




# Multi-site interaction turnover in flea–mammal networks from four continents: Application of zeta diversity concept and multi-site generalised dissimilarity modelling

Boris R. Krasnov<sup>1</sup>  | Irina S. Khokhlova<sup>2</sup> | Mathias S. Kiefer<sup>3</sup> | Daniel Kiefer<sup>4</sup> |  
 Marcela Lareschi<sup>5</sup>  | Sonja Matthee<sup>6</sup> | Juliana P. Sanchez<sup>7</sup>  |  
 Georgy I. Shenbrot<sup>1</sup> | Michal Stanko<sup>8</sup> | Luther van der Mescht<sup>6</sup>

<sup>1</sup>Mitrani Department of Desert Ecology, Swiss Institute of Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

<sup>2</sup>French Associates Institute for Agriculture and Biotechnology of Drylands, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

<sup>3</sup>Comenius University in Bratislava, Bratislava, Slovakia

<sup>4</sup>Comparative Tropical Medicine and Parasitology, Ludwig Maximilian University of Munich, Munich, Germany

<sup>5</sup>Centro de Estudios Parasitológicos y de Vectores, CEPAVE (CCT La Plata-CONICET-UNLP), La Plata, Argentina

<sup>6</sup>Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland, South Africa

<sup>7</sup>Centro de Investigaciones y Transferencia del Noroeste de la Provincia de Buenos Aires—CITNOBA (CONICET-UNNOBA), Pergamino, Argentina

<sup>8</sup>Institute of Parasitology and Institute of Zoology, Slovak Academy of Sciences, Kosice, Slovakia

## Correspondence

Boris R. Krasnov, 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, 84990 Midreshet Ben-Gurion, Israel. Email: [krasnov@bgu.ac.il](mailto:krasnov@bgu.ac.il)

## Present addresses

Mathias S. Kiefer and Daniel Kiefer, 921F ST NW #504, Washington, DC, USA; and Luther van der Mescht, Clinvet International, Uitzich Road, Bainsvlei, 9338 Bloemfontein, Free State, South Africa.

## Funding information

Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación, Grant/Award Number: PICT2010-338; Consejo Nacional de Investigaciones Científicas y Técnicas; Israel Science Foundation, Grant/Award Number: 149/17; Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences; National Research Foundation (NRF) of South Africa, Grant/Award Numbers: 85718,

## Abstract

1. We studied patterns of changes in host–flea interactions measured as total turnover (TT) which can be partitioned into components, namely species turnover (ST), interaction rewiring (RW), and mixed turnover (MX) in networks from Europe, Asia, Africa, and South America, applying a multi-site interaction turnover metric. We also searched for environmental drivers of TT and its components.
2. We asked whether (a) different components contribute differently to TT in rare versus common interactions (in terms of frequency of interaction occurrence); (b) relative roles of turnover components for rare and common interactions differ between continents; and (c) the environmental drivers of interaction turnover differ between turnover components, rare and common interactions, and/or continental networks.
3. Between-network dissimilarity of interactions increased with an increase in the number of compared networks. Pure ST contributed the most to the turnover of rare interactions, whereas the turnover of common interactions was predominated by MX.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *Ecological Entomology* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.

GUN 80764; the Academy of Sciences of the USSR and the Academy of Sciences of the Mongolian People's Republic; Universidad Nacional de La Plata, Grant/Award Number: UNLP N752; Ministry of Education of the Slovak Republic; Slovak Academy of Sciences, Grant/Award Number: VEGA 2/0014/21; Academy of Sciences of the USSR and the Academy of Sciences of the Mongolian People's Republic; Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Grant/Award Number: PIP 0146

Associate Editor: Rob Knell

4. The effects of environmental factors, interaction richness, and spatial distance on TT and its components differed between continental networks, turnover components, and rare versus common interactions. Climate and vegetation exerted the strongest effects on (a) ST for rare (except Asia) and, to a lesser degree, common (South America) interactions, (b) RW for both rare and common interactions in Europe/Asia, and (c) MX for both rare and common interactions (except Africa). Interaction richness and spatial distance mainly influenced ST.
5. We conclude that the patterns of interaction turnover and its components were geographically invariant and did not depend on the identity of the interactors, whereas the drivers of the turnover differed between continental networks because of species-specific responses to the environment.

#### KEYWORDS

dissimilarity, environment, fleas, mammals, multi-site dissimilarity modelling, zeta diversity

## INTRODUCTION

Patterns of species interactions are no less important than species composition for describing ecosystem functioning (Bascompte & Jordano, 2007; Connolly et al., 2011; Jordano & Bascompte, 2013; Kirwan et al., 2009; Montoya et al., 2006; Tylianakis et al., 2008). This recognition has led to a consensus that the sets of these interactions (together with the interactors themselves) should be considered as distinct biological entities (ecological or interaction networks) (reviewed by Delmas et al., 2019). Therefore, spatial and/or temporal variation in community composition can only be understood if variation in both species composition and their interactions are taken into account because (a) species and interactions may respond to different factors, and (b) compositional changes in species and interactions may be governed by different mechanisms (Burkle & Alarcón, 2011; Carstensen et al., 2014; Li et al., 2018; Poisot et al., 2012, 2017; Sabatino et al., 2010). For example, Carstensen et al. (2014) reported that, in Brazilian rupestrian fields, geographical distance correlated positively with beta-diversities of plant-pollinator interactions and plants, but not with beta-diversity of pollinators. Poisot et al. (2017) found that flea-host interactions in the Palearctic networks responded to seasonality of temperature and mean temperature of warmest quarter, whereas flea and host species composition did not.

Although variation in species composition has been studied in a variety of taxa, environments, and geographic regions from long ago till now (e.g. Beck & Chey, 2010; Brown & Nicoletto, 1991; Lamont & Johnson, 2021; Montufar & Pintaud, 2006; Whittaker, 1960), spatial and/or temporal turnover in species interactions only started to be investigated during the last two decades (Carstensen et al., 2014; Dallas & Poisot, 2018; Fründ, 2021; Gravel et al., 2019; Li et al., 2018; Olesen et al., 2008; Petanidou et al., 2008; Poisot et al., 2012, 2015, 2017; Trøjelsgaard et al., 2015). These studies demonstrated that structural measures, including turnover, of different networks respond to different environmental gradients (Pellissier et al., 2018). However, it is still largely unknown whether network measures, such as interaction turnover, in networks represented by the same taxonomic groups

are affected by similar or different environmental factors in different geographic regions. To the best of our knowledge, the effects of environment on interaction turnover in taxonomically similar networks from different geographic regions have never been specifically investigated. Studies of the effects of environment on interaction turnover may provide important insights into the mechanisms governing resource-consumer interactions and their responses to climate change and habitat modification (Burkle et al., 2016, 2022; Novotny, 2009; Poisot et al., 2017; Tylianakis et al., 2010).

The pattern of interaction turnover across space and over time is differently affected by interactions involving species with different degree of commonness or rarity (Bascompte et al., 2003; Carstensen et al., 2014; Novotny, 2009; Poisot et al., 2012). Common, often habitat generalist, species are involved in many interactions (i.e. common interactions) and, thus, are mainly responsible for relative spatial or temporal stability of network structure (e.g. Miele et al., 2020). Rare species (because of low abundance or prevalence, restricted geographic distribution and/or high habitat specificity) are involved in much fewer interactions (i.e. rare interactions) and are often lost from some of networks. Nevertheless, the contribution of rare species to compositional and functional diversity of ecosystems is also substantial (Mouillot et al., 2013). Consequently, understanding spatial or temporal variation in network structure necessitates a metric of interaction turnover that considers interactions involving both common and rare species and allows to distinguish between patterns resulted from each of these interaction categories.

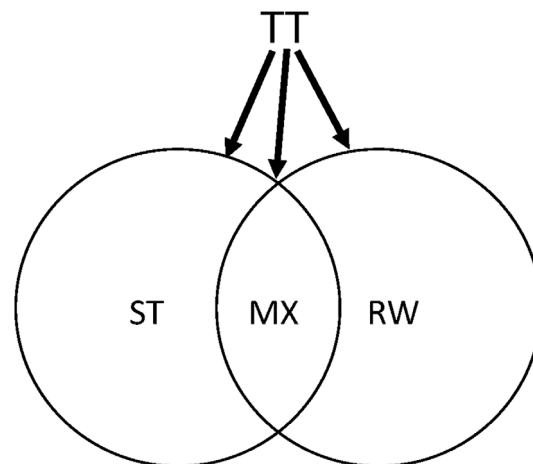
A turnover metric that allows the quantification of variation in the composition of species interactions that vary in the degree of commonness (in terms of relative occurrence) across multiple sites/networks has recently been proposed by Henriksen et al. (2022). This new approach is based on the zeta diversity metric developed by Hui and McGeoch (2014) (see also Latombe et al., 2017; McGeoch et al., 2019). In its original version, zeta diversity (denoted as  $\zeta_i$ ) represents the average number of species shared by  $i$  communities where  $i$  is the so-called zeta order (McGeoch et al., 2019), with zeta order 2 obviously being a pairwise metric. Originally designed for species

composition, the zeta diversity approach can be applied not only to species in communities but also to interactions in ecological networks (McGeoch et al., 2019; see also Krasnov, Korralo-Vinarskaya, et al., 2020).

Developing their multi-site turnover metric, Henriksen et al. (2022) combined the zeta diversity concept with the approaches of Novotny (2009) and Poisot et al. (2012). Novotny (2009) adapted beta diversity indices traditionally used to measure between-community differences in species composition to measure between-network differences in interactions by, for example, using the sum of the interactions unique to one of the two networks divided by the total number of interactions (both unique to one of the two networks and shared between these networks) (i.e. Jaccard similarity) and then calculating the complementary Jaccard dissimilarity index. Given that zeta diversity considers compositional overlap across multiple sites and, therefore, represents turnover as similarity rather than as dissimilarity (McGeoch et al., 2019), Henriksen et al. (2022) proposed to transform the original zeta diversity to zeta dissimilarity ( $\zeta^*$ ), defined as the number of interactions that appear in at least one, but not all, of multiple ( $i$ ) networks divided by the total number of interactions in all networks. Furthermore, Novotny (2009) and Poisot et al. (2012) demonstrated that the interaction turnover (=total interaction turnover, further referred to as TT) can be partitioned into two components (see also CaraDonna et al., 2017; Fründ, 2021). First, the interaction dissimilarity may be due to the absence of one or both interactors from some networks, but they always interact if both are present (species turnover, further referred to as ST). Second, the interaction dissimilarity may arise if a pair of interactors is present in all networks but interact only in some of them (interaction rewiring, further referred to as RW). Henriksen et al. (2022) proposed the third component, mixed turnover (further referred to as MX), when the interaction dissimilarity arises because of species turnover in some networks, whereas in other networks, it arises because of interaction rewiring (see conceptual diagram in Figure 1). MX emerges when multi-site interaction turnover is considered for zeta orders higher than 2 (see Henriksen et al., 2022 and Section 3).

Although other methods of quantifying interaction turnover across multiple networks exist (e.g. Poisot et al., 2012, 2017), the advantage of Henriksen et al.'s (2022) zeta dissimilarity is that it allows one to distinguish between turnover that is mainly due to rare interactions (at lower zeta orders) and turnover that is mainly due to common interactions (at higher zeta orders), similarly to zeta diversity, which detects the relative contributions of rare versus common species to compositional community changes (McGeoch et al., 2019).

Here, we applied Henriksen et al.'s (2022) multi-site interaction turnover metric to explore patterns of interaction turnover and its components and to reveal their environmental drivers in small mammal–flea networks from four continents, namely Europe (eastern Slovakia), Asia (southwestern Mongolia), Africa (western South Africa), and South America (central Patagonia) (further referred to as continental networks). Fleas are holometabolous insect ectoparasites, most abundant and diverse on small burrowing mammals. Flea imagoes are obligatory haematophagous, whereas pre-imaginal fleas are non-



**FIGURE 1** Conceptual schematic diagram demonstrating partitioning of total interaction turnover (TT) into species turnover (ST), interaction rewiring (RW) and mixed turnover (MX). Modified from Henriksen et al. (2022).

parasitic and develop mainly in hosts' burrows/nests. First, we asked whether different turnover components contributed differently to total turnover in rare versus common interactions. In other words, we tested whether the turnover of rare or common interactions is determined, to a greater extent, by ST or RW or both (MT). Second, we asked whether the relative roles of turnover components for rare and common interactions differed between networks situated in different continents. Differences between host–flea networks from different continents can be expected because of different histories of host–flea relationships (Medvedev, 1996, 2005). Third, we asked whether environmental drivers of interaction turnover were similar or different between (a) turnover components, (b) rare and common interactions, and (c) continental networks.

To understand the effect of environmental variation on total interaction turnover and its components, we applied an extension of Multi-Site Generalised Dissimilarity Modelling (MS-GDM) (Latombe et al., 2017) which, in turn, is an extension of generalised dissimilarity modelling (GDM; Ferrier et al., 2007). The development of GDM was aimed at accommodating two types of non-linearity inherent in the shape of compositional turnover along environmental and/or spatial gradients, namely (a) the curvilinearity of the relationship between compositional and environmental dissimilarities at the extreme (i.e. zero or unity) dissimilarity values and (b) the possible variation in the turnover rate along a gradient. The original GDM uses pairwise dissimilarity as a metric of turnover and is, thus, heavily biased to the effect of rare species (Hui & McGeoch, 2014; Latombe et al., 2017). In contrast, MS-GDM employs zeta diversity as a measure of turnover, which allows one to analyse the variation in the compositional turnover of species categories with different degrees of commonness along environmental gradients and/or with geographic distance between assemblages. Furthermore, the relative contribution of each predictor to the explained variation in turnover is expected to vary between zeta orders because of the exclusion of less common species

with an increasing zeta order (Latombe et al., 2017, 2018). We used a modification of the MS-GDM by Henriksen et al. (2022) that considers turnover in interactions rather than in species composition. This modification allowed us to test whether rare and common interactions are affected by similar or different environmental predictors.

## MATERIALS AND METHODS

### Data on host–flea interactions

Data on flea–mammals interactions were taken from surveys of fleas harboured by small mammals carried out in 1986–1996 across 10 sites in eastern Slovakia (Stanko et al., 2002; see map in Appendix S1, Figure S1), in 1981–1984 across 10 sites in southwestern Mongolia (Kiefer et al., 1982, 1984, 1990, 2012; see map in Appendix S1, Figure S2), in 2011–2013 across nine sites in western South Africa (van der Mescht & Matthee, 2017; see map in Appendix S1, Figure S3), and in 2006–2011 across 13 sites in central Argentinian Patagonia (Sanchez, 2012; Sanchez & Lareschi, 2013, 2019; see map in Appendix S1, Figure S4). Details on the sampling design, sampling efforts, and methodology of parasitological examination can be found in the publications cited above. Small mammals were represented by rodents, elephant shrews (in South Africa), shrews (in Slovakia and South Africa), and pikas (in Mongolia). Lists of flea and mammal species in each region can be found in Appendix S2, Table S1. Single records of a given flea species on a given host species were not considered as interactions. To avoid seasonal variation in the species composition of flea assemblages, we used data collected from late spring to early fall (boreal or austral). If a site was sampled more than once, data over years were pooled. In addition, we included, in the analyses, networks represented by at least three host species and at least three flea species (otherwise calculation of zeta-diversity will not be reliable).

### Environmental variables

We described the environment in each region using nine climatic seasonality of air temperature, seasonality of precipitation, mean air temperature of the warmest month, mean precipitation of the wettest month, mean precipitation of the driest month, mean precipitation of the warmest quarter, mean monthly climate moisture index, mean monthly near-surface relative humidity, and mean monthly potential evapotranspiration, and two vegetation-associated variable (net primary production and summer [boreal or austral] normalised difference vegetation index; NDVI). The latter variable is related to the quantity of standing biomass because it reflects the amount of green vegetation. We selected those environmental variables that have been shown to exert strong effects on flea biology (Krasnov, 2008). Although Poisot et al. (2017) reported no effect of air temperature on turnover of flea–mammal interactions, their study was carried out across the entire northern and central Palearctic. The patterns at a smaller scale (e.g. regional) as well as in other biogeographic realms

can be different. Data on climatic variables and net primary production were obtained from CHELSA 2.1 dataset (Brun et al., 2022; Karger et al., 2018). Data on summer NDVI were taken from the VEGETATION Programme (<http://vito-eodata.be>). Environmental data were calculated for each sampling site at resolution of 30 arc seconds. Environmental variables of some categories correlated strongly with each other. These were three variables describing precipitation (mean precipitations of the wettest month, the driest month, and the warmest quarter), three variables describing air humidity (climate moisture index, near-surface relative humidity, and potential evapotranspiration) and two variables describing vegetation (net primary production and NDVI). Consequently, we applied principal component analyses for variables of these three variable categories separately for each continent and substituted the original values of these variables with the scores of the first principal components (*P*, MRHET and VEG, respectively). The eigenvalues of the principal components, proportion of explained variation and their correlations with the original variables can be found in Appendix S2, Tables S2–S5. In all continents, (a) *P* correlated positively with mean precipitations of the wettest month, the driest month and the warmest quarter; (b) MRHET correlated positively with climate moisture index and near-surface relative humidity and negatively with potential evapotranspiration; and (c) VEG correlated positively with both net primary production and NDVI.

### Data analysis: Zeta dissimilarity

For each continent, each local network (i.e. an observed interaction network for a given sample site) was represented by a presence/absence matrix with hosts in rows and fleas in columns. Then, we combined the matrices for each continent into an array using the function “webs2array” of the package ‘bipartite’ (Dormann et al., 2008), implemented in the R Statistical Environment (R Core Team, 2021). We used presence/absence rather than abundance data for several reasons. First, zeta diversity/dissimilarity is an incidence-based metric (Henriksen et al., 2022; McGeoch et al., 2019). Second, for parasites, measurements of incidences seem to be more reliable than measurements of counts/abundances (Gotelli & Rohde, 2002). Third, the results of the analyses of different endo- and ectoparasite communities, harboured by differed hosts and based on either parasite incidences or parasite counts, appeared to be qualitatively similar, with the former often performing better (Krasnov et al., 2021). We calculated the total interaction turnover and its three components (species turnover, interaction rewiring, and mixed turnover) using the R function “intdiv\_zeta” developed by Henriksen et al. (2022). Multi-site dissimilarity in interactions and its components were normalised by the total number of interactions across networks (Henriksen et al., 2022).

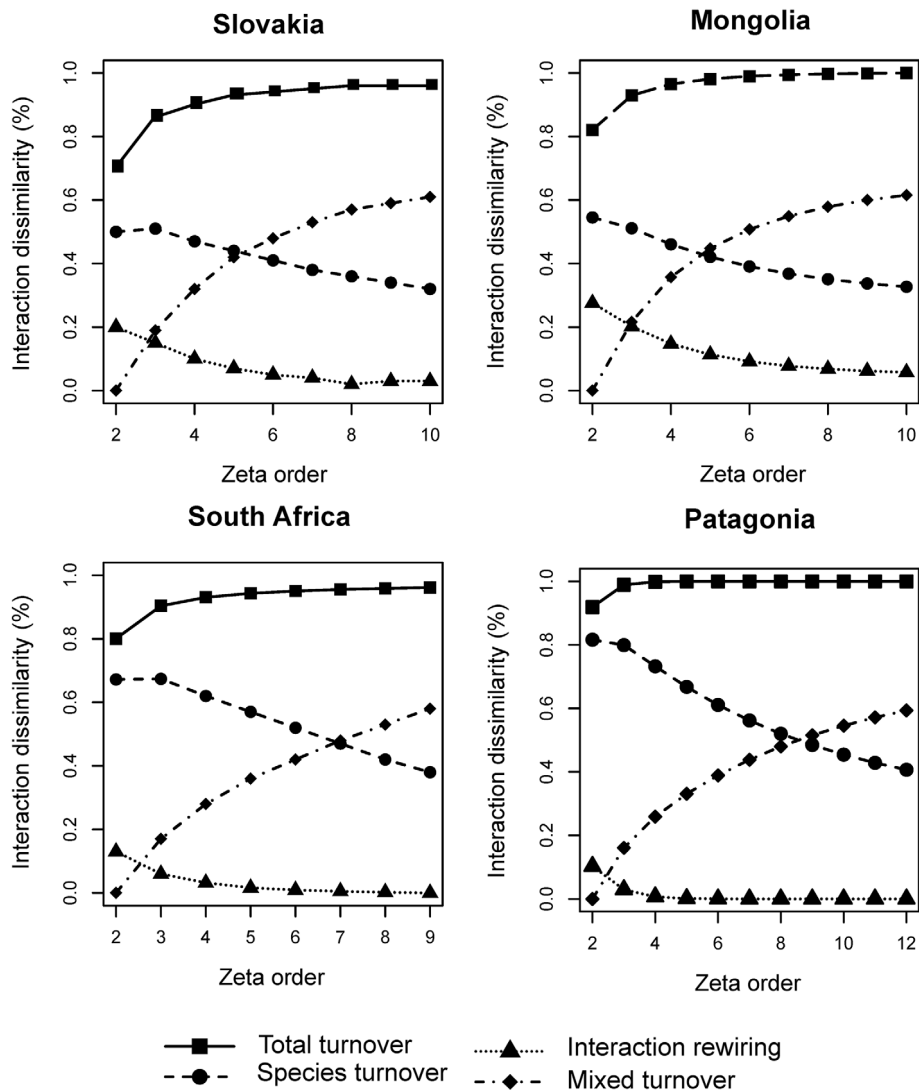
### Data analysis: Multi-site generalised dissimilarity modelling

Similar to generalised dissimilarity modelling (GDM) and the original multi-site GDM (MS-GDM), in the MS-GDM modified by Henriksen

et al. (2022), each environmental or spatial variable is transformed into a number of non-linear, monotonic piecewise functions (I-splines) ranging from 0 to 1. Then, for each combination of networks, the values of zeta dissimilarity are calculated, and the relationship between these values and the differences between the I-splines are analysed using generalised linear modelling (GLM) with a binomial distribution. The I-splines of each variable are then multiplied by their GLM coefficients and summed, thus generating a single monotonic spline. The slope of the I-spline demonstrates the rate of change and its variation along a given gradient, whereas its height (i.e. the sum of the coefficients of the three I-splines of a given variable) represents a predictor's relative importance for the zeta dissimilarity as compared to other predictors (i.e. the total amount of change along a given gradient) (Ferrier et al., 2007; Latombe et al., 2017, 2020). Assuming that the number of shared species or interactions is expected to decrease with an increase in

environmental difference/spatial distance, a negative constraint is enforced on the sign of the I-splines' coefficients (Latombe et al., 2017, 2020).

To run the MS-GDM, we used the R function "intdiv\_msgdm" developed by Henriksen et al. (2022) as a modification of the function "zeta\_msgdm" from the package "zetadiv" (Latombe et al., 2020). We applied MS-GDM separately for networks from each continent, using seasonality of air temperature (ST), seasonality of precipitation (SP), air temperature of the warmest month (T), the three principal components of environmental variables described above (P, MRHET and VEG), geographic distance between sampling sites (D), and, following Henriksen et al. (2022), the interaction richness (IR; the total number of interactions per each network). MS-GDM was applied to zeta orders 2–6 for Slovakia, Mongolia, and South Africa, and to zeta orders 2–5 for Patagonia (because of fewer interactions).



**FIGURE 2** Total interaction turnover and its components (species turnover, interaction rewiring, and mixed turnover) across 10 host–flea networks from Slovakia and Mongolia, nine host–flea networks from South Africa, and 13 host–flea networks from Patagonia. Zeta order: number of networks for which the dissimilarity in interaction composition is calculated.

**TABLE 1** Turnover of host–flea interactions as explained by environmental variables.

ZO	Total interaction turnover			Species turnover			Interaction rewiring			Mixed turnover		
	ED	Pred	$\Sigma_{l-splines}$	ED	Pred	$\Sigma_{l-splines}$	ED	Pred	$\Sigma_{l-splines}$	ED	Pred	$\Sigma_{l-splines}$
2	0.70	ST	-	0.71	ST	-	0.24	ST	-	-	ST	-
		SP	-0.07		SP	-0.17		SP	-0.09		SP	-
		T	-		T	-0.28		T	-		T	-
		P	-0.38		P	-0.23		P	-0.06		P	-
		MRHET	-0.21		MRHET	-		MRHET	-0.02		MRHET	-
		VEG	-0.22		VEG	-0.08		VEG	-0.06		VEG	-
		IR	-0.66		IR	-0.35		IR	-0.08		IR	-
		D	-0.45		D	-0.36		D	-		D	-
3	0.79	ST	-	0.65	ST	-	0.30	ST	-	0.22	ST	-0.01
		SP	-0.10		SP	-0.26		SP	-0.13		SP	-0.06
		T	-		T	-0.19		T	-		T	-0.07
		P	-0.77		P	-0.24		P	-0.05		P	-0.07
		MRHET	-0.17		MRHET	-		MRHET	-		MRHET	-0.01
		VEG	-0.58		VEG	-0.12		VEG	-0.09		VEG	-0.03
		IR	-1.03		IR	-0.41		IR	-0.06		IR	-0.06
		D	-1.00		D	-0.16		D	-		D	-0.03
4	0.77	ST	-	0.61	ST	-	0.30	ST	-	0.30	ST	-0.05
		SP	-0.01		SP	-0.25		SP	-0.11		SP	-0.08
		T	-		T	-0.16		T	-		T	-0.13
		P	-1.10		P	-0.15		P	-0.02		P	-0.15
		MRHET	-0.27		MRHET	-		MRHET	-		MRHET	-0.02
		VEG	-0.77		VEG	-0.09		VEG	-0.12		VEG	-0.11
		IR	-1.30		IR	-0.43		IR	-0.04		IR	-0.11
		D	-0.92		D	-0.04		D	-		D	-0.03
5	0.69	ST	-	0.60	ST	-	0.28	ST	-	0.29	ST	-0.03
		SP	-		SP	-0.32		SP	-0.09		SP	-0.02
		T	-		T	-0.14		T	-		T	-0.11
		P	-1.39		P	-0.12		P	-		P	-0.19
		MRHET	-0.42		MRHET	0.00		MRHET	-		MRHET	-0.15
		VEG	-0.73		VEG	-0.09		VEG	-0.12		VEG	-0.18
		IR	-1.36		IR	-0.38		IR	-0.02		IR	-0.14
		D	-0.75		D	-0.02		D	-		D	-0.02
6	0.58	ST	-	0.62	ST	-	0.27	ST	-	0.29	ST	-
		SP	-0.04		SP	-0.45		SP	-0.06		SP	-0.01
		T	-		T	-0.08		T	-		T	-
		P	-1.19		P	-0.13		P	-		P	-0.26
		MRHET	-0.83		MRHET	-		MRHET	-		MRHET	-0.22
		VEG	-0.42		VEG	-0.13		VEG	-0.10		VEG	-0.27
		IR	-1.40		IR	-0.32		IR	-		IR	-0.14
		D	-0.40		D	-0.03		D	-		D	-

Abbreviations: AIC, Akaike information criterion; ED, explained deviance; MRHET, principal component of three variables describing air humidity (see text for explanations); P, principal component of three precipitation variables (see text for explanations); SP, seasonality of precipitation; ST, seasonality of temperature; T, air temperature of the warmest month; VEG, principal component of two vegetation-related variables (see text for explanations), interaction richness (IR), and geographic distance (D) between 10 sampling sites in eastern Slovakia;  $\Sigma_{l-splines}$ , sum of the coefficients of three l-splines (demonstrates the amplitude of an l-spline).

**TABLE 2** Turnover of host–flea interactions as explained by environmental variables (see Table 1 for abbreviations and explanations), interaction richness (IR), and geographic distance (D) between 10 sampling sites in southwestern Mongolia.

ZO	Total interaction turnover			Species turnover			Interaction rewiring			Mixed turnover		
	ED	Pred	$\Sigma_{I-splines}$	ED	Pred	$\Sigma_{I-splines}$	ED	Pred	$\Sigma_{I-splines}$	ED	Pred	$\Sigma_{I-splines}$
2	0.29	ST	-0.16	0.70	ST	-0.17	0.16	ST	-	-	ST	-
		SP	-		SP	-0.07		SP	-		SP	-
		T	-0.64		T	-0.89		T	-		T	-
		P	-0.42		P	-0.25		P	-0.12		P	-
		MRHET	-		MRHET	-		MRHET	-0.13		MRHET	-
		VEG	-0.06		VEG	-0.35		VEG	-		VEG	-
		IR	-0.15		IR	-0.48		IR	-0.04		IR	-
		D	-		D	-0.01		D	-		D	-
3	0.19	ST	-0.46	0.72	ST	-0.32	0.16	ST	-0.05	0.09	ST	-
		SP	-0.13		SP	-0.18		SP	-		SP	-
		T	-0.92		T	-0.73		T	-0.01		T	-0.01
		P	-0.88		P	-0.07		P	-0.11		P	-0.17
		MRHET	-		MRHET	-		MRHET	-0.17		MRHET	-0.10
		VEG	-0.15		VEG	-0.30		VEG	-0.03		VEG	-
		IR	-0.31		IR	-0.63		IR	-0.09		IR	-0.04
		D	-0.02		D	-		D	-		D	-
4	0.17	ST	-0.91	0.77	ST	-0.35	0.17	ST	-0.10	0.21	ST	-
		SP	-0.34		SP	-0.19		SP	-0.02		SP	-
		T	-0.76		T	-0.53		T	-0.05		T	-0.05
		P	-1.46		P	-		P	-0.10		P	-0.37
		MRHET	-0.27		MRHET	-		MRHET	-0.11		MRHET	-0.15
		VEG	-0.15		VEG	-0.28		VEG	-0.01		VEG	-
		IR	-0.49		IR	-0.59		IR	-0.09		IR	-0.08
		D	-		D	-0.01		D	-		D	-
5	0.21	ST	-1.64	0.80	ST	-0.38	0.18	ST	-0.09	0.29	ST	-0.05
		SP	-0.24		SP	-0.17		SP	-0.03		SP	-
		T	-0.56		T	-0.46		T	-0.05		T	-0.10
		P	-2.10		P	-		P	-0.06		P	-0.56
		MRHET	-0.88		MRHET	-		MRHET	-0.07		MRHET	-0.20
		VEG	-0.08		VEG	-0.24		VEG	-		VEG	-
		IR	-0.94		IR	-0.47		IR	-0.06		IR	-0.13
		D	-		D	-0.01		D	-		D	-
6	0.26	ST	-2.48	0.83	ST	-0.40	0.18	ST	-0.08	0.34	ST	-0.12
		SP	-		SP	-0.14		SP	-0.02		SP	-
		T	-0.20		T	-0.41		T	-0.03		T	-0.18
		P	-2.34		P	-		P	-0.04		P	-0.70
		MRHET	-2.39		MRHET	-		MRHET	-0.06		MRHET	-0.21
		VEG	-0.01		VEG	-0.25		VEG	-		VEG	-
		IR	-1.71		IR	-0.37		IR	-0.05		IR	-0.19
		D	-		D	-0.02		D	-		D	-

Abbreviations: AIC, Akaike information criterion; ED, explained deviance;  $\Sigma_{I-splines}$ : sum of the coefficients of three I-splines (demonstrates the amplitude of an I-spline).

**TABLE 3** Turnover of host–flea interactions as explained by environmental variables (see Table 1 for abbreviations and explanations), interaction richness (IR), and geographic distance (D) between 10 sampling sites in western South Africa.

ZO	Total interaction turnover			Species turnover			Interaction rewiring			Mixed turnover		
	ED	Pred	$\Sigma_{I-splines}$	ED	Pred	$\Sigma_{I-splines}$	ED	Pred	$\Sigma_{I-splines}$	ED	Pred	$\Sigma_{I-splines}$
2	0.49	ST	−0.06	0.39	ST	−0.10	0.04	ST	−0.02	-	ST	-
		SP	−0.47		SP	−0.20		SP	−0.10		SP	-
		T	−0.03		T	−0.34		T	-		T	-
		P	−0.13		P	−0.05		P	-		P	-
		MRHET	−0.22		MRHET	−0.21		MRHET	-		MRHET	-
		VEG	-		VEG	−0.26		VEG	-		VEG	-
		IR	−1.28		IR	−1.20		IR	−0.03		IR	-
		D	-		D	-		D	-		D	-
3	0.56	ST	-	0.44	ST	−0.33	0.10	ST	−0.04	0.08	ST	-
		SP	−0.59		SP	−0.08		SP	−0.10		SP	−0.05
		T	−0.07		T	−0.70		T	-		T	-
		P	-		P	−0.38		P	-		P	-
		MRHET	−0.54		MRHET	−0.27		MRHET	−0.01		MRHET	−0.12
		VEG	0.00		VEG	−0.22		VEG	-		VEG	-
		IR	−1.47		IR	−1.14		IR	−0.02		IR	−0.08
		D	-		D	−0.05		D	-		D	-
4	0.69	ST	−0.06	0.59	ST	−0.32	0.09	ST	−0.01	0.11	ST	-
		SP	−0.39		SP	−0.24		SP	−0.05		SP	−0.12
		T	−0.21		T	−0.56		T	-		T	-
		P	-		P	−0.45		P	-		P	-
		MRHET	−0.55		MRHET	−0.12		MRHET	−0.03		MRHET	−0.21
		VEG	-		VEG	−0.16		VEG	-		VEG	-
		IR	−1.51		IR	−0.77		IR	−0.01		IR	−0.16
		D	-		D	−0.36		D	-		D	-
5	0.72	ST	−0.18	0.62	ST	−0.38	0.08	ST	-	0.11	ST	-
		SP	−0.59		SP	−0.28		SP	−0.01		SP	−0.19
		T	−0.03		T	−0.31		T	−0.02		T	-
		P	-		P	−0.36		P	-		P	-
		MRHET	−0.51		MRHET	−0.02		MRHET	−0.02		MRHET	−0.25
		VEG	-		VEG	−0.20		VEG	-		VEG	-
		IR	−1.67		IR	−0.69		IR	-		IR	−0.23
		D	-		D	−0.34		D	-		D	-
6	0.83	ST	−0.36	0.63	ST	−0.40	0.07	ST	-	0.10	ST	-
		SP	−0.62		SP	−0.38		SP	-		SP	−0.26
		T	-		T	−0.03		T	−0.01		T	-
		P	-		P	−0.27		P	−0.01		P	-
		MRHET	−0.45		MRHET	-		MRHET	-		MRHET	−0.21
		VEG	-		VEG	−0.25		VEG	-		VEG	-
		IR	−1.71		IR	−0.63		IR	-		IR	−0.26
		D	-		D	−0.21		D	-		D	−0.23

Abbreviations: AIC, Akaike information criterion; ED, explained deviance;  $\Sigma_{I-splines}$ : sum of the coefficients of three I-splines (demonstrates the amplitude of an I-spline).



**TABLE 4** Turnover of host–flea interactions as explained by environmental variables (see Table 1 for abbreviations and explanations), interaction richness (IR), and geographic distance (*D*) between 10 sampling sites in central Patagonia.

ZO	Total interaction turnover			Species turnover			Interaction rewiring			Mixed turnover		
	ED	Pred	$\Sigma_{l-splines}$	ED	Pred	$\Sigma_{l-splines}$	ED	Pred	$\Sigma_{l-splines}$	ED	Pred	$\Sigma_{l-splines}$
2	0.67	ST	-0.59	0.70	ST	-0.50	-	ST	-	-	ST	-
		SP	-0.46		SP	-0.34	SP	-	SP		-	
		T	-1.22		T	-0.46	T	-	T		-	
		P	-0.59		P	-0.67	P	-	P		-	
		MRHET	-0.42		MRHET	-0.23	MRHET	-	MRHET		-	
		VEG	-2.30		VEG	-1.44	VEG	-	VEG		-	
		IR	-0.70		IR	-0.67	IR	-	IR		-	
		D	-3.41		D	-3.54	D	-	D		-	
3	0.60	ST	-3.30	0.52	ST	-0.81	-	ST	-	0.07	ST	-0.08
		SP	-0.79		SP	-0.71	SP	-	SP		-	
		T	-1.05		T	-	T	-	T		-0.06	
		P	-1.36		P	-0.77	P	-	P		-	
		MRHET	-1.19		MRHET	0.00	MRHET	-	MRHET		-	
		VEG	-4.30		VEG	-0.76	VEG	-	VEG		-	
		IR	-0.91		IR	-0.39	IR	-	IR		-0.07	
		D	-7.05		D	-1.04	D	-	D		-	
4	0.55	ST	-6.43	0.42	ST	-0.55	0.002	ST	-	0.14	ST	-0.18
		SP	-2.15		SP	-0.84	SP	-0.04	SP		-	
		T	-1.36		T	-	T	-	T		-0.12	
		P	-1.27		P	-0.29	P	-	P		-	
		MRHET	-0.32		MRHET	-	MRHET	-	MRHET		-	
		VEG	-6.23		VEG	-0.47	VEG	-	VEG		-	
		IR	-0.87		IR	-0.41	IR	-0.001	IR		-0.18	
		D	-9.52		D	-0.76	D	-	D		-	
5	0.57	ST	-10.74	0.40	ST	-0.38	0.001	ST	-	0.24	ST	-0.26
		SP	-5.09		SP	-0.97	SP	-0.001	SP		-	
		T	-1.90		T	-	T	-	T		-0.19	
		P	-		P	-	P	-	P		-	
		MRHET	-		MRHET	-	MRHET	-	MRHET		-	
		VEG	-9.01		VEG	-0.32	VEG	-	VEG		-0.05	
		IR	-		IR	-0.47	IR	-0.001	IR		-0.31	
		D	-29.00		D	-0.51	D	-	D		-	

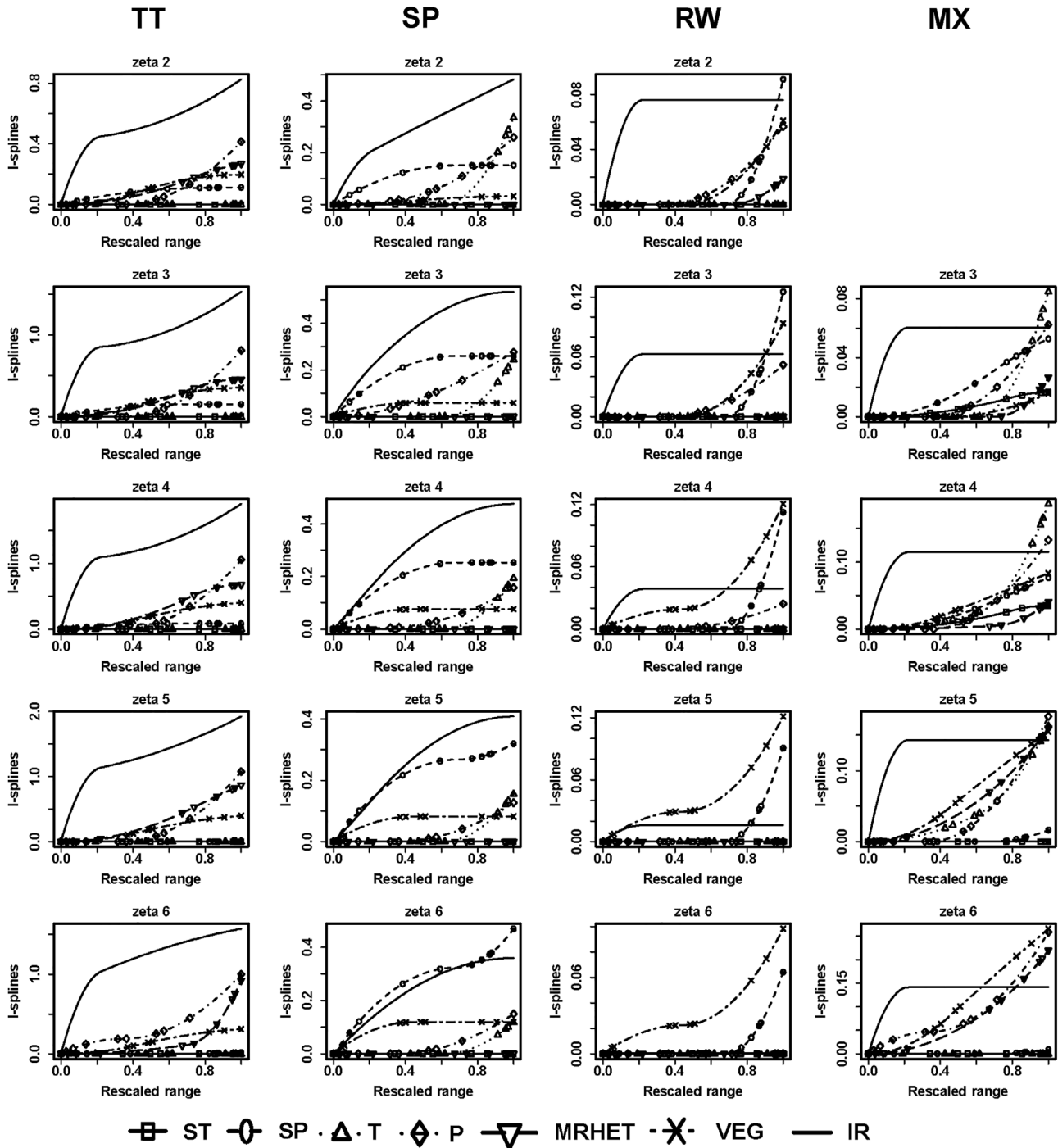
Abbreviations: AIC, Akaike information criterion; ED, explained deviance;  $\Sigma_{l-splines}$ : sum of the coefficients of three l-splines (demonstrates the amplitude of an l-spline).

## RESULTS

In Slovakia, 6 of 22 host and 6 of 24 flea species occurred in all (10) or almost all (8–9) networks, whereas 11 host and nine flea species occurred in one to three networks (Appendix S1, Table S1). In Mongolia, 4 of 18 host and 5 of 25 flea species were characterised by high relative occurrence (recorded in 8 to 10 of 10 networks), whereas the number of species with low relative occurrence (one to three networks) was 9 for hosts and 15 for fleas (Appendix S1, Table S1). In South Africa, only 1 of 10 host and 2 of 21 flea species

were found in all networks, and almost half (4) of host and more than half (15) of flea species occurred in 1–3 networks Appendix S1, Table S1). In Patagonia, no host or flea species appeared in all networks. Instead, 7 of 14 host and 8 of 27 flea species demonstrated intermediate occurrence levels (6–8 of 13 networks), and 4 host and 17 flea species were found in 1–3 networks only (Appendix S1, Table S1).

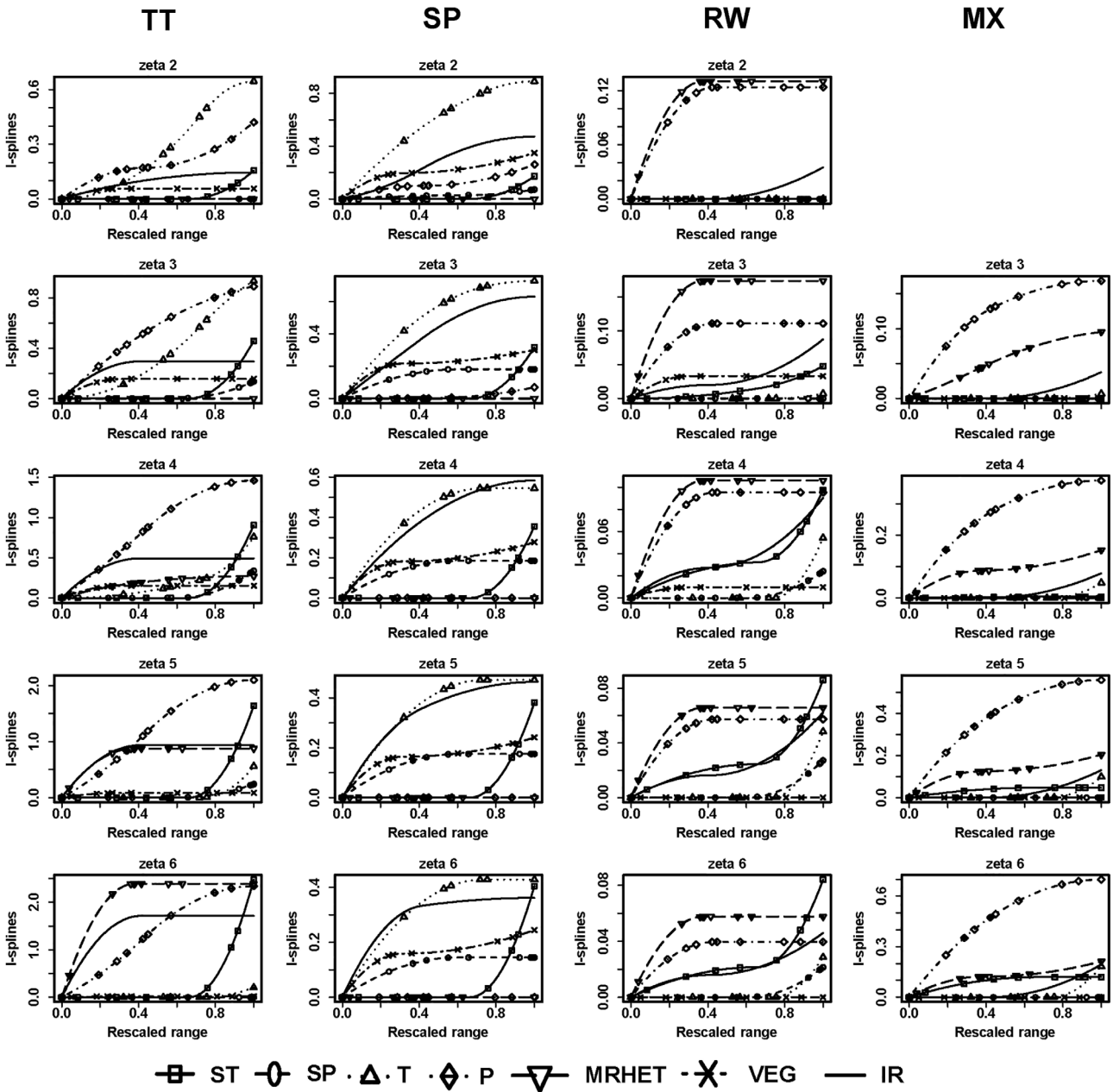
The proportion of interactions shared between pairs of networks (i.e. total interaction turnover) was relatively low for all continents. Nevertheless, it was higher for Slovakian



**FIGURE 3** I-splines produced by the MS-GDMs for total interaction turnover (TT), species turnover (ST), interaction rewiring (RW), and mixed turnover (MX) for host–flea networks from Slovakia across zeta orders (from upper to lower: increasing degree of interaction commonness), showing the relative effects of environmental variables (ST, seasonality of temperature; SP, seasonality of precipitation; T, air temperature of the warmest month; P, principal component of three precipitation variables [see text for explanations]; MRHET, principal component of three variables describing air humidity [see text for explanations]; VEG, principal component of two vegetation-related variables [see text for explanations]) and interaction richness (IR). Predictors are scaled between 0 and 1 (from lowest to highest value). Mixed turnover for zeta order 2 is not shown because the deviance explained by the model equals zero (see Table 1).

networks (about 30%), followed by South African and Mongolian networks (20% and 18%, respectively), and was as low as 8% in Patagonian networks. The proportion of interactions shared by all networks was extremely low for Slovakia and South Africa (4%

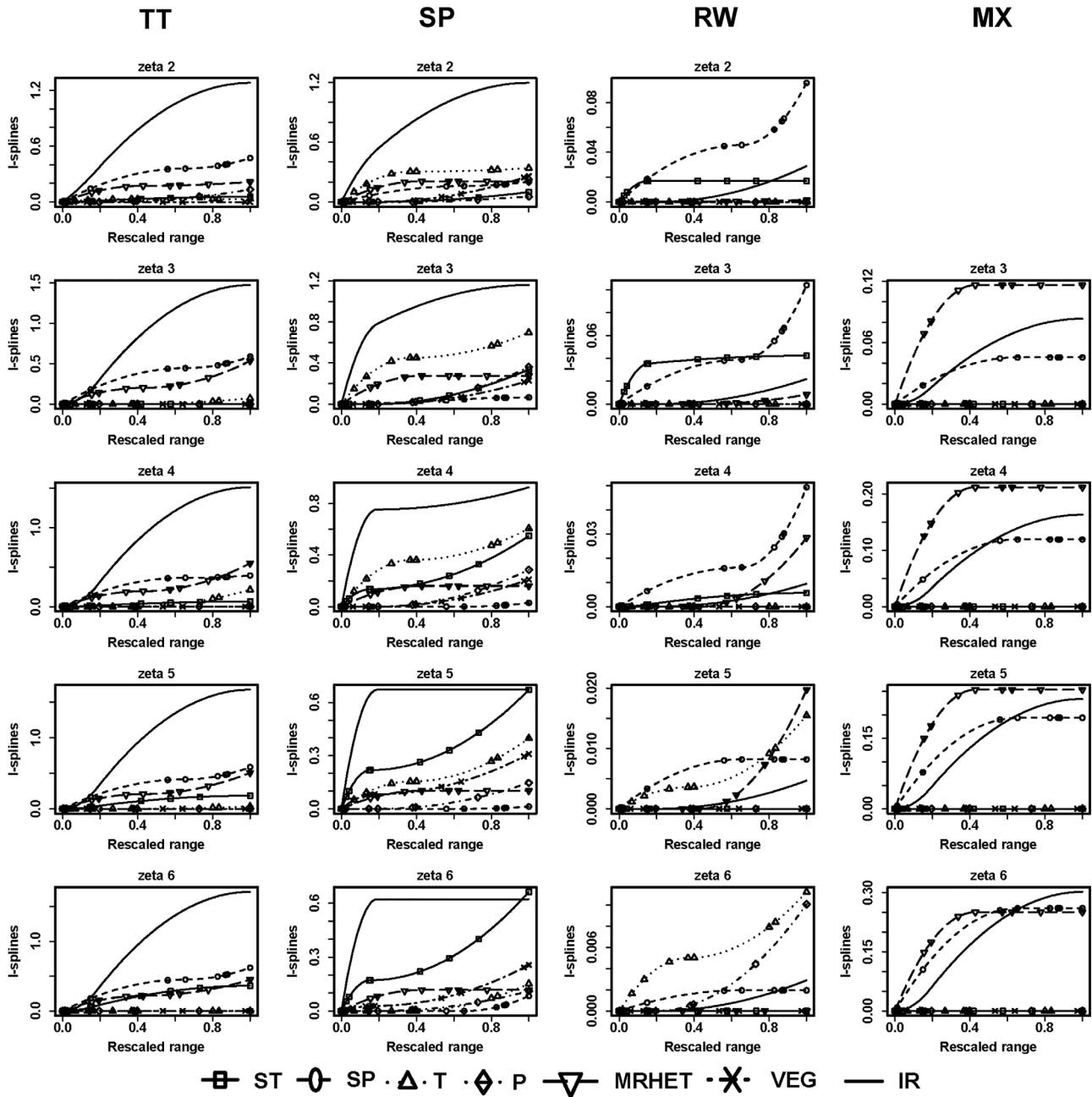
in both), and no interactions were shared by all networks in Mongolia and Patagonia (Figure 1). Moreover, no interactions were shared beyond zeta order 7 in Mongolia and zeta order 3 in Patagonia.



**FIGURE 4** I-splines produced by the MS-GDMs for total interaction turnover (TT), species turnover (ST), interaction rewiring (RW), and mixed turnover (MX) for host–flea networks from Mongolia across zeta orders (from upper to lower: increasing degree of interaction commonness), showing the relative effects of environmental variables and interaction richness (see Figure 1 for abbreviations and explanations). Predictors are scaled between 0 and 1 (from lowest to highest value). Mixed turnover for zeta order 2 is not shown because the deviance explained by the model equals zero (see Table 2).

In all continents, the contribution of species turnover to total interaction turnover steadily decreased with an increase in zeta order (from rare to common interactions), with a concomitant increase in the contribution of mixed turnover (Figure 2). In Slovakia and Mongolia, the contribution of mixed turnover overcame that of species turnover for interactions with an intermediate degree of commonness (i.e. from zeta order 5). In South Africa and Patagonia, the contribution of mixed turnover was higher than that of species turnover mainly for the most common interactions (i.e. from zeta

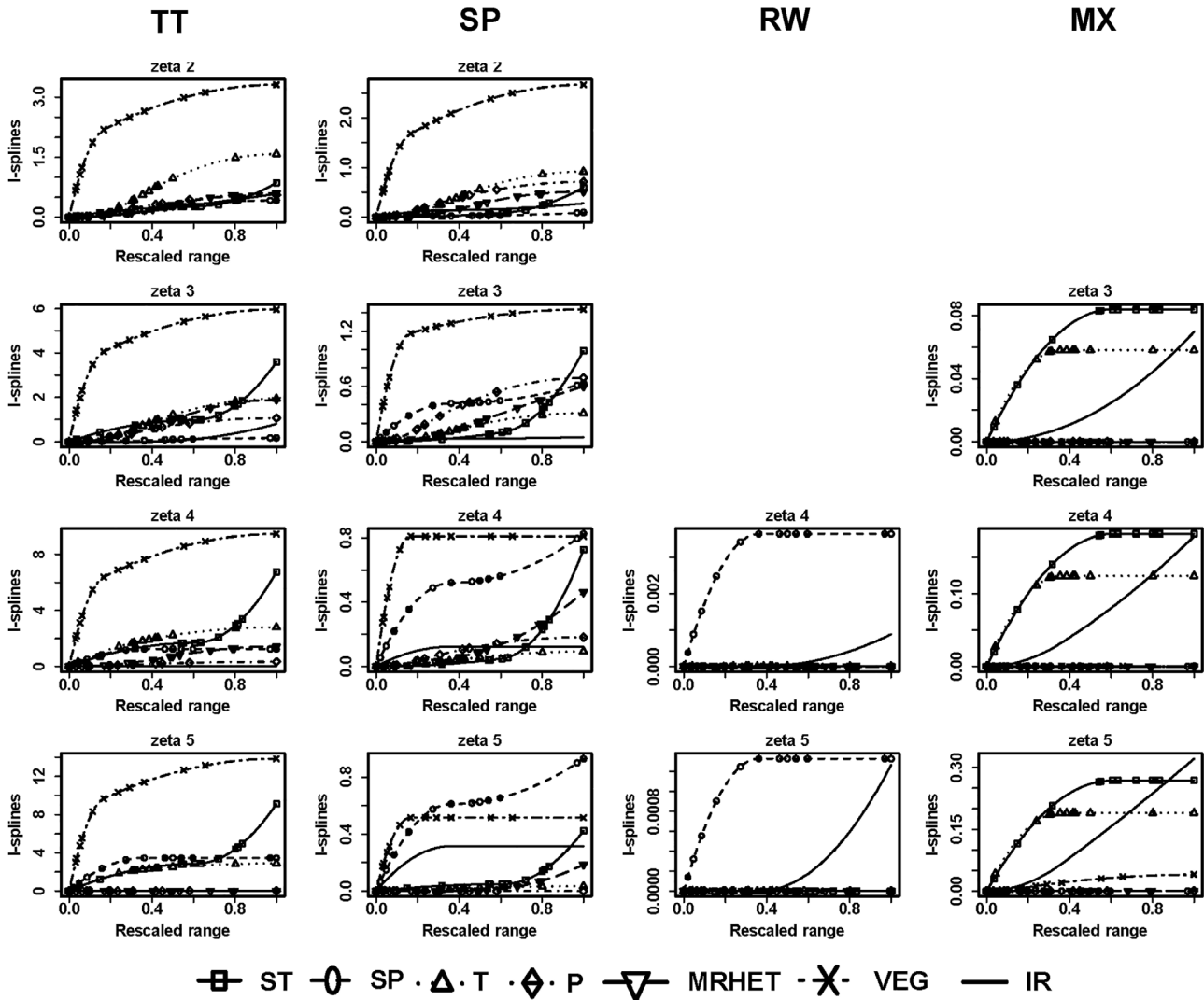
orders 7 and 9, respectively) (Figure 2). The contribution of interaction rewiring was low across zeta orders in all continents. However, it was detectable for rare interactions (from as high as 28% in Mongolia to as low as 10% in Patagonia). For more common interactions, rewiring still contributed to total turnover in Slovakia and Mongolia, but no rewiring was found for the most common interactions in South Africa (zeta order 8 and beyond), as well as for all, except the rarest, interactions in Patagonia (zeta order 4 and beyond) (Figure 1).



**FIGURE 5** I-splines produced by the MS-GDMs for total interaction turnover (TT), species turnover (ST), interaction rewiring (RW), and mixed turnover (MX) for host–flea networks from South Africa across zeta orders (from upper to lower: increasing degree of interaction commonness), showing the relative effects of environmental and interaction richness (see Figure 1 for abbreviations and explanations). Predictors are scaled between 0 and 1 (from lowest to highest value). Mixed turnover for zeta order 2 is not shown because the deviance explained by the model equals zero (see Table 3).

Summaries of the MS-GDM for interaction turnover and its components for host–flea networks from four continents, as influenced by environmental factors, interaction richness, and geographic distance for selected zeta orders 2–6 (Slovakia, Mongolia, and South Africa) and 2–5 (Patagonia), are presented in Tables 1–4. In Slovakia, the total interaction turnover for both rare (i.e. lower zeta orders) and common (i.e. higher zeta orders) interactions was mainly affected by interaction richness and spatial distance and to the lesser degree by precipitation

(Table 1 and Figure 3). The effect of spatial distance on turnover of the most common interactions decreased substantially. In addition, the turnover rate of rare interactions was higher at low and high values of interaction richness, while the turnover rate of common interactions at high values of interaction richness was relatively steady. Interaction richness was the main factor influencing species turnover, although the effect of distance and seasonality of precipitation was also pronounced at zeta order 2 and zeta order 5, respectively



**FIGURE 6** I-splines produced by the MS-GDMs for total interaction turnover (TT), species turnover (ST), interaction rewiring (RW), and mixed turnover (MX) for host–flea networks from Patagonia across zeta orders (from upper to lower: increasing degree of interaction commonness), showing the relative effects of environmental variables and interaction richness (see Figure 1 for abbreviations and explanations). Predictors are scaled between 0 and 1 (from lowest to highest value). Mixed turnover for zeta order 2 and interaction rewiring for zeta orders 2 and 3 are not shown because the deviance explained by each model equals zero (Table 4).

(Table 1 and Figure 3). Environmental variables were more important for interaction rewiring than either interaction richness or spatial distance, whereas both environment and interaction richness affected mixed turnover (Table 1 and Figure 3).

In Mongolia, the total interaction turnover was mostly affected by temperature and precipitation, whereas interaction richness started to play substantial role for the most common interactions (Table 2 and Figure 4). Variation in the interaction turnover rate along the gradients was similar, independent of the degree of interaction commonness except for zeta order 6 (Figure 4). Air temperature (and seasonality of temperature for zeta order 6) and interaction richness were the most important predictors for the species turnover component except for zeta order 2. Interaction rewiring responded mainly to variation in environment (air temperature, precipitation moisture/humidity) as well as to interaction richness for interactions with intermediate

degree of commonness (Table 2 and Figure 4). Precipitation was the strongest factor affecting mixed turnover.

In South Africa, the influence of precipitation seasonality and interaction richness on the total interaction turnover was stronger than that of other predictors, independent of the degree of interaction commonness (Table 3 and Figure 5). Interaction richness, air temperature and precipitation were also strong predictors of species turnover in all zeta orders, while seasonality of temperature and precipitation played an important role in turnover of the most common interactions (Table 3 and Figure 5). The effect of all explanatory variables on interaction rewiring was extremely low (if present at all), with the deviance explained by the model for all zeta orders being not higher than 10% (Table 3). Nevertheless, precipitation seasonality was somewhat important for rare interactions and interactions with intermediate degree of commonness (i.e. zeta orders 2–5), while temperature and

precipitation affected rewiring (albeit to low extent) for the most common interactions (Table 3 and Figure 5). The mixed turnover was mainly influenced by interaction richness and various environmental variables with the strength of effects increasing with an increase in zeta order (i.e. an increase in the degree of interaction commonness) (Table 3 and Figure 5).

In Patagonia, the best predictors of total interaction turnover were spatial distance and vegetation structure, followed by temperature and precipitation seasonality at zeta orders >2 (Table 4 and Figure 6). The same was true for species turnover, while interaction richness exerted a relatively strong effect on this component at the highest zeta order (Table 4 and Figure 6). Interaction rewiring mostly did not respond to any predictor except for precipitation seasonality at zeta orders 4–5 and interaction richness at zeta order 5, although the deviance explained by the models was extremely low and equals zero for zeta orders 2 and 3 (Table 4). The deviance explained by MS-GDM was relatively high for mixed turnover across five (but not fewer) networks, with relatively stronger effects of temperature, temperature seasonality and interaction richness as compared to the remaining predictors (Table 4). The rate of mixed turnover was the highest at the highest air temperatures and the strongest pronounced temperature seasonality (Figure 6).

## DISCUSSION

We found that the patterns of total interaction turnover and the contributions of species turnover, interaction rewiring, and mixed turnover to total turnover were similar in host–flea networks from different continents. On the contrary, the effects of environmental factors, interaction richness, and spatial distance on total interaction turnover and its components differed between continents. Furthermore, these effects also differed between turnover components, as well as between rare and common interactions.

### Contributions of turnover components to total interaction turnover

Pure species turnover contributed mostly to the turnover of rare interactions, whereas the turnover of common interactions was predominated by mixed turnover. These two turnover types contributed equally to the compositional change of interactions with an intermediate degree of commonness. The role of pure interaction rewiring in total turnover was relatively weak and manifested mainly for the turnover of rare interactions but not for interactions with an intermediate or high degree of commonness. Earlier studies demonstrated that the relative contributions of species turnover and interaction rewiring to spatial or temporal interaction turnover may vary from species turnover being relatively stronger than rewiring (e.g. Noreika et al., 2019; Trøjelsgaard et al., 2015) to vice versa (e.g. CaraDonna et al., 2017) to an equal contribution from both components (Lopes et al., 2020). Olesen et al. (2011) showed that the relative roles of species turnover

and rewiring may differ between interaction turnover for generalist, as compared to specialist, species, with rewiring being more characteristic for the former than for the latter. From this perspective, common interactions are expected to involve mainly generalists, whereas rare interactions are expected to involve mainly specialists (or at least one specialist). However, generalist species are not necessarily spatially widespread, while specialists are not necessarily spatially rare because of spatial variation in the level of resource specialisation (e.g. Hughes, 2000). Pure species turnover is a dominant component of the total interaction turnover for species that change their interactions only in the absence of their partners (Henriksen et al., 2022). These interactions are thought to be represented by species characterised by high partner fidelity (Trøjelsgaard et al., 2015). Nevertheless, in the networks with high partner fidelity, the contribution of the rewiring component may be no less important than the contribution of species turnover (Lopes et al., 2020). This seems to be the case for the host–flea networks considered in this study because of the substantial contribution of mixed turnover to the turnover of moderately common and common interactions. The increased contribution of mixed turnover towards the most common interactions might be the result of the increasing number of compared networks, with the dissimilarity between some of them caused by species turnover and between others caused by rewiring.

The roles of interactors in interaction turnover often differ. For example, in some plant–pollinator networks, spatial pollinator-driven turnover appeared to be stronger than plant-driven turnover due to pollinator foraging and/or behavioural flexibility (Noreika et al., 2019; Trøjelsgaard et al., 2015), whereas the opposite was the case for seasonal turnover due to phenological changes in plant species (Norfolk et al., 2015; Simanonok & Burkle, 2014). Given the main focus of this study, we did not test whether interaction turnover was determined mainly by either hosts or fleas or both. However, indirect evidence from other host–parasite networks suggested the predominant role of hosts as drivers of interaction turnover (Lopes et al., 2020), although Dallas and Poisot (2018) argued that different host and parasite species fulfil the same functional roles in interaction networks, so that network structure does not change with compositional turnover of interactors.

The contribution of pure interaction rewiring to the turnover of rare interactions in the Palearctic networks (Slovakia and Mongolia) was two times higher than that in the Afrotropic (South Africa) and the Neotropic (Patagonia) networks. In addition, the contribution of rewiring in the Palearctic networks did not attain zero even when all networks were compared. On the one hand, this result is counterintuitive because host–flea interactions in the Palearctic are relatively more specialised than in other realms so that each Palearctic flea species interacts with fewer host species than fleas inhabiting other realms (Krasnov et al., 2007; Medvedev, 2005); thus, a change in the interacting partner is unlikely for a host-specific flea (e.g. Khokhlova et al., 2012). On the other hand, host–flea (as well as other host–parasite) interactions are asymmetric, with specialist fleas tending to interact with hosts characterised by species-rich parasite assemblages

(i.e. “generalists”) (Vázquez et al., 2005). It is thus possible that the relatively high contribution of rewiring to the turnover of rare interactions in the Palearctic is associated with the high number of host-“generalists” (Olesen et al., 2011). The mean number of flea species per host species in the Palearctic is two times higher than in other biogeographic realms (Medvedev, 2014). In our study, the relative number of host species exploited by a high number (>10) of flea species was higher in Slovakia and Mongolia (six and five, respectively) than in South Africa and Patagonia (three in each). In addition, interaction rewiring may depend on various conditions, including morphological (Maruyama et al., 2014) and phylogenetic constraints (Montesinos-Navarro et al., 2019) and fluctuations in the encounter rate between interactors (Vázquez et al., 2009), thus being system- and region-specific (Henriksen et al., 2022).

### Drivers of interaction turnover

The effects of environmental factors, interaction richness, and spatial distance on the total interaction turnover and its components differed between networks from different continents, as well as between turnover components and between rare and common interactions. For example, total turnover in Mongolian networks was mainly affected by environmental factors, whereas turnover in Slovakian networks responded strongly to interaction richness and spatial distance. In Mongolia, mixed turnover responded to variation in precipitation, whereas interaction rewiring responded to variation in vegetation structure. In Patagonia, the effect of vegetation variables on species turnover component was characteristic for rare but not common interactions.

A comparison of these results with our earlier findings on the effect of environment on variation in flea species composition (albeit carried out at a much larger scale) (Krasnov, Shenbrot, et al., 2020) shows that variation in species composition (i.e. species turnover) and interaction turnover respond to different environmental variables. For example, Krasnov, Shenbrot, et al. (2020) reported that dissimilarity in air temperature contributed the most to the turnover of rare flea species in South America, whereas the turnover of widespread species was also strongly affected by dissimilarity in precipitation. The results of this study for Patagonia suggested that both rare interactions and common interactions were mainly affected vegetation-related factors. Similarly, the turnover of both rare and widespread flea species in Africa was affected by air temperature, but the turnover of rare species responded to dissimilarity in rainfall (Krasnov, Shenbrot, et al., 2020). In this study, we found that the turnover of both rare and common interactions in South Africa was mainly associated with network structure (interaction richness) and seasonality of precipitation. This supports the findings of Poisot et al. (2017) that species interactions and individual species respond to different environmental variables. This means that the information obtained from studies of species differs from that obtained from studies of species interactions and that these two types of studies are complementary (see also Poisot et al., 2017).

The mechanisms of environmental effects on host–flea interactions have been repeatedly discussed (Krasnov, 2008; Krasnov et al., 2019; Krasnov, Shenbrot, et al., 2020). In particular, air temperature and precipitation determine the microclimate of host burrows where fleas’ pre-imaginal development takes place and where imago fleas of many species spend substantial portions of their lives. Vegetation affects soil structure, which, in turn, determines the architecture and substrate of host shelters (e.g. Shenbrot et al., 2002), as well as the structure of hosts’ nests. Furthermore, different small mammals require different vegetation and soil structures for burrow and nest construction (e.g. Laundré & Reynolds, 1993), whereas different fleas have different microclimatic requirements (reviewed in Krasnov, 2008). Consequently, either host or flea species may be absent from a network situated in a locality where environmental conditions are either not suitable for a burrow for that host or the microclimate of a burrow is not suitable for that flea. This will obviously affect the species turnover component. Interaction rewiring might be affected if, for example, environmental conditions allow a given host to construct burrows suitable for a given flea in one but not another locality, where burrows suitable for that flea are constructed by another host species. Therefore, interaction turnover is likely driven by species-specific responses to the environmental gradients (Gravel et al., 2019).

The differential responses to environmental variables in the turnover of rare versus widespread species have previously been shown (Krasnov, Shenbrot, et al., 2020). Henriksen et al. (2022) proved that this is also the case for rare versus common interactions. Our results support these findings. Differences in the effects of environmental gradients on interaction turnover, in dependence on the degree of interaction commonness, might be associated with differential environmental tolerances of the species involved in these interactions. These differences may hypothetically affect both species turnover and interaction rewiring, but no information supporting this explanation is available.

Similarly to the results of Henriksen et al. (2022), network structure (interaction richness) mainly affected the species turnover component. A possible reason for this could be the positive (albeit complex) relationships between species and interaction richness (e.g. Pardikes et al., 2018), so species replacements are likely more probable in richer than in poorer networks.

Relatively strong associations between interaction turnover and spatial distance were found for total turnover and/or its species turnover component in Slovakia and Patagonia but not in Mongolia and South Africa. Earlier studies on the relationship between the distance and (dis)similarity of interactions provided contrasting results. For example, no distance decay of similarity was detected for host-helminth networks at a global scale, although communities of interactors demonstrated this pattern (Dallas & Poisot, 2018). On the contrary, the similarity of mammal–flea interactions in western Siberia decreased with increasing distance between networks (Krasnov, Korallo-Vinarskaya, et al., 2020). Moreover, this latter pattern was mainly true for rare, rather than common, interactions. Inconsistencies between studies of distance decay in interaction similarity might be

explained by differences in spatial scale. For instance, the lack of a distance-dissimilarity pattern at a global scale might arise merely due to variability in the manifestation of this pattern among geographic regions.

The between-continent variation in the effect of environmental factors on interaction turnover is most probably associated with the profoundly different species compositions in both hosts and fleas. These species have different environmental preferences and tolerances, as well as different morphological and physiological constraints. As a result, different species respond to environmental factors in different species-specific ways. As the likely drivers of interaction turnover, these species-specific responses may thus be further translated into continent-specific patterns of interaction dissimilarity along environmental gradients. The roles played by individual host and flea species in interaction turnover warrant further investigation.

It is commonly recognised that network studies are inherently sensitive to undersampling (Chacoff et al., 2012; Henriksen et al., 2019; Jordano, 2016). Henriksen et al. (2022) demonstrated that the multi-site turnover metric, developed by them and applied here, allows more accurate estimations of spatial or temporal variation in interaction networks. This is because this metric distinguishes between the turnover of rare and common interactions and, therefore, offers trustworthy estimates of turnover for common interactions, which, obviously, can be detected with higher certainty than rare interactions. Regarding this study, the patterns found here were surprisingly consistent despite substantial differences in the sampling efforts between continental networks (from 465 host individuals in South Africa to 2380 host individuals in Slovakia). Consequently, we believe that any bias introduced by undersampling and/or differential sampling efforts did not strongly affect our results.

In conclusion, the patterns of host–flea interaction turnover and its components appeared to be consistent, independent of the interactors' identity. However, the drivers of the turnover differed between networks from different continents, probably because of species-specific responses to environmental factors.

## AUTHOR CONTRIBUTIONS

Boris R. Krasnov conceived of the study. Mathias S. Kiefer, Daniel Kiefer, Marcela Lareschi, Sonja Matthee, Juliana P. Sanchez, Michal Stanko, and Luther van der Mescht collected the data. Boris R. Krasnov, Irina S. Khokhlova, and Georgy I. Shenbrot analysed the data. Boris R. Krasnov and Irina S. Khokhlova drafted the manuscript. All authors finalised the manuscript.

## ACKNOWLEDGEMENTS

The authors dedicate this study to late Dr. Matthias Kiefer (in memoriam). We thank Guillaume Latombe for help with the R functions and Golan Bel for help with extracting data from CHELSA. Sampling in Slovakia was supported by the Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences (grant VEGA 2/0014/21 to MS); sampling in Mongolia was supported by the Academy of Sciences of the USSR and the Academy of Sciences of the Mongolian People's Republic (to MSK; grant numbers are not

available); sampling in South Africa was supported by the National Research Foundation (NRF) of South Africa (grants GUN 80764 and 85718 to SM); sampling in Argentina was supported by the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (grant PICT2010-338 to ML), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) (grant PIP 0146 to ML) and Universidad Nacional de La Plata (grant UNLP N752 to ML). The present study was partly supported by the Israel Science Foundation (grant number 149/17 to BRK and ISK).

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data used in these study are available from the cited sources.

## ETHICS STATEMENT

In Slovakia, sampling was done under licences from the Ministry of Environment of the Slovak Republic, nos. 4874/2011–2.2 and 4559/2015–2.3. Sampling in Mongolia was carried out in the framework of the Joint Soviet-Mongolian Complex Biological Expedition of Academy of Sciences of the USSR and the Academy of Sciences of the Mongolian People's Republic, and no special permits were issued. Sampling in South Africa was approved by Stellenbosch University Animal Ethics (reference numbers 2006B01007 and SU-ACUM11-00004) and research permits 0035-AAA007-00423 (Western Cape) and FAUNA 1076/2011 (Northern Cape). Sampling in Patagonia was carried out under permissions from the Dirección de Fauna y Flora Silvestre de la Provincia del Chubut, nos. 34/06, 38/08 and 71/2011.

## ORCID

Boris R. Krasnov  <https://orcid.org/0000-0002-0382-3331>

Marcela Lareschi  <https://orcid.org/0000-0002-5300-9100>

Juliana P. Sanchez  <https://orcid.org/0000-0003-4366-9073>

## REFERENCES

- Bascompte, J. & Jordano, P. (2007) Plant–animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution and Systematics*, 38, 567–593. Available from: <https://doi.org/10.1146/annurev.ecolsys.38.091206.095818>
- Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 9383–9387. Available from: <https://doi.org/10.1073/pnas.16335.76100>
- Beck, J. & Chey, V.K. (2010) Explaining the elevational diversity pattern of geometrid moths from Borneo: a test of five hypotheses. *Journal of Biogeography*, 35, 1452–1464. Available from: <https://doi.org/10.1111/j.1365-2699.2008.01886.x>
- Brown, J.H. & Nicoletto, P.F. (1991) Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist*, 138, 1478–1512. Available from: <https://doi.org/10.1086/285297>
- Brun, P., Zimmermann, N.E., Hari, C., Pellissier, L. & Karger, D. (2022) Data from: CHELSA-BIOCLIM+ a novel set of global climate-related predictors at kilometre-resolution. *EnviDat*. Available from: <https://doi.org/10.16904/envidat.332>



- Burkle, L.A. & Alarcón, R. (2011) The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. *American Journal of Botany*, 98, 528–538. Available from: <https://doi.org/10.3732/ajb.1000391>
- Burkle, L.A., Belote, R.T. & Myers, J.A. (2022) Wildfire severity alters drivers of interaction beta-diversity in plant-bee networks. *Ecography*, 2022, e05986. Available from: <https://doi.org/10.1111/ecog.05986>
- Burkle, L.A., Myers, J.A. & Belote, R.T. (2016) The beta-diversity of species interactions: untangling the drivers of geographic variation in plant-pollinator diversity and function across scales. *American Journal of Botany*, 103, 118–128. Available from: <https://doi.org/10.3732/ajb.1500079>
- CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M. et al. (2017) Interaction rewiring and the rapid turnover of plant-pollinator networks. *Ecology Letters*, 20, 385–394. Available from: <https://doi.org/10.1111/ele.12740>
- Carstensen, D.W., Sabatino, M., Trøjelsgaard, K. & Morellato, L.P.C. (2014) Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. *PLoS One*, 9, e112903. Available from: <https://doi.org/10.1371/journal.pone.0112903>
- Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J. & Padrón, B. (2012) Evaluating sampling completeness in a desert plant-pollinator network. *Journal of Animal Ecology*, 81, 190–200. Available from: <https://doi.org/10.1111/j.1365-2656.2011.01883.x>
- Connolly, J., Cadotte, M.W., Brophy, C., Dooley, Á., Finn, J., Kirwan, L. et al. (2011) Phylogenetically diverse grasslands are associated with pairwise interspecific processes that increase biomass. *Ecology*, 92, 1385–1392. Available from: <https://doi.org/10.1890/10-2270.1>
- Dallas, T. & Poisot, T. (2018) Compositional turnover in host and parasite communities does not change network structure. *Ecography*, 41, 1534–1542. Available from: <https://doi.org/10.1111/ecog.03514>
- Delmas, E., Besson, M., Brice, M.-H., Burkle, L.A., Dalla Riva, G.V., Fortin, M.-J. et al. (2019) Analysing ecological networks of species interactions. *Biological Reviews*, 94, 16–36. Available from: <https://doi.org/10.1111/brv.12433>
- Dormann, C.F., Gruber, B. & Fründ, J. (2008) Introducing the bipartite package: analysing ecological networks. *R News*, 8(2), 8–11.
- Ferrier, S., Manion, G., Elith, J. & 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. Available from: <https://doi.org/10.1111/j.1472-4642.2007.00341.x>
- Fründ, J. (2021) Dissimilarity of species interaction networks: how to partition rewiring and species turnover components. *Ecosphere*, 12, e03653. Available from: <https://doi.org/10.1002/ecs2.3653>
- Gotelli, N.J. & Rohde, K. (2002) Co-occurrence of ectoparasites of marine fishes: null model analysis. *Ecology Letters*, 5, 86–94. Available from: <https://doi.org/10.1046/j.1461-0248.2002.00288.x>
- Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martínez, N.D., Nyman, T. et al. (2019) Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, 42, 401–415. Available from: <https://doi.org/10.1111/ecog.04006>
- Henriksen, M.V., Chapple, D.G., Chown, S.L. & McGeoch, M.A. (2019) The effect of network size and sampling completeness in depauperate networks. *Journal of Animal Ecology*, 88, 211–222. Available from: <https://doi.org/10.1111/1365-2656.12912>
- Henriksen, M.V., Latombe, G., Chapple, D.G., Chown, S.L. & McGeoch, M.A. (2022) A multi-site method to capture turnover in rare to common interactions in bipartite species networks. *Journal of Animal Ecology*, 91, 404–416. Available from: <https://doi.org/10.1111/1365-2656.13639>
- Hughes, J.B. (2000) The scale of resource specialization and the distribution and abundance of lycaenid butterflies. *Oecologia*, 123, 375–383. Available from: <https://doi.org/10.1007/s004420051024>
- Hui, C. & McGeoch, M.A. (2014) Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns. *American Naturalist*, 184, 684–694. Available from: <https://doi.org/10.1086/678125>
- Jordano, P. (2016) Sampling networks of ecological interactions. *Functional Ecology*, 30, 1883–1893. Available from: <https://doi.org/10.1111/1365-2435.12763>
- Jordano, P. & Bascompte, J. (2013) *Mutualistic networks*. Princeton: Princeton University Press.
- Karger, D.N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2018) Data from: climatologies at high resolution for the earth's land surface areas. *EnviDat*. Available from: <https://doi.org/10.16904/envodat.228.v2.1>
- Khokhlova, I.S., Fielden, L.J., Degen, A.A. & Krasnov, B.R. (2012) Ectoparasite fitness in auxiliary hosts: phylogenetic distance from a principal host matters. *Journal of Evolutionary Biology*, 25, 2005–2013. Available from: <https://doi.org/10.1111/j.1420-9101.2012.02577.x>
- Kiefer, D., Stubbe, M., Stubbe, A., Gardner, S.L., Tserenorov, D., Samiya, R. et al. (2012) Siphonaptera of Mongolia and Tuva: results of the Mongolian-German biological expeditions since 1962—years 1999–2003. *Erforschung Biologischer Ressourcen der Mongolei (Halle/Saale)*, 12, 153–167.
- Kiefer, M., Goncharov, A.I. & Lobachev, V.S. (1990) Studies on the fauna and ecology of Siphonaptera in the Mongolian People's Republic. *Nauchnye Doklady Vysshei Shkoly Biologicheskije Nauki (Scientific Reports of Higher Education. Biological Sciences)*, 2, 57–70 (in Russian).
- Kiefer, M., Klimaszewski, S.M. & Krumpal, M. (1982) Zoogeographical regionalization of Mongolia on the basis of flea fauna (Siphonaptera). *Polskie Pismo Entomologiczne*, 52, 13–32.
- Kiefer, M., Krumpal, M., Cendsuren, N., Lobachev, V.S. & Khotolkhu, N. (1984) Checklist, distribution and bibliography of Mongolian Siphonaptera. *Erforschung Biologischer Ressourcen der Mongolei (Halle/Saale)*, 4, 1–123.
- Kirwan, L., Connolly, J., Finn, J.A., Brophy, C., Luscher, A., Nyfeler, D. et al. (2009) Diversity–interaction modeling: estimating contributions of species identities and interactions to ecosystem function. *Ecology*, 90, 2032–2038. Available from: <https://doi.org/10.1890/08-1684.1>
- Krasnov, B.R. (2008) *Functional and Evolutionary Ecology of Fleas. A Model for Ecological Parasitology*. Cambridge: Cambridge University Press.
- Krasnov, B.R., Korallo-Vinarskaya, N.P., Vinarski, M.V. & Khokhlova, I.S. (2020) Spatial and temporal turnover of parasite species and parasite–host interactions: a case study with fleas and gamasid mites parasitic on small mammals. *Parasitology Research*, 119, 2093–2104. Available from: <https://doi.org/10.1007/s00436-020-06726-z>
- Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S. & Poulin, R. (2007) Geographical variation in the ‘bottom-up’ control of diversity: fleas and their small mammalian hosts. *Global Ecology and Biogeography*, 16, 179–186. Available from: <https://doi.org/10.1111/j.1466-8238.2006.00273.x>
- Krasnov, B.R., Shenbrot, G.I., Korallo-Vinarskaya, N.P., Vinarski, M.V., Warburton, E.M. & Khokhlova, I.S. (2019) 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. Available from: <https://doi.org/10.1007/s00436-019-06371-1>
- Krasnov, B.R., Shenbrot, G.I., van der Mescht, L. & Khokhlova, I.S. (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. Available from: <https://doi.org/10.1016/j.ijpara.2020.03.001>
- Krasnov, B.R., Spickett, A., Junker, K., Bugmyrin, S.V., Ieshko, E.P., Bespyatova, L.A. et al. (2021) Parasite counts or parasite incidences? Testing differences with four analyses of infracommunity modelling for seven parasite–host associations. *Parasitology Research*, 120, 2569–2584. Available from: <https://doi.org/10.1007/s00436-021-07217-5>

- Lamont, M. & Johnson, D. (2021) Variation in species composition, size and fitness of two multi-species sea turtle assemblages using different neritic habitats. *Frontiers in Marine Science*, 7, 608740. Available from: <https://doi.org/10.3389/fmars.2020.608740>
- Latombe, G., Hui, C. & McGeoch, M.A. (2017) Multi-site generalised dissimilarity modelling: using zeta diversity to differentiate drivers of turnover in rare and widespread species. *Methods in Ecology and Evolution*, 8, 431–442. Available from: <https://doi.org/10.1111/2041-210X.12756>
- Latombe, G., McGeoch, M.A., Nipperess, D. & Hui, C. (2020) Zetadiv: functions to compute compositional turnover using zeta diversity. R package version 1.2.0. <https://CRAN.R-project.org/package=zetadiv>
- Latombe, G., Richardson, D.M., Pyšek, P., Kučera, T. & Hui, C. (2018) Drivers of species turnover vary with species commonness for native and alien plants with different residence times. *Ecology*, 99, 2763–2775. Available from: <https://doi.org/10.1002/ecy.2528>
- Laundré, J.W. & Reynolds, T.D. (1993) Effects of soil structure on burrow characteristics of five small mammal species. *Great Basin Naturalist*, 53, 358–366. Available from: <https://doi.org/10.2307/41712798>
- Li, D., Poisot, T., Waller, D.M. & Baiser, B. (2018) Homogenization of species composition and species association networks are decoupled. *Global Ecology and Biogeography*, 27, 1481–1491. Available from: <https://doi.org/10.1111/geb.12825>
- Lopes, V.L., Costa, F.V., Rodrigues, R.A., Braga, E.M., Pichorim, M. & Moreira, P.A. (2020) High fidelity defines the temporal consistency of host-parasite interactions in a tropical coastal ecosystem. *Scientific Reports*, 10, 16839. Available from: <https://doi.org/10.1038/s41598-020-73563-6>
- Maruyama, P.K., Vizentin-Bugoni, J., Oliveira, G.M., Oliveira, P.E. & Dalsgaard, B. (2014) Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network. *Biotropica*, 46, 740–747. Available from: <https://doi.org/10.1111/btp.12170>
- McGeoch, M.A., Latombe, G., Andrew, N.R., Nakagawa, S., Nipperess, D. A., Roigé, M. et al. (2019) Measuring continuous compositional change using decline and decay in zeta diversity. *Ecology*, 100, e02832. Available from: <https://doi.org/10.1002/ecy.2832>
- Medvedev, S.G. (1996) Geographical distribution of families of fleas (Siphonaptera). *Entomological Review*, 76, 978–992.
- Medvedev, S.G. (2005) An attempt of a system analysis of the evolution of fleas (Siphonaptera). In: *Meetings in Memory of N.A. Choldokovsky, Issue 57 (2)*. Saint-Petersburg, Russia: Russian Entomological Society and Zoological Institute of the Russian Academy of Sciences. (in Russian).
- Medvedev, S.G. (2014) The Palaearctic centers of taxonomic diversity of fleas (Siphonaptera). *Entomological Review*, 94, 345–358. Available from: <https://doi.org/10.1134/S0013873814030075>
- Miele, V., Ramos-Jiliberto, R. & Vázquez, D.P. (2020) Core-periphery dynamics in a plant-pollinator network. *Journal of Animal Ecology*, 89, 1670–1677. Available from: <https://doi.org/10.1111/1365-2656.13217>
- Montesinos-Navarro, A., Díaz, G., Torres, P., Caravaca, F. & Roldán, A. (2019) Phylogenetic rewiring in mycorrhizal-plant interaction networks increases community stability in naturally fragmented landscapes. *Communications Biology*, 2, 452. Available from: <https://doi.org/10.1038/s42003-019-0700-3>
- Montoya, J.M., Pimm, S.L. & Sole, R.V. (2006) Ecological networks and their fragility. *Nature*, 442, 259–269. Available from: <https://doi.org/10.1038/nature04927>
- Montufar, R. & Pintaud, J.-C. (2006) Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. *Botanical Journal of the Linnean Society*, 151, 127–140. Available from: <https://doi.org/10.1111/j.1095-8339.2006.00528.x>
- Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M. et al. (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, 11, e1001569. Available from: <https://doi.org/10.1371/journal.pbio.1001569>
- Noreika, N., Bartomeus, I., Winsa, M., Bommarca, R. & Öckinger, E. (2019) Pollinator foraging flexibility mediates rapid plant-pollinator network restoration in semi-natural grasslands. *Scientific Reports*, 9, 15473. Available from: <https://doi.org/10.1038/s41598-019-51912-4>
- Norfolk, O., Eichhorn, M.P. & Gilbert, F.S. (2015) Contrasting patterns of turnover between plants, pollinators and their interactions. *Diversity and Distributions*, 21, 405–415. Available from: <https://doi.org/10.1111/ddi.12295>
- Novotny, V. (2009) Beta diversity of plant-insect food webs in tropical forests: a conceptual framework. *Insect Conservation and Diversity*, 2, 5–9. Available from: <https://doi.org/10.1111/j.1752-4598.2008.00035>
- Olesen, J.M., Bascompte, J., Elberling, H. & Jordano, P. (2008) Temporal dynamics in a pollination network. *Ecology*, 89, 1573–1582. Available from: <https://doi.org/10.1890/07-0451.1>
- Olesen, J.M., Stefanescu, C. & Traveset, A. (2011) Strong, long-term temporal dynamics of an ecological network. *PLoS One*, 6, e26455. Available from: <https://doi.org/10.1371/journal.pone.0026455>
- Pardikes, N.A., Lumpkin, W., Hurtado, P.J. & Dyer, L.A. (2018) Simulated tri-trophic networks reveal complex relationships between species diversity and interaction diversity. *PLoS One*, 13, e0193822. Available from: <https://doi.org/10.1371/journal.pone.0193822>
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M. et al. (2018) Comparing species interaction networks along environmental gradients. *Biological Reviews*, 93, 785–800. Available from: <https://doi.org/10.1111/brv.12366>
- Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P. & Pantis, J.D. (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters*, 11, 564–575. Available from: <https://doi.org/10.1111/j.1461-0248.2008.01170.x>
- Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012) The dissimilarity of species interaction networks. *Ecology Letters*, 15, 1353–1361. Available from: <https://doi.org/10.1111/ele.12002>
- Poisot, T., Guéveneux-Julien, C., Fortin, M.-J., Gravel, D. & Legendre, P. (2017) Hosts, parasites and their interactions respond to different climatic variables. *Global Ecology and Biogeography*, 26, 942–951. Available from: <https://doi.org/10.1111/geb.12602>
- Poisot, T., Stouffer, D.B. & Gravel, D. (2015) Beyond species: why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251. Available from: <https://doi.org/10.1111/oik.01719>
- R Core Team. (2021) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Sabatino, M., Maceira, N. & Aizen, M.A. (2010) Direct effects of habitat area on interaction diversity in pollination webs. *Ecological Applications*, 20, 1491–1497. Available from: <https://doi.org/10.1890/09-1626.1>
- Sanchez, J.P. (2012) Sifonápteros Parásitos de los Roedores Sigmodontinos de la Patagonia Norte de la Argentina: Estudios Sistemáticos y Ecológicos. In: *Tesis Doctoral, Facultad de Ciencias Naturales y Museo*. Argentina: Universidad Nacional de La Plata, La Plata.
- Sanchez, J.P. & Lareschi, M. (2013) The fleas (Insecta: Siphonaptera) parasites of sigmodontine rodents (Cricetidae) from Northern Patagonia, Argentina. *Comparative Parasitology*, 80, 110–117. Available from: <https://doi.org/10.1654/4576.1>
- Sanchez, J.P. & Lareschi, M. (2019) Diversity, distribution and parasitism rates of fleas (Insecta: Siphonaptera) on sigmodontine rodents (Cricetidae) from Argentinian Patagonia. *Bulletin of Entomological Research*, 109, 72–83. Available from: <https://doi.org/10.1017/S0007485318000196>

- Shenbrot, G.I., Krasnov, B.R., Khokhlova, I.S., Demidova, T. & Fielden, L.J. (2002) Habitat-dependent differences in architecture and microclimate of the burrows of Sundevall's jird (*Meriones crassus*) (Rodentia: Gerbillinae) in the Negev Desert, Israel. *Journal of Arid Environments*, 51, 265–279. Available from: <https://doi.org/10.1006/jare.2001.0945>
- Simanonok, M.P. & Burkle, L.B. (2014) Partitioning interaction turnover among alpine pollination networks: spatial, temporal, and environmental patterns. *Ecosphere*, 5, 149. Available from: <https://doi.org/10.1890/ES14-00323.1>
- Stanko, M., Miklisová, D., Gouy de Bellocq, J. & Morand, S. (2002) Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia*, 131, 289–295. Available from: <https://doi.org/10.1007/s00442-002-0889-5>
- Trøjelsgaard, K., Jordano, P., Carstensen, D.W. & Olesen, J.M. (2015) Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. *Proceedings of the Royal Society of London B*, 282, 20142925. Available from: <https://doi.org/10.1098/rspb.2014.2925>
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11, 1351–1363. Available from: <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation*, 143, 2270–2279. Available from: <https://doi.org/10.1016/j.biocon.2009.12.004>
- van der Mescht, L. & Matthee, S. (2017) Host range and distribution of small mammal fleas in South Africa, with a focus on species of medical and veterinary importance. *Medical and Veterinary Entomology*, 31, 402–413. Available from: <https://doi.org/10.1111/mve.12239>
- Vázquez, D.P., Blüthgen, N., Cagnolo, L. & Chacoff, N.P. (2009) Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany*, 103, 1445–1457. Available from: <https://doi.org/10.1093/aob/mcp057>
- Vázquez, D.P., Poulin, R., Krasnov, B.R. & Shenbrot, G.I. (2005) Species abundance and the distribution of specialization in host–parasite interaction networks. *Journal of Animal Ecology*, 74, 946–955. Available from: <https://doi.org/10.1111/j.1365-2656.2005.00992.x>
- Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, 30, 279–338. Available from: <https://doi.org/10.2307/1943563>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Maps of sampling localities.

**Appendix S2.** Supplementary tables.

**How to cite this article:** Krasnov, B.R., Khokhlova, I.S., Kiefer, M.S., Kiefer, D., Lareschi, M., Matthee, S. et al. (2023) Multi-site interaction turnover in flea-mammal networks from four continents: Application of zeta diversity concept and multi-site generalised dissimilarity modelling. *Ecological Entomology*, 1–19. Available from: <https://doi.org/10.1111/een.13236>