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HELMINTHOLOGY - ORIGINAL PAPER

Beta diversity of gastrointestinal helminths in two closely related South African rodents: species and site contributions

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Abstract

A fundamental aim of parasite ecology is to understand the mechanisms behind spatial variation in diversity and structure of parasite assemblages. To understand the contribution of individual parasite species and their assemblages to spatial variation in parasite communities, we examined species contributions to beta diversity (SCBD) and local contributions to beta diversity (LCBD) of parasitic gastrointestinal helminths (nematodes and cestodes) in two closely related rodents, *Rhabdomys dilectus* and *Rhabdomys pumilio*, from 20 localities across South Africa. Although the two *Rhabdomys* spp. are morphologically similar, they differ substantially in body size, habitat preference, and sociality. We asked whether the variation in life history traits and infection parameters are associated with SCBD of helminths and whether variation in environmental factors, host population density, and species richness of host communities are associated with LCBD of component assemblages of helminths. We also considered spatial factors to test whether LCBD of helminth assemblages demonstrate geographic structure. We found that the contribution of helminth species parasitic in both hosts to beta diversity significantly increased with characteristic prevalence of these species, whereas mean abundance, type of life cycle, and location in the host's gut had no effect on SCBD. The LCBD of helminth assemblages showed a significant positive correlation with environmental factors in both host species. Our results suggest that predictors of variation in SCBD and LCBD may substantially differ between parasites with different infection parameters and/or parasite communities at different hierarchical scales.

Keywords Beta diversity · *Rhabdomys* · Gastrointestinal helminths · Environment · LCBD · SCBD

Introduction

One of the central aims of parasite ecology is to understand the mechanisms behind spatial variation in diversity and structure of parasite assemblages. This understanding will facilitate the reliability of predictions on disease outbreaks in human, livestock, and wildlife across landscapes (e.g., Altman and Byers 2014; Hoberg and Brooks 2015). Patterns of spatial variation of parasite communities are well known (see Morand and Krasnov 2010 for reviews). These patterns range from the relationship (either positive or negative) between latitude and parasite diversity (Guernier et al. 2004; Krasnov et al. 2004; Lindenfors et al. 2007) to distance decay of similarity in species composition between parasite communities (Poulin 2003; Krasnov et al. 2010). However, the mechanisms behind these patterns are not always fully understood. For example, it is not always clear what the reasons are for one parasite community to be different to another parasite community even if

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these communities share many species and are harbored by the same host species.

The concept of beta diversity was originally introduced by Whittaker (1960, 1972) as the measure of variability in species composition of biological communities across space or time. Since then, his concept has been repeatedly and successfully applied to various questions in community ecology (e.g., Legendre et al. 2005; Legendre 2008; Anderson et al. 2011 and references therein). In particular, beta diversity studies can elucidate mechanisms producing dissimilarities between biological communities (Vellend 2010). These dissimilarities may arise from two different processes, namely (a) turnover or replacement of species and (b) species gains and losses with the latter causing between-community difference in species richness (Harrison et al. 1992; Williams 1996; Lennon et al. 2001; Legendre 2014). In other words, individual species and species assemblages may play different roles in and, thus, contribute differently to total beta diversity (Legendre and de Cáceres 2013). To untangle the influences of individual species and the influences of species assemblages on total beta diversity, Legendre and de Cáceres (2013) developed an approach that allows partitioning of total beta diversity into either (a) species contributions to beta diversity (SCBD), which is the degree of relative importance of individual species for beta diversity or (b) local contributions to beta diversity (LCBD), which is an indicator of the compositional uniqueness of an assemblage as compared to other assemblages (= sites).

The approach of Legendre and de Cáceres (2013) to partition beta diversity into either SCBD or LCBD was successfully applied in studies on beta diversity in various plant and animal taxa (e.g., Tonkin et al. 2016; Heino and Grönroos 2017; Landeiro et al. 2018). It has been found that SCBD may be affected by species-specific traits such as abundance (da Silva et al. 2018), whereas LCBD can be associated with, for example, environmental factors (Tonkin et al. 2016).

Despite the importance of understanding the contribution of individual parasite species and their assemblages to spatial variation in parasite communities, beta diversity separated into SCBD and LCBD components has rarely been applied to parasite communities. To the best of our knowledge, only three studies used this approach for parasites, all of them on haematophagous arthropods (Biguezoton et al. 2016; Poisot et al. 2017; Krasnov et al. 2018). Furthermore, Biguezoton et al. (2016) did not relate either SCBD to species traits or LCBD to site characteristics, whereas Poisot et al. (2017) considered LCBD only and tested for its relationship with climatic variables. Although Krasnov et al. (2018) studied the relationships between SCBD and species traits and the relationships between LCBD and environmental variables and host community structure, this was done on parasite assemblages harbored by entire host communities across large regions (i.e., compound communities of parasites sensu Bush et al. 1997). However, the effects of species traits on SCBD and the effects of site variables on LCBD may differ for beta diversity among parasite communities harbored by different populations of the same host species (i.e., component communities sensu Bush et al. 1997). Furthermore, patterns and correlates of SCBD and LCBD may differ between component communities of parasites belonging to similar taxa but exploiting different host species. This is because characteristics of host species such as sociality and mobility may strongly affect parasite transmission and exchange rates between host individuals and populations (Blasco-Costa et al. 2012; van Schaik and Kerth 2017). This is especially true for endoparasites due to their limited exposure to environmental factors and strong dependence on host spatial behavior (e.g., Ezenwa 2004).

Here, we applied new analyses to an existing dataset on gastrointestinal helminths (nematodes and cestodes) parasitic in two closely related South African rodents, *Rhabdomys dilectus* and *Rhabdomys pumilio* (see Spickett et al. 2017a, b, c). In this study, we examined SCBD of individual helminth species and LCBD of helminth assemblages and asked whether (a) variation in life history traits and infection parameters are associated with SCBD of helminths and (b) variation in environmental factors, host population density, and species richness of host communities are associated with LCBD of component assemblages of helminths. In addition, we took into account spatial factors to test whether LCBD of helminth assemblages demonstrate geographic structure.

Despite close phylogenetic relatedness and morphological similarity of *R. dilectus* and *R. pumilio*, they differ substantially in body size, habitat preference, and sociality. *Rhabdomys dilectus* is about 20% smaller than *R. pumilio* and occur in the mostly mesic eastern, mainly summer rainfall regions of South Africa where the main vegetation type is grassland. This species is solitary with adult males generally having larger home ranges compared to females (Dufour et al. 2015). *Rhabdomys pumilio* inhabits the western winter rainfall region of South Africa where the vegetation is mainly represented by low-medium shrubs. It lives in social groups of up to 30 adult individuals (including only a few breeding females) with both sexes having similar overlapping home ranges (Schradin and Pillay 2005). Due to these between-host differences, we expected differences in the patterns of SCBD and LCBD and their associations with environmental, host-related and spatial factors. Earlier, we explored diversity of helminth assemblages in these two rodents and recorded greater helminth species richness and a lower rate of decrease of similarity in species composition of helminth component communities with increasing geographic distance between these communities in *R. dilectus* than in *R. pumilio* (Spickett et al. 2017a). Consequently, we expected greater variation in SCBD of helminth species and less variation in LCBD of their assemblages in the former than in the latter host.

Materials and methods

Sampling design and helminth recovery

As mentioned above, we used the same data as in Spickett et al. (2017a, b, c). The details on sample design and schedule as well as methods of helminth recovery can be found in these earlier publications. In brief, adult rodents were trapped during spring-summer at 20 localities across South Africa during 2004–2014 (see map in Spickett et al. 2017b). A standardized sampling design was followed throughout. Baited Sherman-type live traps were set 10 m apart in replicated trap lines (50–100 m length). Targeted animals were immediately euthanized by intraperitoneal injection with sodium pentobarbitone (200 mg/kg). Rodents were identified using morphological descriptions and distribution maps (Rambau et al. 2003; Skinner and Chimimba 2005; Stuart and Stuart 2007; du Toit et al. 2012). Carcasses were either frozen in the field and remained frozen until parasite removal in the laboratory, or gastrointestinal tracts (GITs), from and including the oesophagus to the anus, were removed immediately and stored in 70% alcohol for later dissection. Nematode identification was based on morphologically distinguishing characters and using relevant keys and descriptions of various authors. In the case of cestodes, identification was confirmed using molecular analyses where both nuclear (28S ribosomal RNA) and mitochondrial (16S–12S ribosomal RNA) gene fragments were used (Littlewood et al. 2000; von Nickisch-Rosenegk et al. 2001; Lockyer et al. 2003; Galbreath and Hoberg 2012; Haukisalmi et al. 2016, 2018). Helminth faunal diversity comprised nematodes (total 25 species: *R. dilectus* 19 species, *R. pumilio* 11 species) and cestodes (total 9 species: *R. dilectus* 7 species, *R. pumilio* 5 species). Data on the helminth species associated with each species for each of the two rodent species can be found elsewhere (Spickett et al. 2017b). Voucher specimens of each nematode species have been deposited in the National Collection of Animal Helminths at the Agricultural Research Council-Onderstepoort Veterinary Institute, South Africa (accession number: S/2016/38) and cestode species at the Finnish Museum of Natural History, Luomus, Finland (accession numbers KN 3646–KN 3668).

Environmental and host-associated variables

Each sampling locality was characterized by environmental variables as well as variables describing *Rhabdomys* populations and surrounding host communities. Environmental variables included mean altitude; mean, maximal, and minimal air temperatures; summer, autumn, winter, and spring precipitation; and summer, autumn, winter, and spring normalized difference vegetation index (NDVI). The latter index reflects the amount of green vegetation in a sampling site. Elevation data at 1 arc-second grids (approximately 30 m resolution) of the Shuttle Radar Topography Mission (SRTM) were obtained from the online Data Pool, courtesy of the Land Processes Distributed Active Archive Center (LP DAAC), located at USGS/EROS, Sioux Falls, South Dakota (http://lpdaac.usgs.gov). Data on temperature and precipitation were obtained from the WorldClim v1.4 (BioClim) dataset (Hijmans et al. 2005), whereas NDVI data were taken from the VEGETATION Programme (http://free.vgt.vito.be) at 30 arc-seconds grids (approximately 1 km resolution). These variables were averaged within the area of a given locality across grids and extracted for further analyses using QGIS v2.18 (http://qgis.osgeo.org/).

The majority of environmental variables correlated significantly to one another ($r = -0.95$–0.98 for *R. dilectus* and $r = -0.94$–0.98 for *R. pumilio*). Consequently, we applied principal component analyses to environmental variables separately for sites with *R. dilectus* and *R. pumilio* and extracted the two first principal components for each set of variables. Then, we substituted the original values of the environmental variables with the scores of these two principal components, which thus were orthogonal axes of environmental variation across sampling sites (further referred to as environmental variables E1 and E2). An additional nominal environmental variable Biome described the biome to which each sampling site belonged. These were the Grassland, Savanna, and Albany Thicket for *R. dilectus* and the Succulent Karoo, Nama Karoo, and Fynbos for *R. pumilio* (see Spickett et al. 2017b).

A population of *Rhabdomys* in each site was characterized by density of *R. dilectus* or *R. pumilio.* Relative density (RD) was calculated as follows: RD = (100 × the number of hosts)/(the total number of traps × the total number of trap nights), where one trap night equals 12 h (van der Mescht 2011). The rodent community of each sampling site was characterized by the total number of rodent species recorded during the sampling period.

Helminth traits

Variables describing traits of each helminth species were life cycle (direct or indirect), main location in gastrointestinal tract of a host (stomach, small intestine, or cecum/colon), mean abundance, and mean (across sampling sites) prevalence. Most nematodes have a direct life cycle, whereas cestodes and some nematodes have an indirect life cycle, and are dependent on a variety of arthropods as intermediate hosts (Morgan and Hawkins 1951; Yamaguti 1961; Anderson 2000). Location in the host's gut was determined from our observations. The rationale behind using mean abundance as a species trait is that this infection parameter has been proven to be repeatable among populations of the same nematode or cestode species and thus can be considered as a true species character despite some variation (Arneberg et al. 1997; Poulin 2006). Although prevalence appeared to be a less repeatable infection measure than intensity or abundance (Arneberg et al. 1997), mean prevalence nevertheless has been found to vary substantially among, rather than within, helminth species (Arneberg et al. 1997; Poulin 2006) and often positively correlates with intensity (Poulin and Guégan 2000) and abundance (Morand and Guégan 2000).

Spatial variables

To account for spatial structure in beta diversity of helminth assemblages, we used Moran eigenvector maps [= the principal coordinates of neighboring matrices (PCNMs)] (Borcard and Legendre 2002). We built truncated Euclidean distance matrices from geographic coordinates of each sampling site separately for *R. dilectus* and *R. pumilio* and extracted eigenvectors with positive eigenvalues to be used as independent spatial variables in further analysis (Borcard and Legendre 2002). PCNMs allow evaluation of spatial structure over a range of spatial scales from the first to the last eigenvectors reflecting decreasing scales from broader to finer (Borcard and Legendre 2002). We extracted seven and six positive eigenvectors for sites in which *R. dilectus* and *R. pumilio*, respectively, were sampled using the package "vegan" (Oksanen et al. 2018) implemented in the R Statistical Environment (R Core Team 2018). We tested for spatial autocorrelation in PCNMs using Moran's I test from the R package "ape" (Paradis et al. 2004) and retained only those with significant spatial autocorrelation (3 PCNMs for each rodent species) for the main analysis (Borcard et al. 2011).

Data analyses

The number of helminth species recorded in each sampling site did not correlate with the number of rodents examined ($r = -0.007$ for *R. dilectus* and $r = -0.01$ for *R. pumilio*). For each rodent species, we constructed a site-by-species matrix in which each cell represented prevalence of a given helminth species in a given site. These values were then Hellinger-transformed, that is, the square root was taken of the quotient of the value of each cell and its row sum. This transformation gives low weights to species with low prevalence and many zeros across site. We did not use mean abundances of helminth species because these values cannot be compared between species belonging to different clades, orders, and phyla. Then, we calculated species and site (= local) contributions to beta diversity of helminths (SCBD and LCBD, respectively), using the approach of Legendre and de Cáceres (2013). This approach is based on the suggestion of Ellison (2010) to calculate beta diversity without prior calculations of alpha diversity and gamma diversity (see Whittaker 1960) by using the total variance of the site-by-species community matrix as a single-number beta diversity estimate (e.g., Legendre et al. 2005). This total variance is estimated by computing a matrix of squared deviations from the column means. The sum of all values of this matrix divided by ($n - 1$) (where n is the number of sampling units) represents an index of total beta diversity (Legendre et al. 2005). Using total variation of the site-by-species matrix as an index of overall beta diversity allows one to estimate the contribution of individual species (SCBD) and of individual sampling units (= sites) (LCBD) to this quantity. The relative contribution of a particular species to overall beta diversity is thus computed as the quotient of the sum of squares corresponding to this species and the total sum of squares. Similarly, the relative contribution of a particular site to overall beta diversity is computed as the quotient of the sum of squares corresponding to this site and the total sum of squares. In other words, the sums of squares corresponding to individual species or individual sites represent partitioning of beta diversity among species or among sites, respectively. Calculations of SCBD and LCBD were done using function "beta.div" implemented in the R package "adespatial" (Dray et al. 2018).

The effects of helminth trait variables on SCBD and environmental, host-associated and spatial variables on LCBD were tested using beta-regression and a logit-link function implemented in the R package "betareg" (Cribari-Neto and Zeileis 2010). Beta-regression approach is necessary for models with a response variable ranging from 0 to 1 but without attaining either 0 or 1 values because this approach takes into account heteroscedasticity and skewness characteristics for variables of this type (Cribari-Neto and Zeileis 2010). We ran beta-regressions separately for data on helminths of *R. dilectus* and *R. pumilio* as well as separate models for continuous and categorical (life cycle and location in host's gut for SCBD and biome for LCBD) variables. Furthermore, for the sake of better understanding the effects of different predictors, we ran separate models for environmental, host-associated and spatial predictors on LCBD. If the effect of the categorical predictor was significant, we compared the average contributions to beta diversity between groups with Tukey HSD test using the R packages "emmeans" (Lenth 2019) and "lmtest" (Zeileis and Hothorn 2002).

In addition, we repeated the analyses while constructing site-by-species matrices using incidence (= presence/absence) rather than prevalence of helminths. These analyses provided similar results, and we report here only the results of analyses of the prevalence site-by-species matrices.

Results

The two axes produced by principal component analyses of environmental variables explained 89.56% and 88.77% of variation across sampling sites for *R. dilectus* and *R. pumilio*, respectively. For *R. dilectus*, E1 correlated negatively with altitude and positively with minimal air temperature, winter precipitation, and spring and winter NDVI, whereas E2 correlated negatively with mean air temperatures and positively with summer precipitation (see details in Supplementary Material, Table S1). For *R. pumilio*, E1 represented mainly an increase in precipitation (in all seasons) and summer and autumn NDVI and a decrease in maximal air temperature, whereas E2 represented an increase in minimal air temperature and a decrease in altitude (see details in Supplementary Material, Table S1).

Total beta diversity of helminth assemblages was 0.72 in *R. dilectus* and 0.62 in *R. pumilio*. Contribution of helminth species to total beta diversity ranged from 0.001 to 0.17 in *R. dilectus* and from 0.002 to 0.19 in *R. pumilio* being, on average, 0.038 and 0.062, respectively. Contribution of approximately 40% of helminths harbored by *R. dilectus* (10 of 26 species) and 50% of helminths harbored by *R. pumilio* (eight of 16 species) to beta diversity was greater than average. Results of beta-regressions analyses showed that contribution of helminth species parasitic in both hosts to beta diversity significantly increased with characteristic prevalence of these species (Table 1, Fig. 1), whereas mean abundance, type of life cycle, and location in the host's gut had no effect on SCBD.

Site contributions to beta diversity ranged from 0.07 to 0.18 and from 0.05 to 0.19 in helminth assemblages of *R. dilectus* and *R. pumilio*, respectively. Above-average (0.12 and 0.10, respectively) contribution to beta diversity was found in four of 10 assemblages of both hosts. LCBD of helminth assemblages was significantly negatively correlated with both environmental factors in both *R. dilectus* and E1 in *R. pumilio* (Table 2, see illustrative example with E1 in Fig. 2). No effect of density of *Rhabdomys* spp. or total rodent species richness in a site on LCBD was found (Table 2). In *R. dilectus*, LCBD of helminth assemblage did not depend on the biome in which this assemblage resided. On the contrary, helminth assemblages of *R. pumilio* inhabiting fynbos contributed significantly less to total beta diversity than assemblages from the Succulent and Nama Karoo (Tukey's HSD tests, $p < 0.001$; Fig. 3).

Significant and negative associations between LCBD of local helminth assemblages of *R. dilectus* and *R. pumilio* and spatial variables were found for PCNMs 2 and 1, respectively (Table 2). Distribution of PCNMs and their values together with values of LCBD is presented in Fig. 4.

Discussion

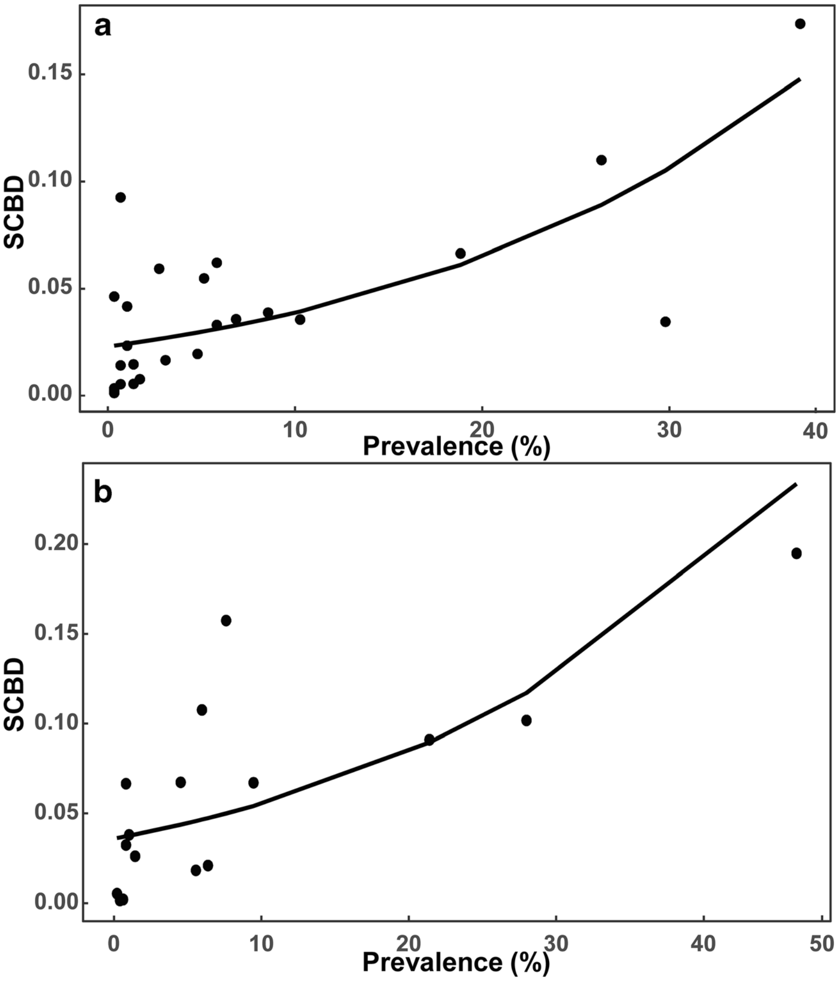
Contrary to our expectation, total beta diversity, variation in both SCBD and LCBD of helminths and their associations with species traits and environmental, host-associated and spatial variables were similar between the two rodent species. Furthermore, we found a positive association between helminth species prevalence and its SCBD, whereas LCBD of a component helminth community was mainly driven by environmental, but not host-associated factors and demonstrated spatial structure at broad scale.

Positive association between prevalence and SCBD means that highly (on average) prevalent helminths tended to contribute more to total beta diversity than less prevalent helminths. Species with high mean prevalence also demonstrated high occupancy in terms of sampling sites in which they were recorded (correlation between mean prevalence and proportion of sites where a given species was found was 0.67 and 0.76 for helminths of *R. dilectus* and *R. pumilio*, respectively). Positive (either curvilinear or linear) relationship between site occupancy and SCBD has also been found for stream insects by Heino and Grönroos (2017). They argue that this

Table 1 Summary of beta-regression analyses of the effect of continuous (prevalence and mean abundance) and categorical (life cycle and location in host's gut) traits of helminth species harbored by *R. dilectus* (RD) and *R. pumilio* (RP) on their contributions to beta diversity (SCBD). Variable "life cycle" was represented by two categories (direct (D) and indirect (I)) and variable "location in host's gut" by three categories for *R. dilectus* (stomach (ST), small intestine (SI), and cecum/colon (CC)) and two categories (SI and CC) for *R. pumilio*. $^*p < 0.01$

Host	Predictor	Estimate ± SE	z	Pseudo-r^2 of a model
RD	Prevalence	0.05 ± 0.001*	3.20*	
	Mean abundance	0.01 ± 0.02	0.49	
				0.32
	Life cycle (D)	0.13 ± 0.32	0.39	0.006
	Location in the gut (SI/ST)	0.74 ± 0.49/0.43 ± 0.53	1.51/1.81	0.30
RP	Prevalence	0.05 ± 0.02*	2.87*	
	Mean abundance	− 0.002 ± 0.003	− 0.73	
				0.35
	Life cycle (D)	0.54 ± 0.42	1.26	0.07
	Location in the gut (SI)	0.20 ± 0.55	0.35	0.008

Fig. 1 Relationships between the contribution to total beta diversity of helminth species (SCBD) harbored by *R. dilectus* (**a**) and *R. pumilio* (**b**) and their characteristic prevalence



relationship may arise from a positive relationship between abundance and occupancy, so that species showing high occupancy are also characterized by high local abundance and a large variation in abundance across sites which, in turn, results in high SCBD values. Vilmi et al. (2017) reported similar results for diatom communities, emphasizing the importance of common species for beta diversity (see also Krasnov et al. 2018 for fleas). Nevertheless, mean abundance of a helminth species was not associated with SCBD despite a positive relationship between prevalence and mean abundance ($r = 0.80$ and $r = 0.76$ for *R. dilectus* and *R. pumilio*, respectively; see also Morand and Guégan 2000). Moreover, examination of the distribution of data points in Fig. 1 suggests that highly prevalent helminths generally demonstrated high SCBD, while SCBD of less prevalent helminths varied from low to high. Life histories of the majority of helminth species are unknown, so it is difficult to provide more detailed explanations.

Neither the type of life cycle nor pattern of host exploitation was found to affect SCBD. This can be explained by the fact that a given life cycle (direct or indirect) or the preferable microhabitat inside the host's gut is shared by multiple helminth species with either high or low SCBD. Although the helminth species with the highest SCBD in both *R. dilectus* and *R. pumilio* was a nematode with a direct life cycle (*Neoheligmonella capensis* and *Heligmonina spira*, respectively), helminth species with lower SCBD in both hosts were those with direct and indirect life cycles. Regarding preferred within-host microhabitat, small intestine and stomach in *R. dilectus* and small intestine and cecum/colon in *R. pumilio* were infected by helminths with either higher or lower SCBD.

LCBD of helminth assemblages appeared to be determined mainly by environmental factors, whereas density of the hosts or diversity of host communities did not have any effect. Significant relationships between LCBD and environmental variables were previously found in studies of LCBD for communities of free-living species (Heino and Grönroos 2017; Vilmi et al. 2017; da Silva et al. 2018; Landeiro et al. 2018) and parasites (Poisot et al. 2017; but see Krasnov et al. 2018). In general, higher LCBD of helminth assemblages were associated with sites situated at higher altitude, higher maximal but lower mean and minimal air temperatures, lower precipitation, and smaller amount of green vegetation. These environmental

Table 2 Summary of beta-regression analyses of the effect of environmental variables [continuous—model E, categorical (biome)—model B], host-associated variables (model H), and spatial variables (model SP) on contributions of helminth assemblages harbored by *R. dilectus* (RD) and *R. pumilio* (RP) to beta diversity (LCBD). Environmental variables were the first two principal components (E1 and E2; see text for explanations). Host-associated variables were density of a *Rhabdomys* species (DR) and total rodent species richness (RSR). Spatial variables were represented by positive eigenvectors (PCNMs) calculated from distances between regions (see text for explanations). Variable "biome" was represented by three categories for *R. dilectus* (Grassland (GL), Savanna (SV), Albany Thicket (AT)) or *R. pumilio* (Succulent Karoo (SK), Nama Karoo (NK), Fynbos (F)). *$p < 0.01$

Host	Model	Predictor	Estimate ± SE	z	Pseudo-r^2 of a model
RD	E	E1	− 0.23 ± 0.08*	− 2.92*	
		E2	− 0.15 ± 0.07	− 2.14*	
					0.61
	H	DR	0.04 ± 0.14	0.30	
		RSR	0.04 ± 0.09	0.48	
					0.03
	SP	PCNM1	0.25 ± 0.21	1.16	
		PCNM2	− 0.80 ± 0.20*	− 4.07*	
		PCNM7	0.13 ± 0.18	0.46	
					0.66
		Biome (GL/SV)	− 0.14 ± 0.25/0.20 ± 0.26	− 0.58/077	
RP	E	E1	− 0.40 ± 0.13*	− 3.13*	
		E2	− 0.17 ± 0.12	− 1.32	
					0.61
	H	DR	− 0.08 ± 0.10	− 0.82	
		RSR	0.01 ± 0.10	0.10	
					0.08
	SP	PCNM1	− 1.27 ± 0.30*	− 4.18*	
		PCNM2	0.20 ± 0.26	0.77	
		PCNM6	0.05 ± 0.37	0.14	
					0.67
		Biome (NK/SK)	1.26 ± 0.16*/0.94 ± 0.12*	7.77*/7.64*	0.008

factors unlikely affect adult helminths residing in a host's gut but undoubtedly can influence free-living infective stages (e.g., eggs and/or larvae) as well as intermediate hosts of species with indirect life cycles. In particular, free-living infective stages of directly transmitted nematodes are susceptible to desiccation (Stromberg 1997) and as a result the occurrence and distribution of these nematodes have been associated with environmental conditions such as precipitation (Froeschke et al. 2010), relative humidity (Dybing et al. 2013), and vegetation cover (Dybing et al. 2013). For example, the environmental factors that influence the occurrence of helminth species in red foxes (*Vulpes vulpes*) varied within taxonomic groups (e.g., nematodes) with the percentage of native vegetation cover being the most important for *Toxocara canis*, while *Toxascaris leonina* was affected mainly by average humidity (Dybing et al. 2013). In addition, a comparative habitat type study on rodents (*Mastomys natalensis* and *Mastomys erythroleucus*) in Senegal, recorded distinctly different habitat types for the two most abundant and prevalent nematodes (*Neoheligmonella* sp. and *Trichuris* sp.). A significantly higher prevalence was recorded for *Neoheligmonella* sp. in high-cover natural savanna vegetation compared to low-cover rural villages, while the opposite was true for *Trichuris* sp. (Brouat et al. 2007). Vegetation cover and type also influence the distribution of arthropods, which often act as intermediate hosts (Procheş and Cowling 2007; Botha et al. 2016), and this would explain the importance of vegetation related variables in the distribution of helminths with indirect life cycles (Torre et al. 2013). Moreover, eggs, infective larval stages or intermediate hosts of different helminth species may tolerate environmental conditions differently.

Species-specific variation in environmental tolerance ranges may explain why helminth assemblages in *R. pumilio* in Karoo-like vegetation contributed more to LCBD compared to assemblages in Fynbos. Environmental conditions associated with the Succulent and Nama Karoo are characterized by lower annual rainfall (224.2 mm and 267.8 mm, respectively) than Fynbos (505.5 mm). In addition, vegetation cover is also generally sparser in the former two compared to the latter (Cramer and Hoffman 2015). These environmental conditions may not be suitable for many helminth species, especially those with free-living stages. Those species that

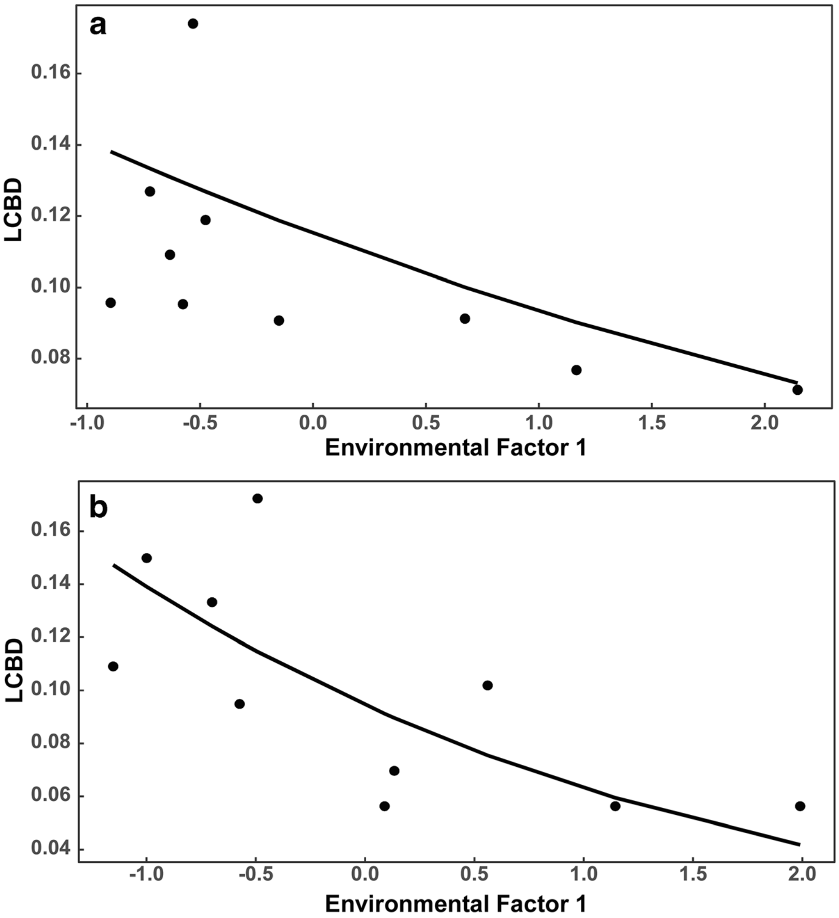


Fig. 2 Relationship between the contribution of local helminth assemblages of *R. dilectus* (**a**) and *R. pumilio* (**b**) to total beta diversity (LCBD) and the first principal component of environmental variables (environmental factor 1)

are able to survive in harsher conditions are likely more specialized (e.g., prefer specific environmentally adapted intermediate hosts) and are adapted to extreme climates. In the present study, four of the six helminth species that occur in the north-eastern Karoo-like assemblages are cestodes with indirect life cycles (*Raillietina trapezoides*, *Meggittina baeri*, *Skrjabinotaenia occidentalis*, and an unknown *Skrjabinotaenia* sp.) and the remaining two species were nematodes that may be self-transmitted through coprophagy and/or grooming (*Syphacia* sp. and *Aspiculuris shikoloueta*). Other species such as *R. trapezoides* seem to persist in a dry and arid environment and are harbored by multiple desert adapted rodent hosts (Faleh et al. 2012). Excepting *Syphacia* sp., *A. shikoloueta*, and *R. trapezoides*, the abovementioned helminths were absent from the Fynbos assemblages. The absence of a significant effect of a biome on LCBD in *R. dilectus* may be due to more similar environmental conditions in the three occupied biomes (Grassland, Savanna, and Albany Thicket) as evident in their mean annual rainfall (619.1, 626.3, and 812.2 mm, respectively) and overall high vegetation cover (Cramer and Hoffman 2015).

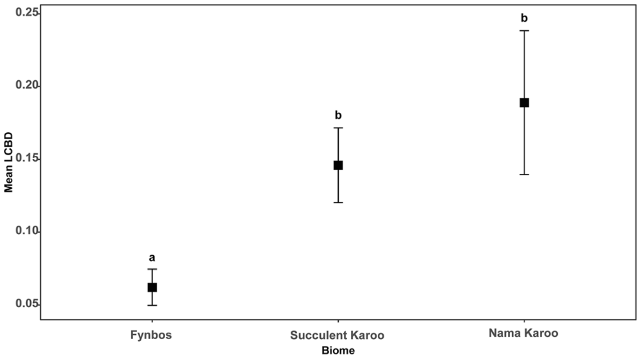


Fig. 3 Mean contributions of local helminth assemblages harbored by *R. pumilio* and situated in different biomes to total beta diversity (LCBD). Letters denote significant differences

In addition, environmental factors may affect helminth communities via their effect on host individuals or populations. For example, food availability that undoubtedly differs under different environmental conditions may affect the immunity of the hosts (Vestey et al. 1993; Krasnov et al. 2005). Variation in food availability may also lead to among-site variation in rodent mobility and home range size (Schradin and Pillay 2006) which, in turn, may cause among-site differences in spatial distribution of helminth eggs and/or larvae and, consequently, to higher or lower LCBD. As mentioned above, we did not find any effect of host density or species richness of host community on LCBD of helminth assemblages. One of the reasons for this can be

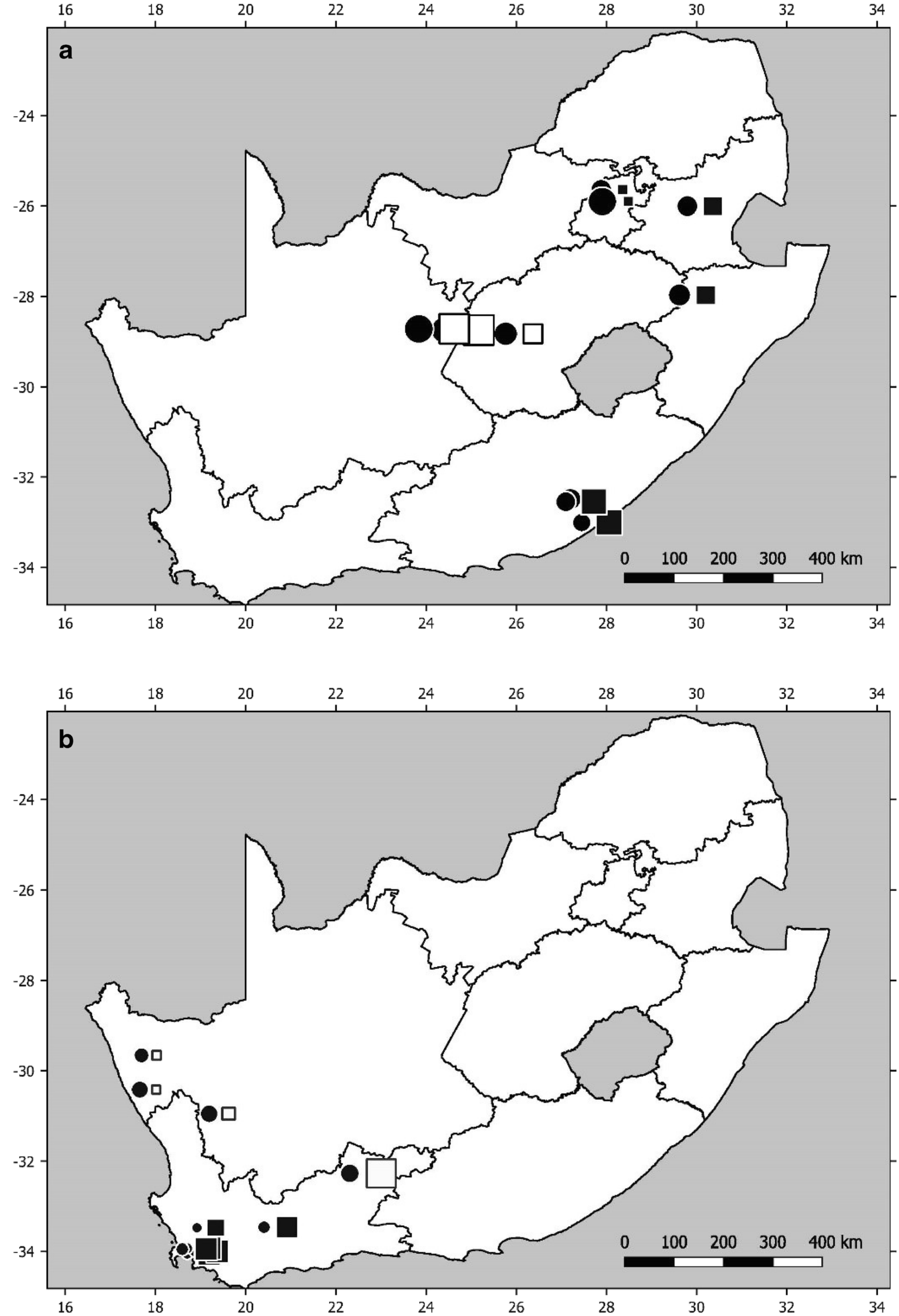


Fig. 4 Map of values of the PCNM variables (squares) and LCBD (circles) of helminth assemblages of *R. dilectus* (**a**, PCNM2) and *R. pumilio* (**b**, PCNM1). Sizes of squares and circles are proportional to values. Black squares—positive values of PCNM, white squares—negative values of PCNM

strong effects of environmental factors that might mask host-associated effects. Nevertheless, some host-associated factors can affect helminth diversity. For example, alpha diversity of helminth infracommunities (i.e., in an individual host) in *Rhabdomys* spp. has been shown to be affected by host reproductive status (slightly higher in reproducing animals) but not host sex (Spickett et al. 2017b). The effect of host-associated factors on beta diversity is less clear, although some indirect evidence suggested that spatial variation in helminth species composition could, to some extent, be driven by host spatial behavior (Spickett et al. 2017a).

Earlier studies on the contribution of ectoparasite assemblages to beta diversity produced contrasting results. Poisot et al. (2017) found that LCBD of flea assemblages were mainly affected by environmental factors, whereas Krasnov et al. (2018) showed that the effect of host species composition on flea LCBD was much stronger than that of the environment. Substantial difference in analytical approach could be the main reason behind this discrepancy (see discussion in Krasnov et al. 2018). Contrary to Poisot et al. (2017) and Krasnov et al. (2018) that considered the entire pool of parasites exploiting the entire pool of hosts in a region, here we focused on parasite assemblages of the same host species (= component communities). Consequently, the effect of the surrounding host community on LCBD of component parasite communities could be much weaker (if any) than in the case of compound communities.

Spatial patterns in LCBD can be, at least partly, explained by spatial structure of environmental gradients. For example, examination of Fig. 4a allows one to envisage a west-east and a north-south gradient of LCBD for helminth communities of *R. dilectus* with predominantly north-western assemblages contributing more than predominantly south-eastern assemblages to beta diversity. This suggests that, for example, north-western helminth assemblages comprised of species either absent from, or less prevalent in other assemblages. For example, *Heligmonina boomkeri* was recorded in the northern and north-eastern populations (Gauteng and KwaZulu-Natal (Grassland vegetation)) but was absent from the south-eastern populations of *R. dilectus* (Albany Thicket vegetation). Similarly, Fig. 4b illustrates a north-south gradient of LCBD for helminth assemblages of *R. pumilio* with generally higher LCBD of more northern assemblages (except for an easternmost outlier). This may result from species assemblages from northern populations that are relatively more unique than those of southern populations. For example, *H. spira* and *N. capensis* were never recorded in helminth assemblages of northern (Karoo-like vegetation) populations, but both were highly prevalent in almost all southern populations (Fynbos vegetation). Moreover, the gradient of LCBD seems to be more pronounced for helminth communities of *R. pumilio* than for *R. dilectus*, likely due to a sharp north-south increase of precipitation (from 17 mm/year in the north to 73.58 mm/year in the south for *R. pumilio* vs 59.94 mm/year in the north to 65.06 mm/year in the south for *R. dilectus*) and NDVI (from 0.25 in the north to 0.54 in the south for *R. pumilio* vs 0.44 in the north to 0.65 in the south for *R. dilectus*) throughout most of the distribution of the former than the latter host (see also Cramer and Hoffman 2015).

In conclusion, SCBD of a helminth species could be predicted from its infection parameters, but not from life history traits. Counterintuitively, LCBD of an assemblage of intestinal helminths could be predicted from the climatic conditions and vegetation of the surrounding environment. Comparison of our results to that of a similar study on ectoparasites (Krasnov et al. 2018) suggests that predictors of variation in SCBD and LCBD may substantially differ between parasites of different life history and/or parasite communities at different hierarchical scales.

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Data accessibility The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

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Compliance with ethical standards

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

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (Stellenbosch University - Research Ethics Committee: Animal Care and Use, permit numbers 2006B01007 and SU-ACUM11-00004 and Onderstepoort Veterinary Institute - Animal Ethics Committee, permit number AEC32.11).

References

Altman I, Byers JE (2014) Large-scale spatial variation in parasite communities influenced by anthropogenic factors. Ecology 95:1876–1887. https://doi.org/10.1890/13-0509.1

Anderson RC (2000) Nematode parasites of vertebrates. Their development and transmission, 2nd edn. CABI, Wallingford

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol Lett 14:19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Arneberg P, Skorping A, Read AF (1997) Is population density a species character? Comparative analyses of the nematode parasites of mammals. Oikos 80:289–300. https://doi.org/10.2307/3546597

Biguezoton A, Adehan S, Adakal H, Zoungrana S, Farougou S, Chevillon C (2016) Community structure, seasonal variations and interactions between native and invasive cattle tick species in Benin and Burkina Faso. Parasit Vectors 9:43. https://doi.org/10.1186/s13071-016-1305-z

Blasco-Costa I, Waters JM, Poulin R (2012) Swimming against the current: genetic structure, host mobility and the drift paradox in trematode parasites. Mol Ecol 21:207–217. https://doi.org/10.1111/j.1365-294X.2011.05374.x

Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol Model 153:51–68. https://doi.org/10.1016/S0304-3800(01)00501-4

Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R, 2nd edn. Springer, New York. https://doi.org/10.1007/978-3-319-71404-2

Botha M, Siebert SJ, van den Berg J (2016) Do arthropod assemblages fit the grassland and savanna biomes of South Africa? S Afr J Sci 112:1–10. https://doi.org/10.17159/sajs.2016/20150424

Brouat C, Kane M, Diouf M, Bâ K, Sall-Dramé R, Duplantier JM (2007) Host ecology and variation in helminth community structure in *Mastomys* rodents from Senegal. Parasitology 134:437–450. https://doi.org/10.1017/S003118200600151X

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583. https://doi.org/10.2307/3284227

Cramer MD, Hoffman MT (2015) The consequences of precipitation seasonality for Mediterranean-ecosystem vegetation of South Africa. PLoS One 10:1–21. https://doi.org/10.1371/journal.pone.0144512

Cribari-Neto F, Zeileis A (2010) Beta regression in R. J Stat Softw 34:1–24. https://doi.org/10.18637/jss.v034.i02

da Silva PG, Hernández MIM, Heino J (2018) Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. Divers Distrib 24:1674–1686. https://doi.org/10.1111/ddi.12785

Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guenard G, Jombart T, Larocque G, Legendre P, Madi N, Wagner HH (2018) adespatial: multivariate multiscale spatial analysis. R package version 0.2–0. https://CRAN.R-project.org/package=adespatial

du Toit N, Jansen van Vuuren B, Matthee S, Matthee CA (2012) Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia: Muridae) from southern Africa with implications for taxonomy. Mol Phylogenet Evol 65:75–86. https://doi.org/10.1016/j.ympev.2012.05.036

Dufour CMS, Meynard C, Watson J, Rioux C, Benhamou S, Perez J, du Plessis JJ, Avenant N, Pillay N, Ganem G (2015) Space use variation in co-occurring sister species: Response to environmental variation or competition? PLoS One 10:1–15

Dybing NA, Fleming PA, Adams J (2013) Environmental conditions predict helminth prevalence in red foxes in Western Australia. Int J Parasitol Parasites Wildl 2:165–172. https://doi.org/10.1016/j.ijppaw.2013.04.004

Ellison AM (2010) Partitioning diversity. Ecology 91:1962–1963. https://doi.org/10.1890/09-1692.1

Ezenwa VO (2004) Host social behavior and parasitic infection: a multifactorial approach. Behav Ecol 15:446–454. https://doi.org/10.1093/beheco/arh028

Faleh AB, Annabi A, López S, Said K, Ribas A (2012) On the helminth parasites of the genus *Jaculus* (Rodentia: Dipodidae) in Tunisia: a preliminary survey study. Leb Sci J 13:107–110

Froeschke G, Harf R, Sommer S, Matthee S (2010) Effects of precipitation on parasite burden along a natural climatic gradient in southern Africa – implications for possible shifts in infestation patterns due to global changes. Oikos 119:1029–1039. https://doi.org/10.1111/j.1600-0706.2009.18124.x

Galbreath KE, Hoberg EP (2012) Return to Beringia: parasites reveal cryptic biogeographic history of North American pikas. Proc R Soc Lond B Biol 279:371–378. https://doi.org/10.1098/rspb.2011.0482

Guernier V, Hochberg ME, Guégan JF (2004) Ecology drives the worldwide distribution of human infectious diseases. PLoS Biol 2:e186. https://doi.org/10.1371/journal.pbio.0020186

Harrison S, Ross SJ, Lawton JH (1992) Beta-diversity on geographic gradients in Britain. J Anim Ecol 61:151–158. https://doi.org/10.2307/5518

Haukisalmi V, Hardman LM, Fedorov VB, Hoberg EP, Henttonen H (2016) Molecular systematics and Holarctic phylogeography of cestodes of the genus *Anoplocephaloides* Baer, 1923 s. s. (Cyclophyllidea, Anoplocephalidae) in lemmings (*Lemmus*, *Synaptomys*). Zool Scr 45:88–102. https://doi.org/10.1111/zsc.12136

Haukisalmi V, Ribas A, Junker K, Spickett A, Matthee S, Henttonen H, Jrijer J, Halajian A, Ander JL, Nakao M (2018) Molecular systematics and evolutionary history of catenotaeniid cestodes (Cyclophyllidea). Zool Scr 47:221–230. https://doi.org/10.1111/zsc.1227

Heino J, Grönroos M (2017) Exploring species and site contributions to beta diversity in stream insect assemblages. Oecologia 183:151–160. https://doi.org/10.1007/s00442-016-3754-7

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. https://doi.org/10.1002/joc.1276

Hoberg EP, Brooks DR (2015) Evolution in action: climate change, biodiversity dynamics and emerging infectious disease. Philos Trans R Soc B 370:20130553. https://doi.org/10.1098/rstb.2013.0553

Krasnov BR, Shenbrot GI, Khokhlova IS, Degen AA (2004) Flea species richness and parameters of host body, host geography and host "milieu". J Anim Ecol 73:1121–1128. https://doi.org/10.1111/j.0021-8790.2004.00883.x

Krasnov BR, Khokhlova IS, Arakelyain MS, Degen AA (2005) Is a starving host tastier? Reproduction in fleas parasitizing food-limited rodents. Funct Ecol 19:625–631. https://doi.org/10.1111/j.1365-2435.2005.01015.x

Krasnov BR, Mouillot D, Shenbrot GI, Khokhlova IS, Poulin R (2010) Deconstructing spatial patterns in species composition of ectoparasite communities: the relative contribution of host composition, environmental variables and geography. Glob Ecol Biogeogr 19:515–526. https://doi.org/10.1111/j.1466-8238.2010.00529.x

Krasnov BR, Shenbrot GI, Warburton EM, van der Mescht L, Surkova EN, Medvedev SG, Pechnikova N, Ermolova N, Kotti BK, Khokhlova IS (2018) Species and site contributions to beta diversity in fleas parasitic on the Palearctic small mammals: ecology, geography and host species composition matter the most. Parasitol 146:653–661. https://doi.org/10.1017/S0031182018001944

Landeiro VL, Franz B, Heino J, Siqueira T, Bini LM (2018) Species-poor and low-lying sites are more ecologically unique in a hyperdiverse Amazon region: evidence from multiple taxonomic groups. Divers Distrib 24:966–977. https://doi.org/10.1111/ddi.12734

Legendre P (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. J Plant Ecol 1:3–8. https://doi.org/10.1093/jpe/rtm001

Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. Glob Ecol Biogeogr 23:1324–1334. https://doi.org/10.1111/geb.12207

Legendre P, de Cáceres M (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol Lett 16: 951–963. https://doi.org/10.1111/ele.12141

Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecol Monogr 75:435–450. https://doi.org/10.1890/05-0549

Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. J Anim Ecol 70:966–979. https://doi.org/10.1046/j.0021-8790.2001.00563.x

Lenth R (2019) emmeans: estimated marginal means, aka least-squares means. R package version 1.3.2. https://CRAN.R-project.org/package=emmeans

Lindenfors P, Nunn CL, Jones KE, Cunningham AA, Sechrest W, Gittleman JL (2007) Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. Glob Ecol Biogeogr 16:496–509. https://doi.org/10.1111/j.1466-8238.2006.00301.x

Littlewood DT, Curini-Galletti M, Herniou EA (2000) The interrelationships of Proseriata (Platyhelminthes: Seriata) tested with molecules and morphology. Mol Phylogenet Evol 16:449–466. https://doi.org/10.1006/mpev.2000.0802

Lockyer AE, Olson PD, Littlewood DTJ (2003) Utility of complete large and small subunit rRNA genes in resolving the phylogeny of the Neodermata (Platyhelminthes): implications and a review of the cercomer theory. Biol J Linn Soc 78:155–171. https://doi.org/10.1046/j.1095-8312.2003.00141.x

Morand S, Guégan JF (2000) Distribution and abundance of parasite nematodes: Ecological specialisation, phylogenetic constraint or simply epidemiology? Oikos 88:563–573. https://doi.org/10.1034/j.1600-0706.2000.880313.x

Morand S, Krasnov BR (eds) (2010) The biogeography of host-parasite interactions. Oxford Univ. Press, Oxford

Morgan BB, Hawkins PA (1951) Veterinary helminthology. Burgess Publishing Company, Minneapolis

Oksanen J, Blanchet G, Friendly M, Kindt P, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) vegan: community ecology package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290. https://doi.org/10.1093/bioinformatics/btg412

Poisot T, Guéeveneux-Julien C, Fortin M-J, Gravel D, Legendre P (2017) Hosts, parasites and their interactions respond to different climatic variables. Glob Ecol Biogeogr 26:242–251. https://doi.org/10.1111/geb.12602

Poulin R (2003) The decay of similarity with geographical distance in parasite communities of vertebrate hosts. J Biogeogr 30:1609–1615. https://doi.org/10.1046/j.1365-2699.2003.00949.x

Poulin R (2006) Variation in infection parameters among populations within parasite species: intrinsic properties versus local factors. Int J Parasitol 36:877–885. https://doi.org/10.1016/j.ijpara.2006.02.021

Poulin R, Guégan J-F (2000) Nestedness, anti-nestedness and the relationship between prevalence and intensity in ectoparasite assemblages of marine fish: a special model of species coexistence. Int J Parasitol 30:1147–1152. https://doi.org/10.1016/S0020-7519(00)00102-8

Procheş Ş, Cowling R (2007) Do insect distributions fit our biomes? S A J Sci 103:258–261

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/

Rambau RV, Robinson TJ, Stanyon R (2003) Molecular genetics of *Rhabdomys pumilio* subspecies boundaries: mtDNA phylogeography and karyotypic analysis by fluorescence in situ hybridization. Mol Phylogenet Evol 28:564–575. https://doi.org/10.1016/S1055-7903(03)00058-7)

Schradin C, Pillay N (2005) Intraspecific variation in the spatial and social organization of the African striped mouse. J Mammal 86: 99–107. https://doi.org/10.1644/1545-1542(2005)086<0099:IVITSA>2.0.CO;2

Schradin C, Pillay N (2006) Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. Behav Ecol 17:452–458. https://doi.org/10.1093/beheco/arj04

Skinner JD, Chimimba CT (2005) The mammals of the southern African subregion, 3rd edn. Cambridge University Press, Cape Town

Spickett A, Junker K, Krasnov BR, Haukisalmi V, Matthee S (2017a) Intra- and interspecific similarity in species composition of helminth communities in two closely-related rodents from South Africa. Parasitology 144:1211–1220. https://doi.org/10.1017/S003118201700049X

Spickett A, Junker K, Krasnov BR, Haukisalmi V, Matthee S (2017b) Helminth parasitism in two closely related South African rodents: abundance, prevalence, species richness and impinging factors. Parasitol Res 116:1395–1409. https://doi.org/10.1007/s00436-017-5419-9

Spickett A, Junker K, Krasnov BR, Haukisalmi V, Matthee S (2017c) Community structure of helminth parasites in two closely related South African rodents differing in sociality and spatial behaviour. Parasitol Res 116:2299–2312. https://doi.org/10.1007/s00436-017-5538-3

Stromberg BE (1997) Environmental factors influencing transmission. Vet Parasitol 72:247–264. https://doi.org/10.1016/S0304-4017(97)00100-3

Stuart C, Stuart T (2007) Field guide to mammals of southern Africa, revised edition. Struik Nature, Cape Town

Tonkin JD, Heino J, Sundermann A, Haase P, Jähnig SC (2016) Context dependency in biodiversity patterns of central German stream metacommunities. Freshw Biol 61:607–620. https://doi.org/10.1111/fwb.12728

Torre I, Arrizabalaga A, Feliu C, Ribas A (2013) The helminth infracommunities of the wood mouse (*Apodemus sylvaticus*) two years after the fire in Mediterranean forests. Helminthologia 50(1): 27–38.https://doi.org/10.2478/s11687-013-0104-8

van der Mescht L (2011) Ectoparasite assemblage of the four-striped mouse, *Rhabdomys pumilio*: the effect of anthropogenic habitat transformation and temporal variation. Stellenbosch University, MSc Dissertation

van Schaik J, Kerth G (2017) Host social organization and mating system shape parasite transmission opportunities in three European bat species. Parasitol Res 116:589–599. https://doi.org/10.1007/s00436-016-5323-8

Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol 85:183–206. https://doi.org/10.1086/652373

Vestey MR, McMurry ST, Lochmiller RL (1993) Influence of dietary protein on selected measures of humoral and cellular immunity in the cotton rat *Sigmodon hispidus*. Can J Zool 71:579–586. https://doi.org/10.1139/z93-079

Vilmi A, Karjalainen SM, Heino J (2017) Ecological uniqueness of stream and lake diatom communities shows different macroecological patterns. Divers Distrib 23:1042–1053. https://doi.org/10.1111/ddi.12594

von Nickisch-Rosenegk M, Brown WM, Boore JL (2001) Complete sequence of the mitochondrial genome of the tapeworm *Hymenolepis diminuta*: gene arrangements indicate that platyhelminths are eutrochozoans. Mol Biol Evol 18:721–730. https://doi.org/10.1093/oxfordjournals.molbev.a003854

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30:279–338. https://doi.org/10.2307/1943563

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251. https://doi.org/10.2307/1218190

Williams PH (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. Proc R Soc B 263:579–588. https://doi.org/10.1098/rspb.1996.0087

Yamaguti S (1961) Systema helminthum. III. The nematode parasites of vertebrates, part I. Interscience Publishers, New York

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7–10 https://CRAN.R-project.org/doc/Rnews/