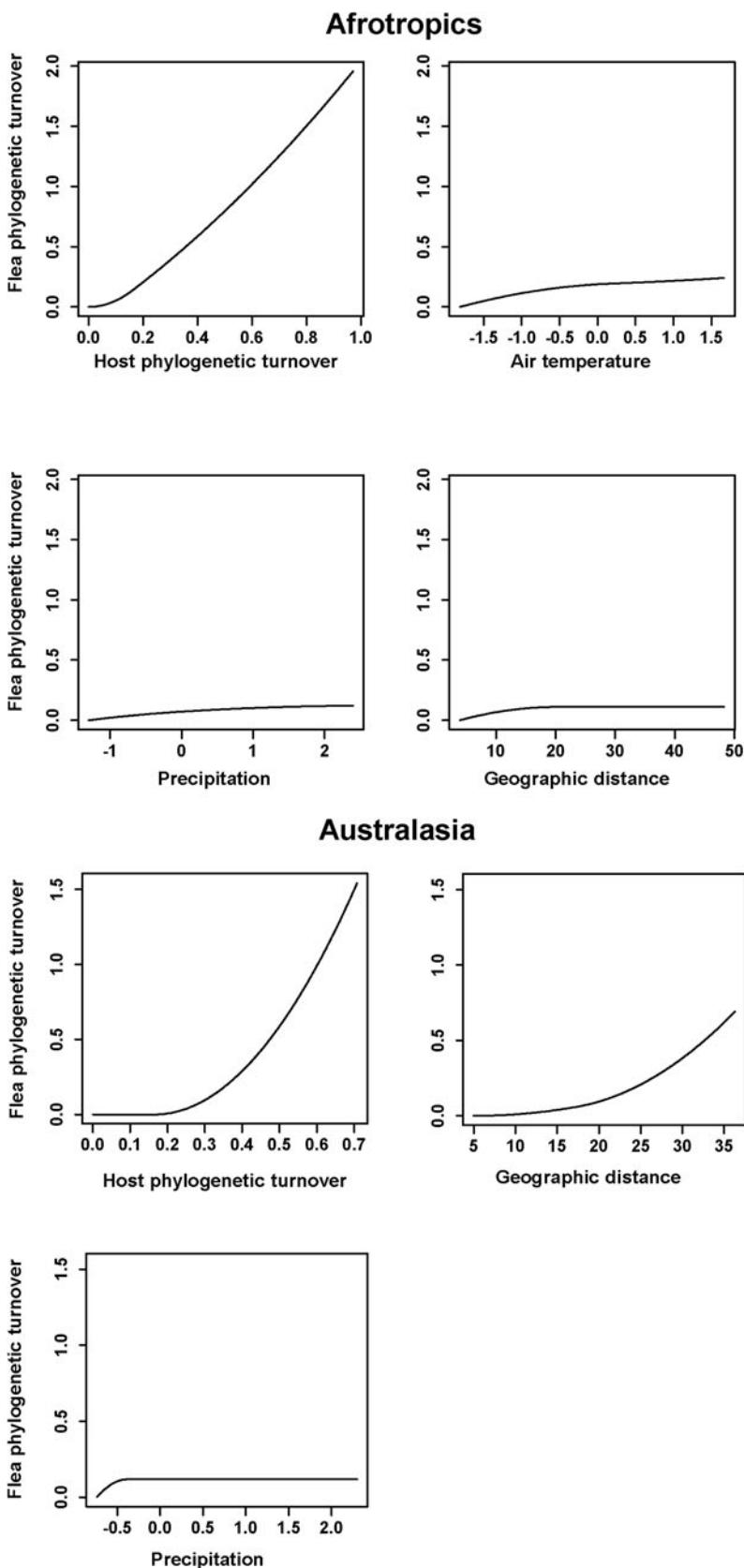
Fig. 1. Generalized dissimilarity model-fitted I-splines (partial regression fits) of host phylogenetic turnover, environmental variables and geographic distance as predictors of flea phylogenetic turnover across the Afrotropics and the Australasia. The steeper slope of the transformed relationship on a given section of the gradient indicates a greater rate of turnover.

Geographic distance was, in general, a better predictor of phylogenetic turnover for hosts than for fleas. Its importance varied between realms in both fleas and hosts. In addition, it had no effect on the phylogenetic turnover of hosts in the Afrotropics. This supports earlier observations that the famous pattern of distance decay of community similarity (Nekola and White, 1999) is not universal in terms of either compositional similarity or phylogenetic similarity (Pérez-del-Olmo *et al.*, 2009; Maestri *et al.*, 2017).

We found only a weak relationship between flea phylogenetic originality and host specificity and only in terms of host species richness and only in the Palaearctic (although some trend could be envisaged in the Nearctic). The main reason behind the general

Indomalaya

Nearctic
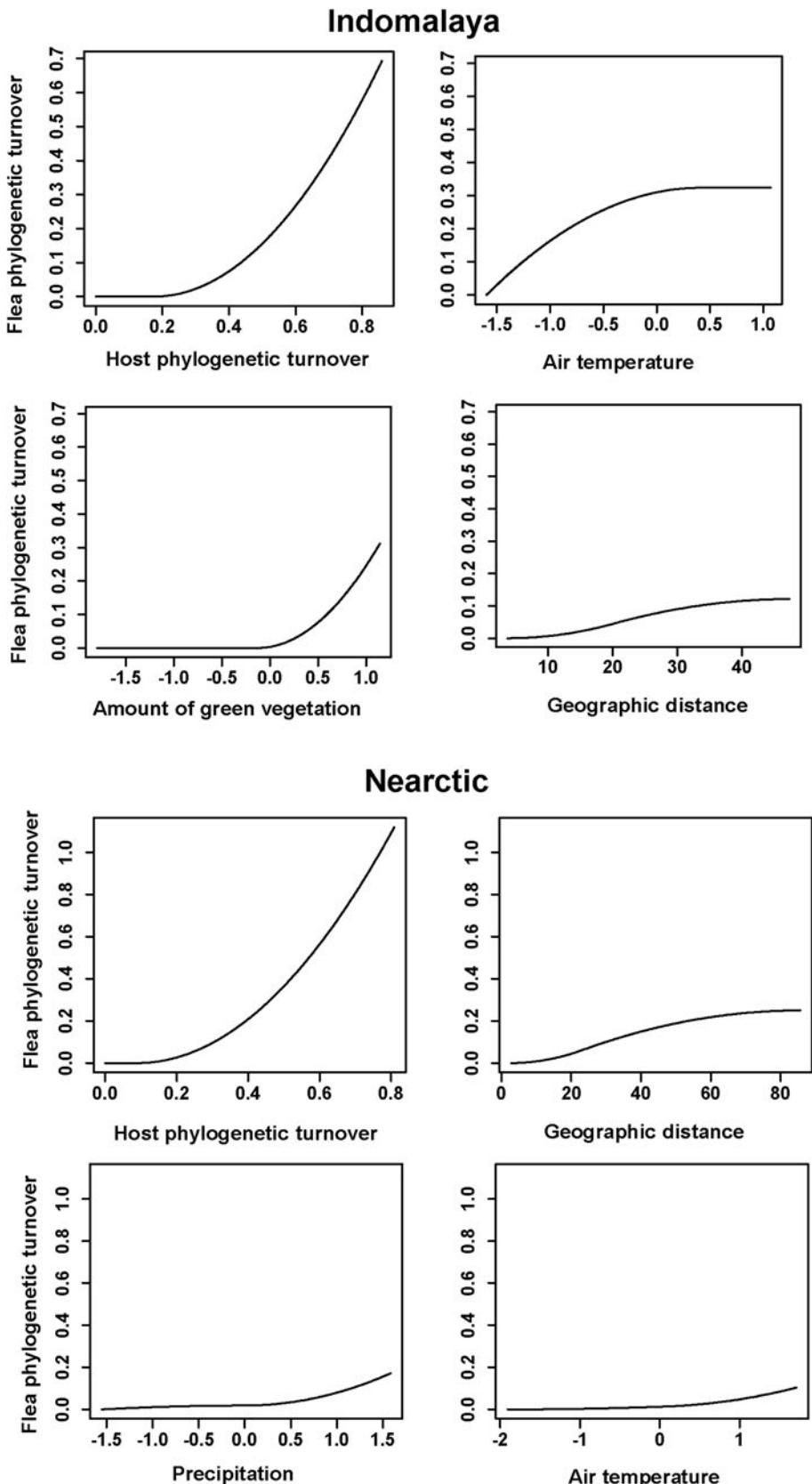
Fig. 2. Generalized dissimilarity model-fitted I-splines (partial regression fits) of host phylogenetic turnover, environmental variables and geographic distance as predictors of flea phylogenetic turnover across the Indomalaya and the Nearctic. The steeper slope of the transformed relationship on a given section of the gradient indicates a greater rate of turnover.

lack of association between parasite phylogenetic originality and host specificity could be that host specificity, to a great extent, correlates with parasite traits rather than with their phylogenetic position. For example, reproductive output, in terms of clutch size, correlates with host specificity in copepods (Doherty *et al.*, 2022). Similarly, the number of host species used by facultatively haematophagous gamasid mites correlated with their body size

(Krasnov *et al.*, 2013). In other words, parasite host specificity might be related to its functional rather than its phylogenetic originality, while phylogenetic originality does not necessarily reflect functional originality (Pavoine *et al.*, 2017). The relationships between a parasite's functional originality and its host specificity remain to be investigated. Nevertheless, the case of the Palaearctic fleas may be linked to the fact that diversification of the largest
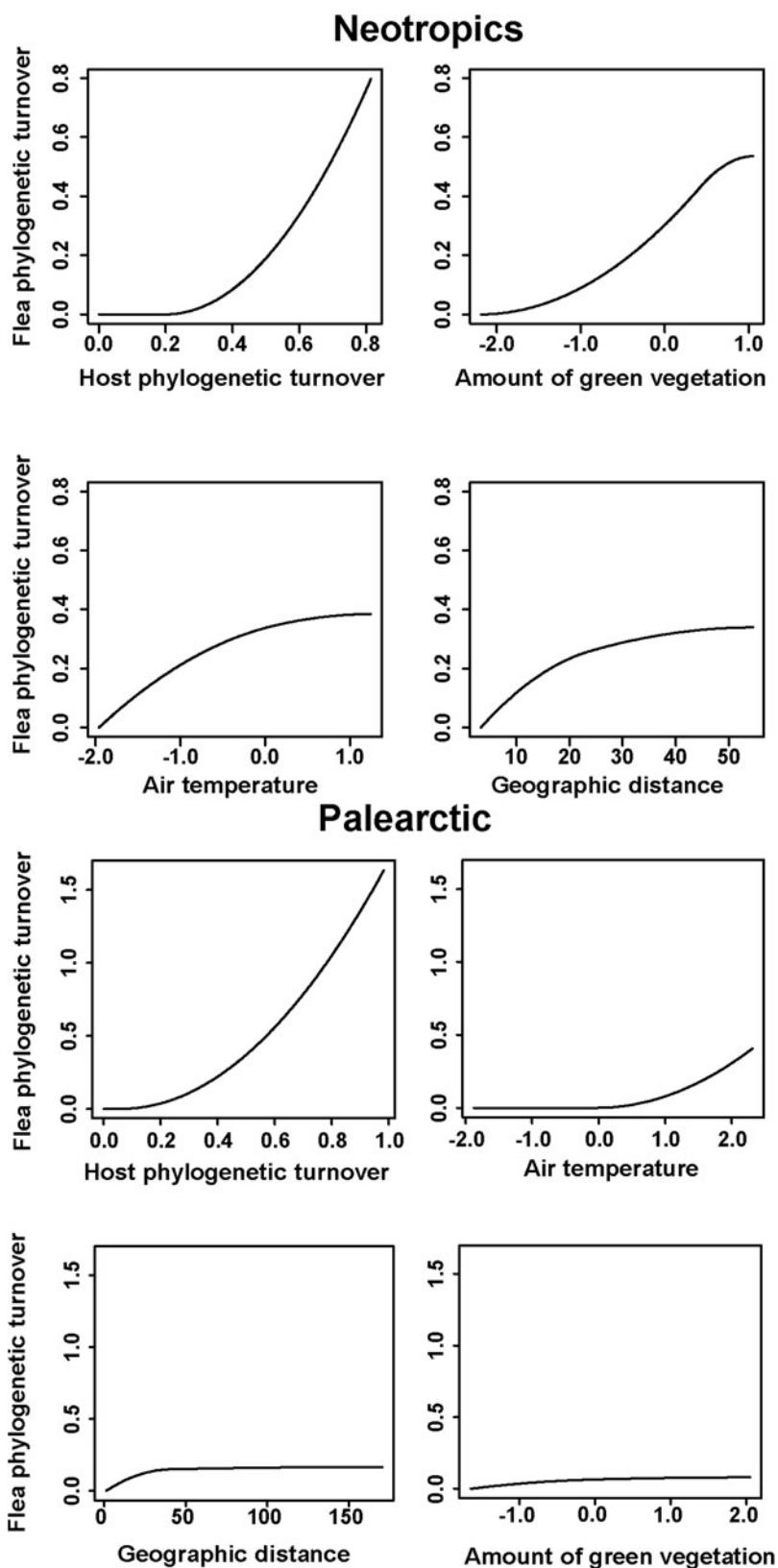
Fig. 3. Generalized dissimilarity model-fitted I-splines (partial regression fits) of host phylogenetic turnover, environmental variables and geographic distance as predictors of flea phylogenetic turnover across the Neotropics and the Palaearctic. The steeper slope of the transformed relationship on a given section of the gradient indicates a greater rate of turnover.

flea families likely occurred in this realm and started as late as in the Eocene (Medvedev, 2005). As a result, the distribution of flea species according to the degree of their phylogenetic originality was strongly asymmetrical in the Palaearctic (skewness = 3.94) followed by that in the Nearctic (3.38), with less asymmetry in the remaining realms (2.33–3.24). The high asymmetry of this distribution could have resulted in a significant relationship between phylogenetic originality and the size of a host spectrum.

Relationships between the phylogenetic originality of a host species and either the compositional or phylogenetic diversity of their flea assemblages, albeit weak, were found in 4 of the 6 realms. These might have resulted from the aforementioned chain of associations between phylogenetic originality, geographic range size and diversity of flea assemblages (Feliu *et al.*, 1997; Veron *et al.*, 2021). Surprisingly, the trend of increased phylogenetic flea diversity in the most phylogenetically original hosts in the Nearctic was
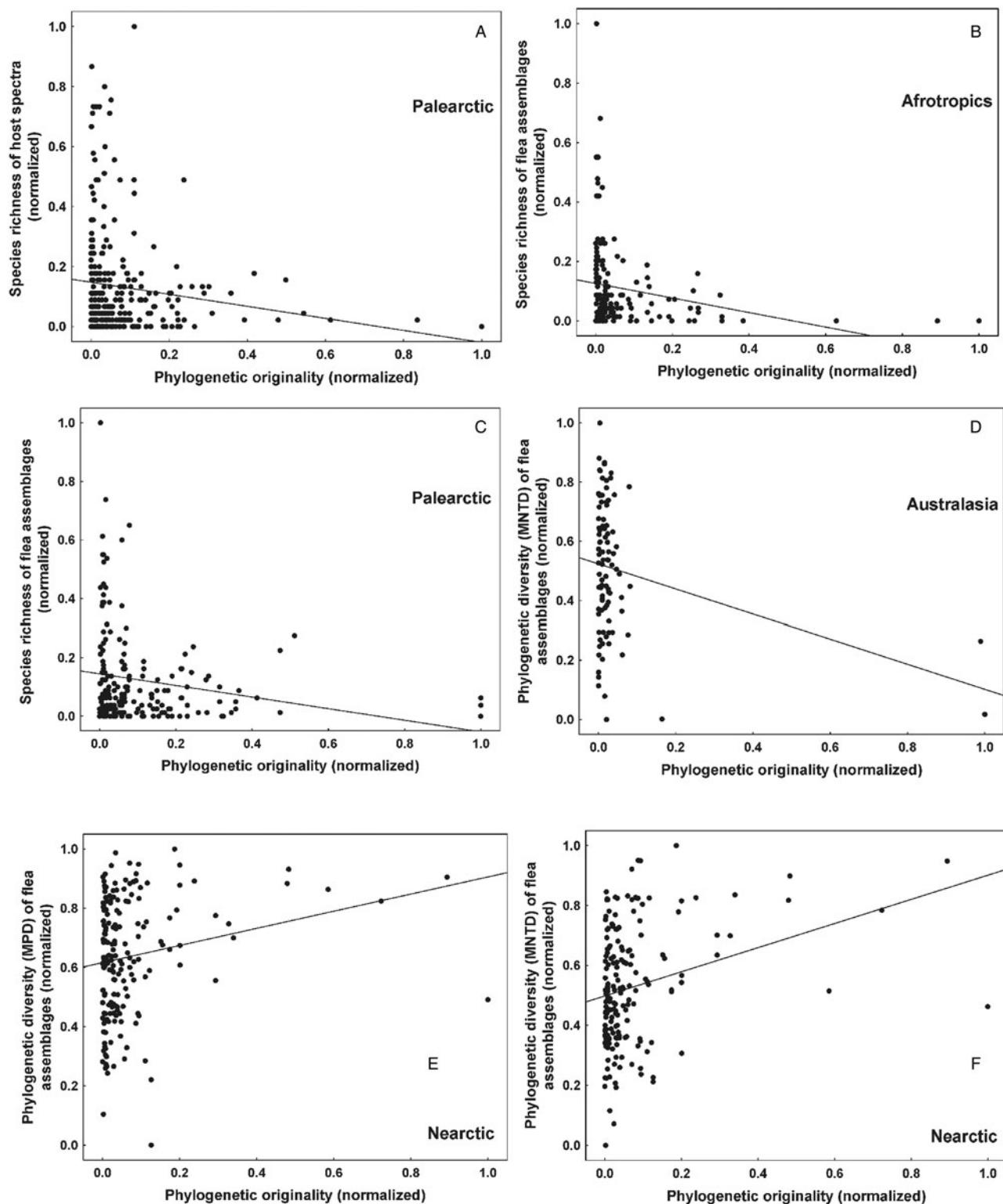
Fig. 4. Relationship between the phylogenetic originality of a flea species and the number of host species it exploits in the Palaearctic (A), between the phylogenetic originality of a host species and the number of flea species it harbours in the Afrotropics (B) and the Palaearctic (C), between the phylogenetic originality of a host species and the phylogenetic diversity of its flea assemblage measured as either MPD or MNTD in the Australasia (D) and the Nearctic (E, F). MPD, mean pairwise distance; MNTD, mean nearest-taxon distance (see text for explanations).

opposite to the patterns found in the Australasia. This difference is difficult to explain, although it suggests differential histories of flea evolution in different realms. Our knowledge of the historical patterns of flea evolution and dispersal is insufficient. However, these opposite trends might somehow be associated with the fact that flea fauna in the Nearctic is represented by a large number of species belonging to the youngest family (Ceratophyllidae), whereas many Australasian fleas belong to the basal flea families Macropsyllidae, Stephanocircidae, Pygiopsyllidae, Stivaliidae and Lycopsyllidae (Medvedev, 2005; Zhu *et al.*, 2015).

In conclusion, the results of our study suggest that fleas' phylogenetic turnover is determined, to a great extent, by the phylogenetic turnover of their hosts, whereas environmental factors are less important. Comparison of the results of this study with those of

Table 3. Relationship between the phylogenetic originality of a host species (HPO) and either the species richness (FSR) or phylogenetic diversity of its flea assemblage (MPD or MNTD) in 4 biogeographic realms (only significant models are shown)

Realm	Diversity metric	Equation	R^2	F	P
Afrotropics	FSR	$0.13 - 0.24 \times HPO$	0.06	9.22	0.003
Palaearctic	FSR	$0.14 - 0.20 \times HPO$	0.04	7.54	0.007
Australasia	MNTD	$0.52 - 0.42 \times HPO$	0.07	7.35	0.008
Nearctic	MPD	$0.62 + 0.29 \times HPO$	0.04	7.45	0.006
	MNTD	$0.50 + 0.40 \times HPO$	0.08	15.27	0.0001

MPD, mean pairwise distance; MNTD, mean nearest-taxon distance (Tucker *et al.*, 2017).

earlier studies (e.g. Krasnov *et al.*, 2019*a*) suggests that the phylogenetic alpha- and beta-diversity of parasites are controlled by different rules (see also Krasnov *et al.*, 2019*b*). In addition, phylogenetic patterns in the order Siphonaptera are manifested mainly at the level of regional assemblages rather than at the level of individual species.

References

Adlard RD, Miller TL and Smit NJ (2015) The butterfly effect: parasite diversity, environment, and emerging disease in aquatic wildlife. *Trends in Parasitology* 31, 160–166.

Bass D, Stentiford GD, Littlewood DTJ and Hartikainen H (2015) Diverse applications of environmental DNA methods in parasitology. *Trends in Parasitology* 31, 499–513.

Beveridge I and Chilton NB (2001) Co-evolutionary relationships between the nematode subfamily Cloacininae and its macropodid marsupial hosts. *International Journal for Parasitology* 31, 976–996.

Brown JH (1984) On the relationship between abundance and distribution of species. *American Naturalist* 124, 255–279.

Cadotte MW and Davies TJ (2010) Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions* 16, 376–385.

Caira JN and Jensen K (2001) An investigation of the co-evolutionary relationships between onchobothriid tapeworms and their elasmobranch hosts. *International Journal for Parasitology* 31, 960–975.

Castiglione S, Serio C, Piccolo M, Mondanaro A, Melchionna M, Febbraro MD, Sansalone G, Wroe S and Raia P (2020) The influence of domestication, insularity and sociality on the tempo and mode of brain size evolution in mammals. *Biological Journal of the Linnean Society* 132, 221–231.

Chown SL and Gaston KJ (1997) The species-body size distribution: energy, fitness and optimality. *Functional Ecology* 11, 365–375.

Chown SL, Addo-Bediako A and Gaston KJ (2002) Physiological variation in insects: large-scale patterns and their implications. *Comparative Biochemistry and Physiology B* 131, 587–602.

Clark NJ (2018) Phylogenetic uniqueness, not latitude, explains the diversity of avian blood parasite communities worldwide. *Global Ecology and Biogeography* 27, 744–755.

Doherty J, Milotic M, Filion A and Eriksson A (2022) Host specificity and the reproductive strategies of parasites. *Parasitology* 149, 534–541.

Eriksson A, Doherty JF, Fischer E, Graciolli G and Poulin R (2019) Hosts and environment overshadow spatial distance as drivers of bat fly species composition in the Neotropics. *Journal of Biogeography* 47, 736–747.

Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61, 1–10.

Feliu C, Renaud F, Catzeflis F, Hugot J-P, Durand P and Morand S (1997) Comparative analysis of parasite species richness of Iberian rodents. *Parasitology* 115, 453–466.

Ferrier S, Manion G, Elith J and Richardson K (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions* 13, 252–264.

Fick SE and Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302–4315.

Fitzpatrick M, Mokany K, Manion G, Nieto-Lugilde D and Ferrier S (2022) gdm: Generalized dissimilarity modelling. https://mfitzpatrick.al.umces.edu/gdm/, https://github.com/fitzLab-AL/gdm/.

Gibert C, Shenbrot G, Stanko M, Khokhlova IS and Krasnov BR (2021) Dispersal-based versus niche-based processes as drivers of flea species composition on small mammalian hosts: inferences from species occurrences at large and small scales. *Oecologia* 197, 471–484.

Gotelli NJ and Entsminger GL (2001) Swap and fill algorithms in null model analysis: rethinking the Knight's Tour. *Oecologia* 129, 281–291.

Gower JC and Legendre P (1986) Metric and Euclidean properties of dissimilarity coefficients. *Journal of Classification* 3, 5–48.

Hadfield JD, Krasnov BR, Poulin R and Nakagawa S (2014) A tale of two phylogenies: comparative analyses of ecological interactions. *American Naturalist* 183, 174–187.

Hafner MS and Nadler SA (1988) Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* 332, 258–259.

Hafner MS and Nadler SA (1990) Cospeciation in host-parasite assemblages: comparative analysis of rates of evolution and timing of cospeciation events. *Systematic Zoology* 39, 192–204.

Hafner MS and Page RD (1995) Molecular phylogenies and host-parasite cospeciation: gophers and lice as a model system. *Philosophical Transactions of the Royal Society of London B* 349, 77–83.

Isaac NJ, Turvey ST, Collen B, Waterman C and Baillie JE (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE* 2, e296.

Isaac NJ, Redding DW, Meredith HM and Safi K (2012) Phylogenetically-informed priorities for amphibian conservation. *PLoS ONE* 7, e43912.

Kamiya T, O'Dwyer K, Nakagawa S and Poulin R (2014) Host diversity drives parasite diversity: meta-analytical insights into patterns and causal mechanisms. *Ecography* 37, 689–697.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP and Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464.

Krasnov B (2018) Flea and host species in different regions of four biogeographic realms. Mendeley Data, V1. http://dx.doi.org/10.17632/dzyvrp7kfh.1.

Krasnov BR, Shenbrot GI, Medvedev SG, Khokhlova IS and Vatschenok VS (1998) Habitat-dependence of a parasite-host relationship: flea assemblages

in two gerbil species of the Negev Desert. *Journal of Medical Entomology* 35, 303–313.

Krasnov BR, Shenbrot GI, Khokhlova IS and Degen AA (2004a) Relationship between host diversity and parasite diversity: flea assemblages on small mammals. *Journal of Biogeography* 31, 1857–1866.

Krasnov BR, Shenbrot GI, Khokhlova IS and Degen AA (2004b) Flea species richness and parameters of host body, host geography and host 'milieu'. *Journal of Animal Ecology* 73, 1121–1128.

Krasnov BR, Poulin R, Shenbrot GI, Mouillot D and Khokhlova IS (2005) Host specificity and geographic range in haematophagous ectoparasites. *Oikos* 108, 449–456.

Krasnov BR, Vinarski MV, Korallo-Vinarskaya NP and Khokhlova IS (2013) Ecological correlates of body size in gamasid mites parasitic on small mammals: abundance and niche breadth. *Ecography* 36, 1042–1050.

Krasnov BR, Shenbrot GI, Khokhlova IS, Stanko M, Morand S and Mouillot D (2015) Assembly rules of ectoparasite communities across scales: combining patterns of abiotic factors, host composition, geographic space, phylogeny and traits. *Ecography* 38, 184–197.

Krasnov BR, Shenbrot GI, Khokhlova IS and Degen AA (2016) Trait-based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. *Oikos* 125, 29–38.

Krasnov BR, Shenbrot GI, van der Mescht L, Warburton EM and Khokhlova IS (2019a) Phylogenetic and compositional diversity are governed by different rules: a study of fleas parasitic on small mammals in four biogeographic realms. *Ecography* 42, 1000–1011.

Krasnov BR, Shenbrot GI, Korallo-Vinarskaya NP, Vinarski MV, Warburton EM and Khokhlova IS (2019b) The effects of environment, hosts and space on compositional, phylogenetic and functional beta-diversity in two taxa of arthropod ectoparasites. *Parasitology Research* 118, 2107–2120.

Krasnov BR, Shenbrot GI, van der Mescht L and Khokhlova IS (2020) Drivers of compositional turnover are related to species' commonness in flea assemblages from four biogeographic realms: zeta diversity and multi-site generalised dissimilarity modelling. *International Journal for Parasitology* 50, 331–344.

Krasnov BR, Shenbrot GI and Khokhlova IS (2022a) Regional flea and host assemblages form biogeographic, but not ecological, clusters: evidence for a dispersal-based mechanism as a driver of species composition. *Parasitology* 149, 1450–1459.

Krasnov BR, Shenbrot GI and Khokhlova IS (2022b) Phylogenetic signals in flea-host interaction networks from four biogeographic realms: differences between interactors and the effects of environmental factors. *International Journal for Parasitology* 52, 475–484.

Lawton J (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* 28, 23–39.

Llopis-Belenguer C, Pavoine S, Blasco-Costa I and Balbuena JA (2020) Assembly rules of helminth parasite communities in grey mullets: combining components of diversity. *International Journal for Parasitology* 50, 1089–1098.

López-Berrizbeitia MF, Acosta-Gutiérrez R and Díaz MM (2020) Fleas of mammals and patterns of distributional congruence in northwestern Argentina: a preliminary biogeographic analysis. *Heliyon* 6, e04871.

MacArthur RH (1958) Population ecology of some warblers of Northeastern coniferous forests. *Ecology* 39, 599–619.

MacArthur RH (1964) Environmental factors affecting bird species diversity. *American Naturalist* 98, 387–397.

Maddison WP and Maddison DR (2021) Mesquite: a modular system for evolutionary analysis. Version 3.70. http://www.mesquiteproject.org.

Maestri R, Shenbrot GI and Krasnov BR (2017) Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. *Journal of Biogeography* 44, 1880–1890.

Maestri R, Shenbrot GI, Warburton EM, Khokhlova IS and Krasnov BR (2020) Contrasting responses of beta diversity components to environmental and host-associated factors in insect ectoparasites. *Ecological Entomology* 45, 594–605.

Marshall AG (1981) *The Ecology of Ectoparasitic Insects*. London, UK: Academic Press.

Martins PM, Poulin R and Gonçalves-Souza T (2021) Integrating climate and host richness as drivers of global parasite diversity. *Global Ecology and Biogeography* 30, 196–204.

May R (1990) Taxonomy as destiny. *Nature* 347, 129–130.

McNew SM, Barrow LN, Williamson JL, Galen SC, Skeen HR, DuBay SG, Gaffney AM, Johnson AB, Bautista E, Ordoñez P, Schmitt CJ, Smiley

A, Valqui T, Bates JM, Hackett SJ and Witt CC (2021) Contrasting drivers of diversity in hosts and parasites across the tropical Andes. *Proceedings of the National Academy of Sciences of the USA* 118, e2010714118.

Medvedev SG (2005) *An Attempted System Analysis of the Evolution of the Order of Fleas (Siphonaptera)*. Lectures in Memoriam N. A. Kholodkovsky, No. 57. Saint Petersburg, Russia: Russian Entomological Society and Zoological Institute of Russian Academy of Sciences (in Russian).

Miller JT, Jolley-Rogers G, Mishler BD and Thornhill AH (2018) Phylogenetic diversity is a better measure of biodiversity than taxon counting. *Journal of Systematics and Evolution* 56, 663–667.

Mokany K, Ware C, Woolley SNC, Ferrier S and Fitzpatrick MC (2022) A working guide to harnessing generalized dissimilarity modelling for biodiversity analysis and conservation assessment. *Global Ecology and Biogeography* 31, 802–821.

Morrone JJ and Gutiérrez A (2005) Do fleas (Insecta: Siphonaptera) parallel their mammal host diversification in the Mexican transition zone? *Journal of Biogeography* 32, 1315–1325.

Nekola JC and White PS (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26, 867–878.

Nipperess DA, Faith DP and Barton K (2010) Resemblance in phylogenetic diversity among ecological assemblages. *Journal of Vegetation Science* 21, 809–820.

Ochiai A (1957) Zoogeographic studies on the soleoid fishes found in Japan and its neighbouring regions. *Bulletin of the Japanese Society for the Science of Fish* 22, 526–530.

Paterson AM, Gray RD and Wallis GP (1993) Parasites, petrels and penguins: does louse presence reflect seabird phylogeny? *International Journal for Parasitology* 23, 515–526.

Pavoine S (2016) A guide through a family of phylogenetic dissimilarity measures among sites. *Oikos* 125, 1719–1732.

Pavoine S (2020) adiv: An R package to analyse biodiversity in ecology. *Methods in Ecology and Evolution* 11, 1106–1112.

Pavoine S and Izsak J (2014) New biodiversity measure that includes consistent interspecific and intraspecific components. *Methods in Ecology and Evolution* 5, 165–172.

Pavoine S, Ollier S and Dufour AB (2005) Is the originality of a species measurable? *Ecology Letters* 8, 579–586.

Pavoine S, Bonsall MB, Dupaix A, Jacob U and Ricotta C (2017) From phylogenetic to functional originality: guide through indices and new developments. *Ecological Indicators* 82, 196–205.

Pérez-del-Olmo A, Fernández M, Raga JA, Kostadinova A and Morand S (2009) Not everything is everywhere: the distance decay of similarity in a marine host-parasite system. *Journal of Biogeography* 36, 200–209.

Peters RH (1983) *The Ecological Implications of Body Size*. Cambridge, UK: Cambridge University Press.

Poulin R, Krasnov BR and Mouillot D (2011) Host specificity in phylogenetic and geographic space. *Trends in Parasitology* 27, 355–361.

Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology* 21, 24–43.

R Core Team (2022) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing, https://www.R-project.org.

Revell LJ (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3, 217–223.

Ricotta C and Szeidl L (2009) Diversity partitioning of Rao's quadratic entropy. *Theoretical Population Biology* 76, 299–302.

Rosauer DF, Ferrier S, Williams KJ, Manion G, Keogh JS and Laffan SW (2013) Phylogenetic generalised dissimilarity modelling: a new approach to analysing and predicting spatial turnover in the phylogenetic composition of communities. *Ecography* 37, 21–32.

Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge, UK: Cambridge University Press.

Roy BA (2001) Patterns of association between crucifers and their flower-mimic pathogens: host jumps are more common than coevolution or cospeciation. *Evolution* 55, 41–53.

Russo L, Miller AD, Tooker J, Bjornstad ON and Shea K (2017) Quantitative evolutionary patterns in bipartite networks: vicariance, phylogenetic tracking or diffuse co-evolution? *Methods in Ecology and Evolution* 9, 761–772.

Schmidt-Nielsen K (1984) *Scaling. Why is Animal Size So Important?* Cambridge, UK: Cambridge University Press.

Selbach C, Jorge F, Dowle E, Bennett J, Chai X, Doherty JF, Eriksson A, Filion A, Hay E, Herbison R, Lindner J, Park E, Presswell B, Ruehle

B, Sobrinho PM, Wainwright E and Poulin R (2019) Parasitological research in the molecular age. *Parasitology* **146**, 1361–1370.

Surkova EN, Warburton EM, van der Mescht L, Khokhlova IS and Krasnov BR (2018) Body size and ecological traits in fleas parasitic on small mammals in the Palearctic: larger species attain higher abundance. *Oecologia* **188**, 559–569.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M and Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.

Thieltges DW, Hof C, Dehling DM, Brändle M, Brandl R and Poulin R (2011) Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna. *Global Ecology and Biogeography* **20**, 675–682.

Traub R (1980) The zoogeography and evolution of some fleas, lice and mammals. In Traub R and Starcke H (eds), *Fleas*. Proceedings of the International Conference on Fleas, Ashton Wold, England, June, 1977. Rotterdam, The Netherlands: A. A. Balkema, pp. 93–172.

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M and Mazel F (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* **92**, 698–715.

Upham NS, Esselstyn JA and Jetz W (2019) Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology* **17**, e3000494.

Vane-Wright RI, Humphries CJ and Williams PH (1991) What to protect? Systematics and the agony of choice. *Biological Conservation* **55**, 235–254.

Veron S, Kondratyeva A, Robuchon M, Grandcolas P, Govaerts R, Haevermans T, Pellens R and Mouchet M (2021) High evolutionary and functional distinctiveness of endemic monocots in world islands. *Biodiversity and Conservation* **30**, 3697–3715.

Watters GT (1992) Unionids, fishes, and the species-area curve. *Journal of Biogeography* **19**, 481–490.

Whiting MF, Whiting AS, Hastriter MW and Dittmar K (2008) A molecular phylogeny of fleas (Insecta: Siphonaptera): origins and host associations. *Cladistics* **24**, 677–707.

Zhu Q, Hastriter MW, Whiting MF and Dittmar K (2015) Fleas (Siphonaptera) are Cretaceous, and evolved with Theria. *Molecular Phylogenetics and Evolution* **90**, 129–139.