

Searching for common patterns in parasite ecology: species and host contributions to beta-diversity in helminths of South African ungulates and fleas of South American rodents

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Highlights

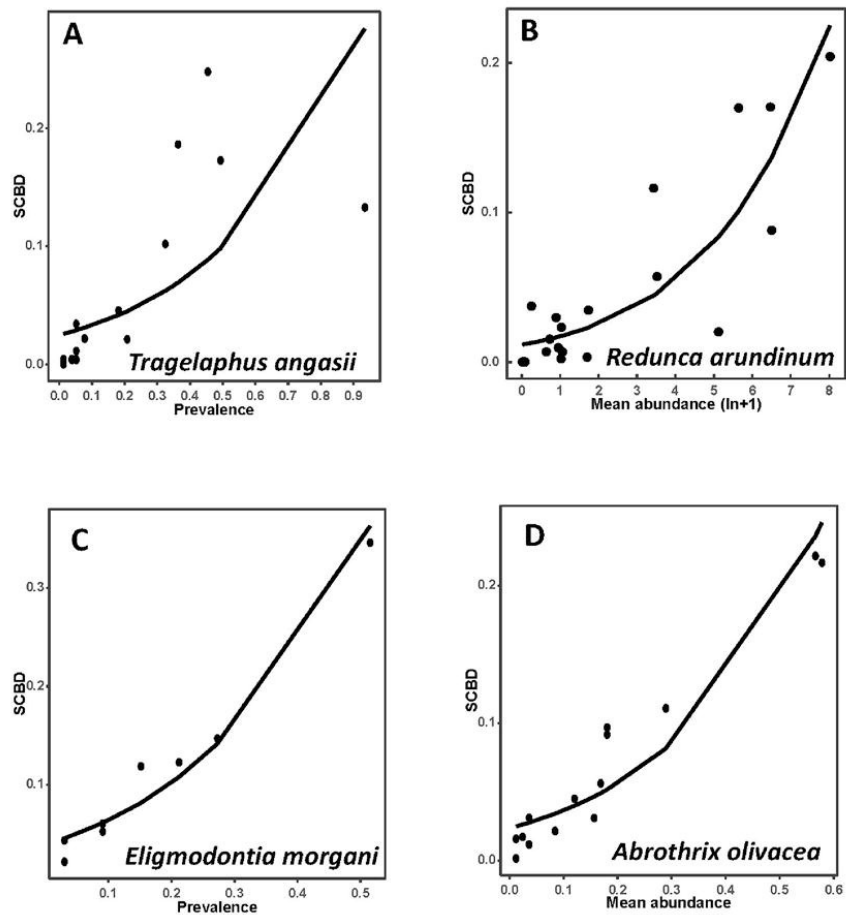
- Morphological and ecological attributes of parasite species did not contribute to parasite beta-diversity.
- Contribution of parasite species to their beta-diversity depended on mean abundance and/or prevalence.
- The effect of host sex or age on their contribution to parasite beta-diversity was detected in a few species only.

Abstract

We searched for common patterns in parasite ecology by investigating species and host contributions to the beta-diversity of infracommunities (=assemblages of parasites harboured by a host individual) in helminths of three species of South African ungulates and fleas of 11 species of South American rodents, assuming that a comparison of patterns in distinctly different parasites and hosts would allow us to judge the generality or, at least, commonness of these patterns. We used data on species' composition and numbers of parasites and asked whether (i) parasite species' attributes (life cycle, transmission mode, and host specificity in helminths; possession of sclerotized combs, microhabitat preference, and host specificity in fleas) or their population structure (mean abundance and/or prevalence) and (ii) host characteristics (sex and age) affect parasite and host species' contributions to parasite beta-diversity (SCBD and HCBD, respectively). We found that parasite species' morphological and ecological attributes were mostly not associated with their SCBD. In contrast, parasite SCBD, in both ungulates and rodents, significantly increased with either parasite mean abundance or prevalence or both. The effect of host characteristics on HCBD was detected in a few hosts only. In general, parasite infracommunities' beta-diversity appeared to be driven by variation

in parasite species rather than the uniqueness of the assemblages harboured by individual hosts. We conclude that some ecological patterns (such as the relationships between SCBD and parasite abundance/prevalence) appear to be common and do not differ between different host-parasite associations in different geographic regions, whereas other patterns (the relationships between SCBD and parasite species' attributes) are contingent and depend on parasite and host identities.

Graphical abstract



Keywords: Beta-diversity; Contribution; Parasites; Hosts; Helminths; Fleas; Ungulates; Rodents

1. Introduction

One of the most important tasks of any scientific discipline is to reveal general rules that can explain a broad range of facts and phenomena. Ecology is a young science compared, for example, with physics or chemistry. Moreover, ecological systems are enormously complex and affected by multiple extrinsic and intrinsic factors. Even so, some general rules, patterns, and laws determining the abundance, distribution, and diversity of living organisms have been revealed, mainly in the past 50 years (e.g., Brown, 1995, Rosenzweig, 1995, Gaston, 2003, Vandermeer and Goldberg, 2013). Although interest in parasites as agents causing diseases in humans, livestock, and wildlife has a long history, parasite ecology has fallen somewhat behind the ecology of free-living organisms. One of the reasons for this is that parasitism as a consumer strategy originated independently in multiple plant and animal lineages and, often, several times in the same lineage (Poulin, 2007a). As a result, parasites appear in an enormous variety of forms, belonging to different taxa and differing in their origin, patterns of parasitism, and life histories, and they represent a large (if not the largest) proportion of global biodiversity (Windsor, 1998, Dobson et al., 2008, Carlson et al., 2020). Nevertheless, the past three decades have witnessed an outpouring of studies on the ecology of various parasite taxa (Poulin, 2021). This paved the way for one of the first attempts to elucidate general rules governing parasite ecology, undertaken by Poulin (2007b), who concluded that general laws likely exist at the level of parasite populations and host-parasite interaction networks, but that patterns characteristic at the level of parasite communities do not appear to be universal.

The search for common patterns in parasite ecology is usually carried out by reviewing the results of different studies (e.g., Poulin, 2007b, Morand, 2015) or as formal meta-analyses (e.g., Kamiya et al., 2014a, Kamiya et al., 2014b). Empirical studies have compared ecological patterns in different parasites often considered species belonging to the same higher taxon (e.g., Fantozzi et al., 2022) or those that have similar strategies of parasitism (e.g., intestinal helminths or haematophagous arthropods) in hosts belonging to the same (e.g., de Bellocq et al., 2003) or different taxonomic units (e.g., Dallas et al., 2019a, Dáttilo et al., 2020). Ecological patterns in parasites with distinctly different strategies of parasitism (e.g., ectoparasites and endoparasites) in substantially different hosts have been considered in the same study less often (e.g., Vázquez et al., 2005, Vázquez et al., 2007, Dallas et al., 2019b, Brian and Aldridge, 2021, Krasnov et al., 2021). However, elucidating common patterns in parasite ecology requires comparison of the same patterns between substantially different host-parasite associations.

Here, we searched for common patterns in parasite ecology by investigating parasite species and host contributions to the beta-diversity of parasite infracommunities (=assemblages of parasites harboured by a host individual). Beta-diversity is the measure of variability in the species composition of plant, animal, or microbial communities across space or time (Whittaker, 1960, Whittaker, 1972). In the case of parasite communities, beta-diversity reflects the difference in species identities and their numbers between infra-, component (=assemblage of all parasites harboured by a population of conspecific hosts), or compound (=assemblage of all parasites harboured by a host community) communities. Given that many infra-, component, and compound (the latter in case of taxonomically similar hosts across similar environments) communities obviously share many parasite species, the ultimate reasons behind the differences between communities are not always clear. It is commonly accepted that there are two main mechanisms producing these differences (Carvalho et al., 2012, Legendre and de Cáceres, 2013, Legendre, 2014; but see Baselga et al., 2007, Baselga, 2010). These mechanisms are (i) species replacement (=turnover), causing differences in species composition, and (ii) species gains/losses causing differences in species composition. This

suggests differential contributions of individual species and their assemblages to beta-diversity (Legendre and de Cáceres, 2013). To estimate the effects of species and their assemblages on beta-diversity, Legendre and de Cáceres (2013) proposed partitioning total beta-diversity into (i) species' contributions (SCBD; the degree of the relative importance of individual species for between-community differences) and (ii) local contributions (LCBD; the degree of the compositional uniqueness of a given assemblage relative to other assemblages). Studies of SCBD and LCBD in various communities of free-living species demonstrated that SCBD can be associated with species' traits, whereas LCBD can be associated with the environment in which a given community exists (Heino and Grönroos, 2017, da Silva et al., 2018, Xia et al., 2022).

The concept of beta-diversity partitioning into SCBD and LCBD has rarely been applied to parasite communities. Furthermore, SCBD and LCBD were mainly considered at the scale of parasite component (Biguezoton et al., 2016, Spickett et al., 2019) or compound (Poisot et al., 2017, Krasnov et al., 2019) communities. and only once at the scale of a single host species' infracommunities (Junker et al., 2023). In the latter case, LCBD can be renamed as HCBD (host contributions to beta-diversity) because it reflects the compositional uniqueness of parasite assemblages in individual hosts and, consequently, may depend on host characteristics similar to the dependence of classical LCBD on sampling sites' environmental characteristics (e.g., Poisot et al., 2017).

Here, we used data on species composition and numbers in the endoparasite (helminths) infracommunities of three species of ungulates from South Africa and the ectoparasite (fleas) infracommunities of 11 species of rodents from South America. We asked whether (i) parasite species attributes (life cycle, transmission mode, and host specificity in helminths and possession of sclerotized combs, microhabitat preference, and host specificity in fleas) or their population structure (mean abundance and/or prevalence) and (ii) host characteristics (sex and age) affect parasite species contributions and host contributions to beta-diversity (SCBD and HCBD, respectively).

2. Materials and methods

2.1. Data on parasite distribution among host individuals

We used data on helminths from three species of South African ungulates and fleas from 11 species of South American rodents (eight species from Patagonia and four species from northwestern Argentina). South African ungulates included the nyala (*Tragelaphus angasii*), common reedbeek (*Redunca arundinum*), and common warthog (*Phacochoerus africanus*). Patagonian rodents comprised the hairy soft-haired mouse (*Abrothrix hirta*), olive grass mouse (*Abrothrix olivacea*), Patagonian akodont (*Akodon iniscatus*), Morgan's gerbil mouse (*Eligmodontia morgani*), eastern Patagonian laucha (*Eligmodontia typus*), gray leaf-eared mouse (*Graomys griseoflavus*), yellow-rumped leaf-eared mouse (*Phyllotis xanthopygus*), and the bunny rat (*Reithrodon auritus*). Rodents from northwestern Argentina included the white-throated grass mouse (*Akodon simulator*), Spegazzini's akodont (*Akodon spegazzinii*), and Brenda's colilargo (*Oligoryzomys brendae*).

In South Africa, culling is a routine management process aimed at regulating wildlife populations. This provided an opportunity to obtain data on parasites of multiple wildlife species, which would have been otherwise unavailable. We used data collected during culling operations targeting the above-mentioned ungulate species. In particular, gastrointestinal

helminths of *T. angasii* and *R. arundinum* were investigated in three and two localities, respectively, in KwaZulu-Natal Province during 1983–1984 (see map in Supplementary Fig. S1), whereas helminths of *P. africanus* were collected in two localities in Mpumalanga and Limpopo Provinces during 1980–1981 and 1988–1989, respectively, as well as in one locality in KwaZulu-Natal Province in 2015 (see map in Supplementary Fig. S1). Details on sampling procedures and helminth recovery can be found in earlier publications (Horak et al., 1988, Boomker et al., 1989, Boomker et al., 1991a, Boomker et al., 1991b, Junker et al., 2019, Junker et al., 2022, Junker et al., 2023). Earlier, we used part of these data on helminths of *P. africanus* and considered a similar question (Junker et al., 2023). Here, we increased the dataset for this host with the assumption that this will produce more reliable results.

In South America, data on fleas parasitic on rodents were obtained from short-term (three consecutive nights) sampling carried out during 2005–2011 at 4–7 sampling sites per host species in Patagonia and 1998–2013 at 5–7 sampling sites per host species in northwestern Argentina (see maps in Supplementary Figs. S2–S3). Similar to the South African data, details on sampling procedures, parasitological examination, and identification of both fleas and hosts can be found in earlier publications (Sanchez, J.P., 2013. Sifonápteros parásitos de los roedores sigmodontinos de la Patagonia Norte de la Argentina: estudios sistemáticos y ecológicos. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; Sanchez and Lareschi, 2013, Sanchez and Lareschi, 2019; López Berrizbeitia, M.F., 2018. Sifonápteros de micromamíferos (Didelphimorphia, Chiroptera y Rodentia) del Noroeste Argentino: sistemática y distribución. Doctoral Thesis. San Miguel de Tucumán: Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán. Tucumán, Argentina; López Berrizbeitia and Díaz, 2019, Krasnov et al., 2023). Information on sample size and total number of parasite species for each host species is presented in Table 1.

Table 1. The number of examined and infected individuals of each host species and parasite species richness (PSR) of helminth infracommunities of South African ungulates (HSAU), and flea infracommunities of Patagonian and northwestern Argentinian rodents (FPR and FNAR, respectively). In South Africa, helminths were recorded in each individual host. In South America, the number includes only hosts from which at least one flea was collected.

Communities	Host	Total host number	Infected hosts	PSR
HSAU	<i>Tragelaphus angasii</i>	77	77	19
	<i>Redunca arundinum</i>	56	56	21
	<i>Phacochoerus africanus</i>	130	130	17
FPR	<i>Abrothrix hirta</i>	71	45	15
	<i>Abrothrix olivacea</i>	164	83	15
	<i>Akodon iniscatus</i>	68	31	9
	<i>Eligmodontia morgani</i>	72	33	10
	<i>Eligmodontia typus</i>	128	58	11
	<i>Graomys griseoflavus</i>	99	57	10
	<i>Phyllotis xanthopygus</i>	62	26	10
	<i>Reithrodon auritus</i>	25	23	14
FNAR	<i>Akodon simulator</i>	67	13	6
	<i>Akodon spegazzinii</i>	41	12	12
	<i>Oligoryzomys brendae</i>	93	12	5

2.2. Parasite species attributes and population characteristics

Each helminth species was characterized by three attributes, namely (i) life cycle (direct or indirect); (ii) transmission mode (trophic, percutaneous invasion, or vectorial); and (iii) ranked host specificity (high: one or two host species of the same family across a helminth's geographic range, intermediate: multiple hosts from one or two orders, low: multiple hosts from three or more orders). Information on life cycles and transmission mode was taken from various literature sources (e.g., Reinecke, 1983, Riley, 1986, Anderson, 2000). Each flea species was characterized by three attributes. These were (i) the occurrence of sclerotized combs (no combs or both pronotal and genal combs), (ii) ranked host specificity (high: from one to five host species across a flea's geographic range, intermediate: from six to 19 host species, low: more than 20 host species), and (iii) microhabitat preference (a flea's preference to spend most of its life in a host's hair, in a host's burrow/nest, or no clear preference). Sclerotized combs allow a flea to anchor itself in the host's hair and withstand host grooming efforts (Krasnov, 2008). Data on the total number of host species exploited across a flea's geographic range and microhabitat preference were obtained from Krasnov et al. (2022) and Krasnov et al. (2024), respectively.

The population structure of each helminth and flea species was characterized by mean abundance (mean number of parasites per host individual, independent of whether a host was infected or not) and prevalence. Abundance has been shown to be a true species attribute of both helminth and flea species because, across parasite populations, it varied in relatively narrow species-specific boundaries (Arneberg et al., 1997, Krasnov et al., 2006, Poulin, 2006). Prior to analyses, helminth abundance data were $(\ln + 1)$ -transformed to account for substantial variation in mean abundance between helminth species. Prevalence (at least for helminths) appeared to be less conserved within a species than mean abundance (Arneberg et al., 1997); nevertheless, its variation between species was shown to be substantially lower than that within species (Poulin, 2006).

2.3. Host characteristics

Each individual host was characterized by its sex and age. An age category (young versus adult) was attributed to each host based on body size and mass, changes in pelage, horn confirmation and length and/or dentition (for ungulates; Howard, P.C., 1983. An integrated approach to the management of common reedbeek on farmland in Natal. Ph.D. thesis, Univ. of Natal, Pietermaritzburg, South Africa; Anderson, 1986, Rudman et al., 2018) or body mass, body length, and reproductive state (for rodents).

2.4. Data analyses

For each host species, data were pooled across localities in which this host was sampled. This was done because data for each separate locality (especially for South America) were scarce and, thus, could produce unreliable results. We constructed host individuals \times parasite species matrices for each host species, where the entries were the counts of parasites. Then, we calculated SCBD and HCBBD (Legendre and de Cáceres, 2013) using the "beta.div" function (with option method="log.chord") implemented in the "adespatial" package (Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., Wagner, H.H., 2023. adespatial: Multivariate multiscale spatial analysis. R package version 0.2-23. <https://CRAN.R-project.org/package=adespatial>) of the R Statistical Environment (R Core Team, 2023. R: A language and environment for statistical

computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>). The option `method="log.chord"` allows one to log-transform the composition data prior to analysis with the chord distance (Legendre and Borcard, 2018), thus reducing the asymmetry of the species distributions.

The effects of parasite attributes and population variables on SCBD and host-associated variables on HCBD were analysed using beta-regressions. We applied beta-regressions because our response variables ranged from zero to unity and did not attain these extreme values. For parasites, we ran beta-regressions separately for species attributes and population variables. First, we tested for the overall effects of (i) parasite species attributes and population variables on SCBD and (ii) host characteristics on HCBD across all host species. This was done using general linear mixed-effects models implemented in the R package “`glmmTMB`” (Brooks et al., 2017) with option `family = beta_family(link="logit")` and host species as random effect. For models testing the effects of (i) parasite population variables on SCBD and (ii) host characteristics on HCBD, we pooled data on all host species. Modelling the effects of parasite species’ attributes on SCBD was carried out separately for helminths and fleas because the two parasite groups were characterised by different species’ attributes.

Then, to understand if and how (i) the parasite species’ attributes and/or population variables were associated with SCBD and (ii) host age and/or sex were associated with HCBD, we ran separate models for each host species using the R package “`betareg`” (Cribari-Neto and Zeileis, 2010). For each host species and for either SCBD or HCBD, and either species’ attribute or population variables (for SCBD), we constructed models with all combinations of explanatory variables, and then selected the best model using the “`model.sel`” and “`get.models`” functions, based on Akaike Information Criteria (AIC) implemented in the R package “`MuMIn`” (Bartoń, K. 2023. `MuMIn`: multi-model inference. R package version 1.47.5, <https://CRAN.R-project.org/package=MuMIn>). $P < 0.05$ was considered statistically significant.

3. Results

The dissimilarity between ungulate individuals in their helminth infracommunities was substantially lower than that between rodent individuals in their flea infracommunities (Mann-Whitney test; $z = -2.49$, $P = 0.01$) (Table 2). In almost all hosts, the contribution of parasite species (SCBD) to beta-diversity was higher than that of host individuals (HCBD), even when the numbers of parasite species and host individuals were similar (across host species, Mann-Whitney test; $z = 9.41$, $P < 0.001$) (Table 2).

Table 2. Total beta-diversity (BD) and mean species and host contribution to BD (SCBD and HCBD, respectively; in parentheses: range of values) of helminth infracommunities of South African ungulates (HSAU) and flea infracommunities of Patagonian and northwestern Argentinian rodents (FPR and FNAR, respectively).

Communities	Host	BD	SCBD	HCBD
HSAU	<i>Tragelaphus angasii</i>	0.43	0.05 (0.0002–0.25)	0.01 (0.006–0.03)
	<i>Redunca arundinum</i>	0.35	0.05 (0.0002–0.20)	0.02 (0.004–0.07)
	<i>Phacochoerus africanus</i>	0.34	0.06 (0.0001–0.21)	0.008 (0.001–0.04)
FPR	<i>Abrothrix hirta</i>	0.81	0.07 (0.0014–0.18)	0.02 (0.01–0.03)
	<i>Abrothrix olivacea</i>	0.76	0.07 (0.001–0.22)	0.01 (0.006–0.22)
	<i>Akodon iniscatus</i>	0.76	0.11 (0.01–0.26)	0.03 (0.02–0.05)
	<i>Eligmodontia morgani</i>	0.70	0.10 (0.02–0.35)	0.03 (0.01–0.06)
	<i>Eligmodontia typus</i>	0.57	0.09 (0.006–0.37)	0.02 (0.002–0.04)
	<i>Graomys griseoflavus</i>	0.62	0.10 (0.005–0.27)	0.02 (0.007–0.04)
	<i>Phyllotis xanthopygus</i>	0.84	0.10 (0.01–0.21)	0.04 (0.02–0.05)
	<i>Reithrodon auritus</i>	0.76	0.07 (0.005–0.18)	0.04 (0.03–0.07)
FNAR	<i>Akodon simulator</i>	0.73	0.17 (0.03–0.23)	0.08 (0.4–0.11)
	<i>Akodon spegazzinii</i>	0.81	0.08 (0.008–0.28)	0.08 (0.05–0.12)
	<i>Oligoryzomys brendae</i>	0.72	0.20 (0.06–0.38)	0.08 (0.04–0.15)

Models testing overall across-host species effects of parasite species attributes and their population variables on SCBD and host characteristics on HCBD demonstrated that, in general, SCBD was associated with parasite abundance and prevalence, but not parasite species' attributes (except host specificity in helminths), whereas HCBD was not associated with any host characteristic (Table 3). Separate within-host species analyses supported this. In particular, parasite species' morphological and ecological attributes mostly did not affect their contribution to their infracommunities' beta-diversity, except the host specificity of helminths in one out of three host species, the microhabitat preference of fleas in two out of 11 host species, and the occurrence of sclerotized combs in fleas in one out of 11 host species (Table 4). In these hosts, the contribution to beta-diversity was higher in (i) highly host-specific helminths (Fig. 1) and (ii) fleas preferring to spend most of their time in a host's hair or possessing sclerotized combs (see illustrative examples in Fig. 2). On the contrary, the SCBD of both helminths and fleas significantly increased with either their mean abundance (in South African *P. africanus* and two of 11 species of South American rodents) or prevalence (in South African *T. angasii* and nine of 11 species of South American rodents) or both (in South African *R. arundinum*) (see illustrative examples in Fig. 3).

Table 3. Summary of mixed-effects beta-regression models of the effect of (i) parasite species attributes and population structure on their contribution to beta-diversity (SCBD) and (ii) host characteristics on their contribution to beta-diversity (HCBD) in helminth infracommunities in South African ungulates and flea infracommunities of South American rodents. The effects of parasite species' attributes on SCBD were analysed separately for helminths and fleas (see section 2.4 for explanations). Parasite species' attributes are as follows.

SCBD/HCBD	Host	Predictor	Coefficient	S.E.	z	p	
SCBD	All	Prevalence	3.15	0.23	15.28	<0.01	
		Abundance	0.40	0.04	10.34	<0.01	
	Helminths	LC	0.59	0.30	-1.90	0.06	
		TM (trophic)	-0.28	0.41	-0.69	0.49	
		TM (vectorial)	-0.24	0.63	-0.39	0.70	
		HSPh (low)	-0.78	0.39	-2.01	0.04	
		HSPh (intermediate)	-0.43	0.37	-1.18	0.23	
		Fleas	MP (body)	-0.10	0.18	-0.53	0.59
	MP (nest)		-0.33	0.63	-0.52	0.60	
	Combs		0.17	0.17	0.99	0.33	
	HSPf (low)		0.27	0.18	1.47	0.14	
	HSPf (intermediate)		0.08	0.24	0.32	0.75	
	HSBD		Sex	0.003	0.48	0.07	0.94
			Age	-0.05	0.05	-0.11	0.91

For helminths: LC, life cycle; TM, transmission mode; HSPh, host specificity (see section 2.2 for explanations). For fleas: HSPf, host specificity; MP, microhabitat preference; Combs, occurrence of combs; and HSPf, host specificity (see section 2.2 for explanation). Reference levels for nominal variables were “high” for HSPh and HSPf, “direct” for LC, “percutaneous invasion” for TM, “no clear microhabitat preference” for MP, and “two combs” for Combs. Hosts characteristics are age (reference level “adult”) and sex (reference level “female”).

Table 4. Summary of the best beta-regression models of the effect of parasite species' attributes and population structure on their contribution to the beta-diversity (SCBD) of helminth infracommunities in South African ungulates and flea infracommunities of South American rodents. Only models with significant coefficients are shown.

Parasites	Host	Predictor	Coefficient	S.E.	z	Pseudo R ²
Helminths	<i>Tragelaphus angasii</i>	Prevalence	2.93	0.69	4.26	0.53
		<i>Redunca arundinum</i>	Abundance	0.27	0.07	3.66
	<i>Phacochoerus africanus</i>	Prevalence	1.70	0.59	2.90	
		Abundance	0.38	0.06	6.55	0.63
		Host specificity	-1.31	0.47	-2.77	0.28
Fleas	<i>Abrothrix hirta</i>	Prevalence	10.52	1.57	6.68	0.69
		<i>Abrothrix olivacea</i>	Abundance	8.90	1.03	8.69
	<i>Akodon iniscatus</i>	MP	-1.57	0.54	-2.88	0.71
		Prevalence	11.06	2.27	4.87	0.65
	<i>Eligmodontia morgani</i>	Prevalence	11.16	0.81	13.70	0.90
	<i>Eligmodontia typus</i>	Prevalence	8.56	1.32	6.50	0.57
	<i>Graomys griseoflavus</i>	MP	-1.39	0.59	-2.37	0.59
		Abundance	3.02	0.45	6.63	0.71
	<i>Phyllotis xanthopygus</i>	Prevalence	16.89	2.80	6.04	0.73
	<i>Reithrodon auritus</i>	Prevalence	5.34	0.93	5.75	0.66
	<i>Akodon simulator</i>	Prevalence	16.26	6.08	2.67	0.61
	<i>Akodon spegazzinii</i>	Combs	0.97	0.46	2.12	0.34
		Prevalence	26.68	4.33	6.16	0.67
	<i>Oligoryzomys brendae</i>	Prevalence	30.63	6.55	4.67	0.76

MP, microhabitat preference; and Combs, occurrence of combs (for fleas, see section 2.2 for explanation). Reference levels for these nominal variables were “high” for host specificity, “no clear microhabitat preference” for MP, and “two combs” for Combs.

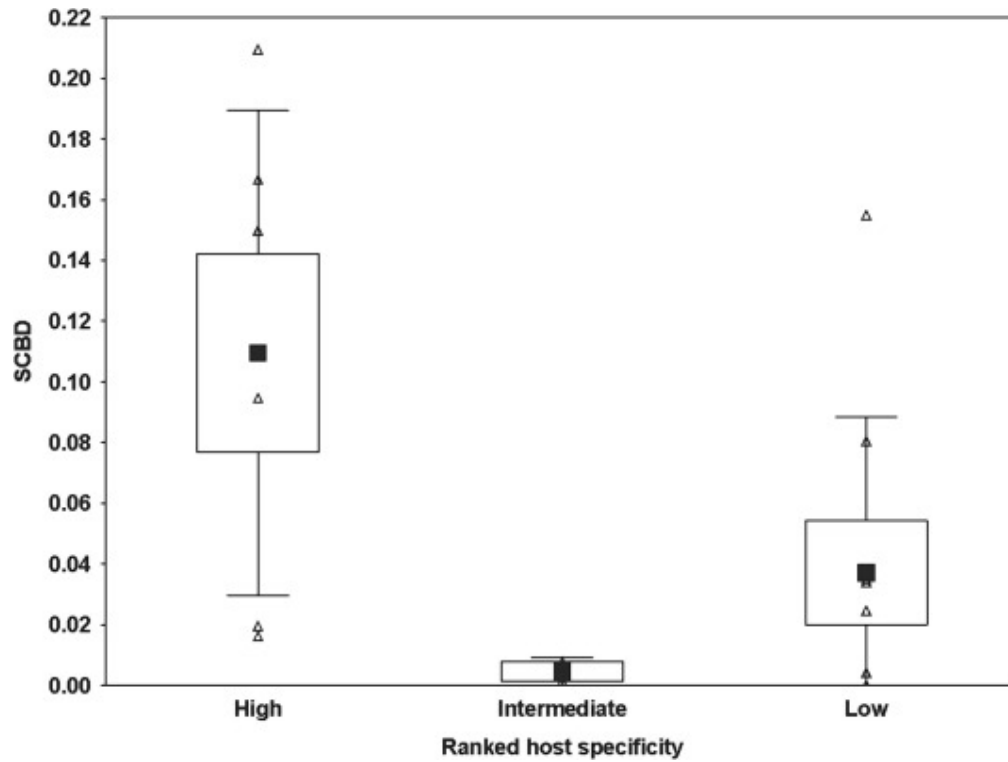


Fig. 1. Contribution of helminth species with different levels of host specificity to the beta-diversity (SCBD) of their infracommunities harboured by *Phacochoerus africanus* (see section 2.2 for explanation). Closed squares, means; boxes, \pm S.E.; whiskers, \pm S.D.; triangles, raw data.

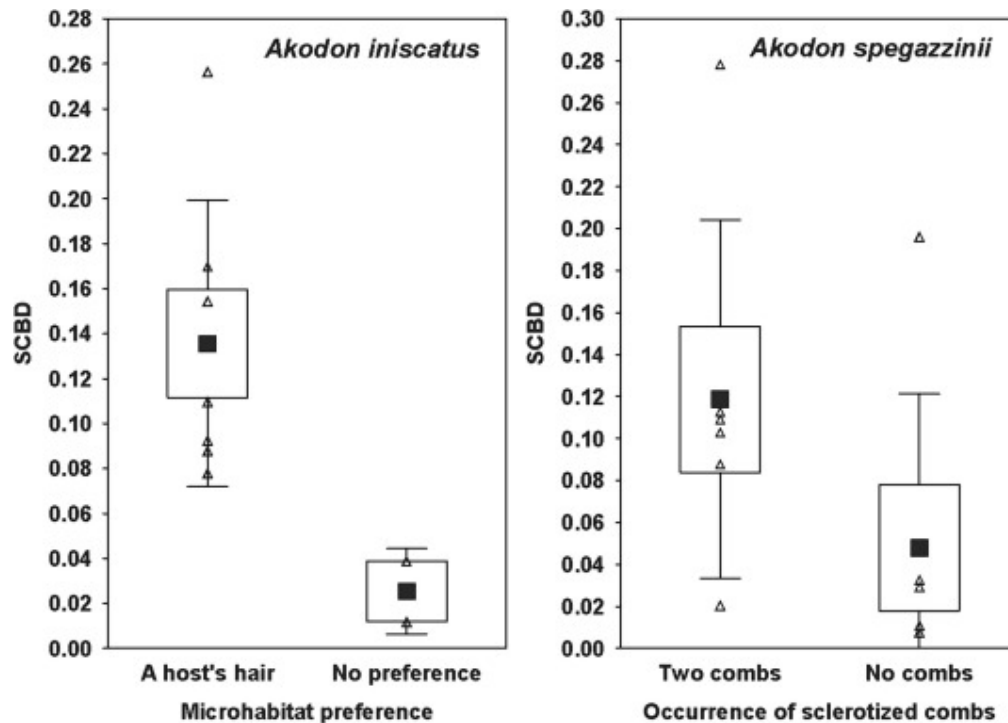


Fig. 2. Contribution of flea species with different microhabitat preferences (for *Akodon iniscatus*) and possession or not of sclerotized combs (for *Akodon spegazzinii*) to the beta-diversity (SCBD) of their infracommunities. Closed squares, means; boxes, \pm S.E.; whiskers, \pm S.D.; triangles, raw data.

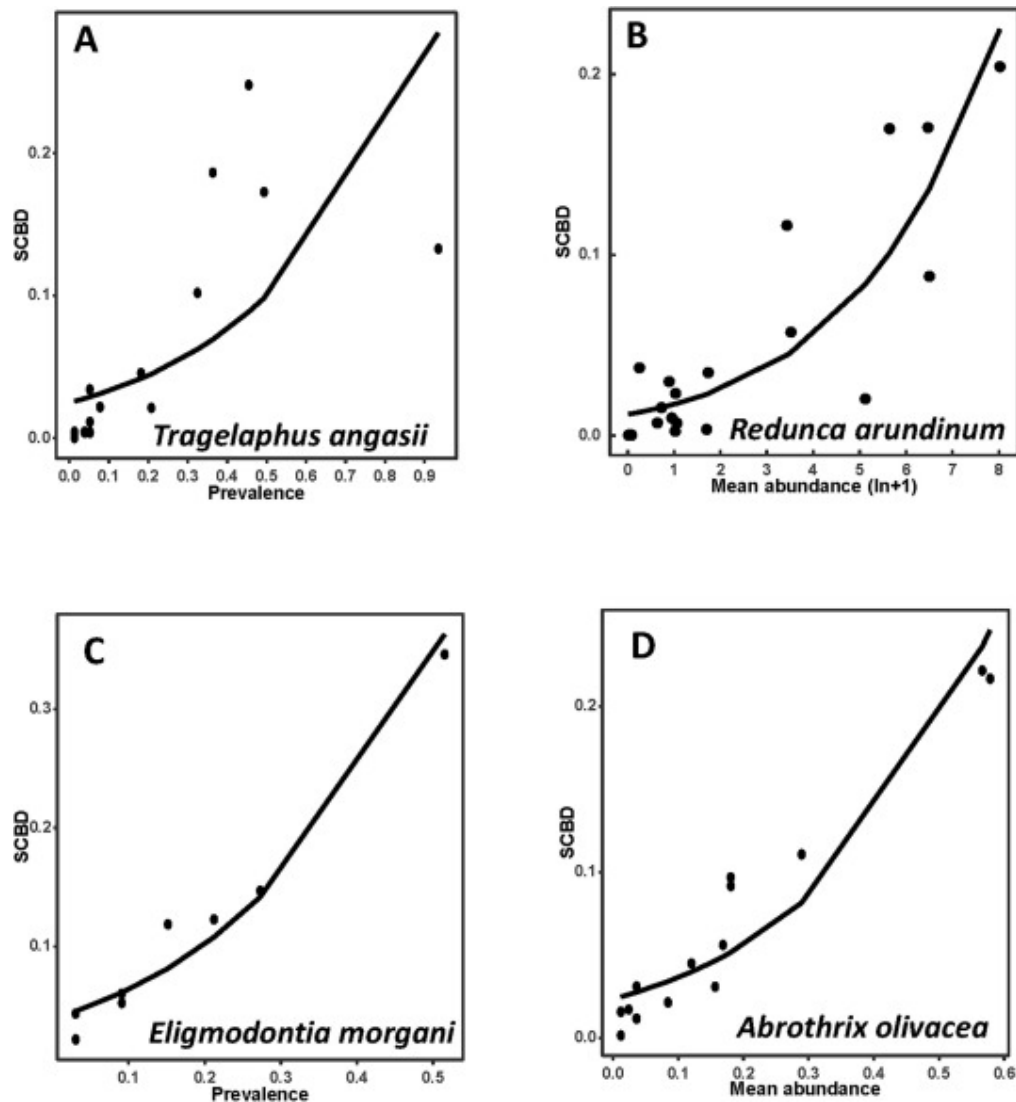


Fig. 3. Relationships between parasite prevalence or abundance and their contribution to the beta-diversity (SCBD) of helminth infracommunities in *Tragelaphus angasii* (A) and *Redunca arundinum* (B) and of flea infracommunities in *Eligmodontia morgani* (C) and *Abrothrix olivacea* (D).

An effect of host characteristics on their contribution to parasite infracommunities' beta-diversity was found, for helminths, in two of the three species of ungulates (age) and, for fleas, in two of 11 species of rodents (either age only or both sex and age) (Table 5). In all these hosts, HCBBD was higher in (i) young hosts than in adult hosts (Fig. 4, Fig. 5) and (ii) female hosts than in male hosts (Fig. 5; note values of coefficients in Table 5).

Table 5. Summary of the best beta-regression models of the effect of host sex and age on their contribution to the beta-diversity (HCBD) of helminth infracommunities in South African ungulates and flea infracommunities of South American rodents. Only models with significant coefficients are shown. Reference levels for nominal variables were male (for sex) and young (for age).

Parasites	Host	Predictor	Coefficient	S.E.	z	Pseudo R^2
Helminths	<i>Tragelaphus angasii</i>	Age	0.20	0.08	2.44	0.07
	<i>Phacochoerus africanus</i>	Age	0.21	0.10	2.02	0.05
Fleas	<i>Reithrodon auritus</i>	Sex	-0.22	0.09	-2.58	0.55
		Age	0.44	0.08	5.20	
	<i>Akodon spegazzinii</i>	Sex	-0.37	0.18	-2.09	0.24

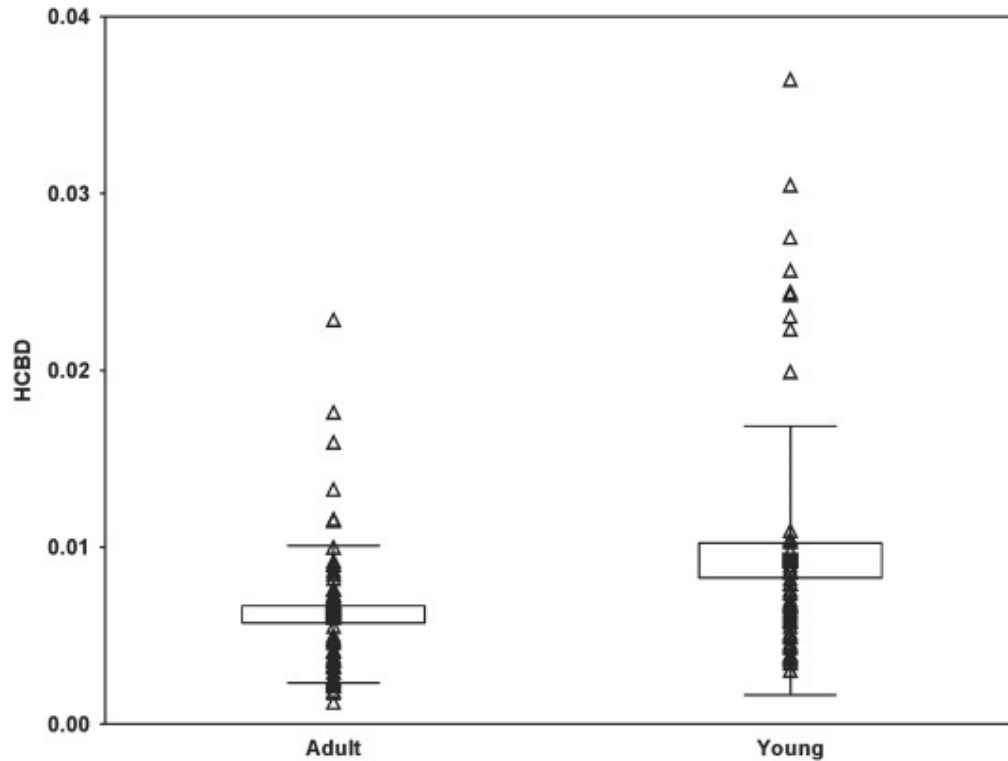


Fig. 4. Contribution of young and adult *Phacochoerus africanus* to the beta-diversity (HCBD) of helminth infracommunities. Closed squares, means; boxes, \pm S.E.; whiskers, \pm S.D.; triangles, raw data.

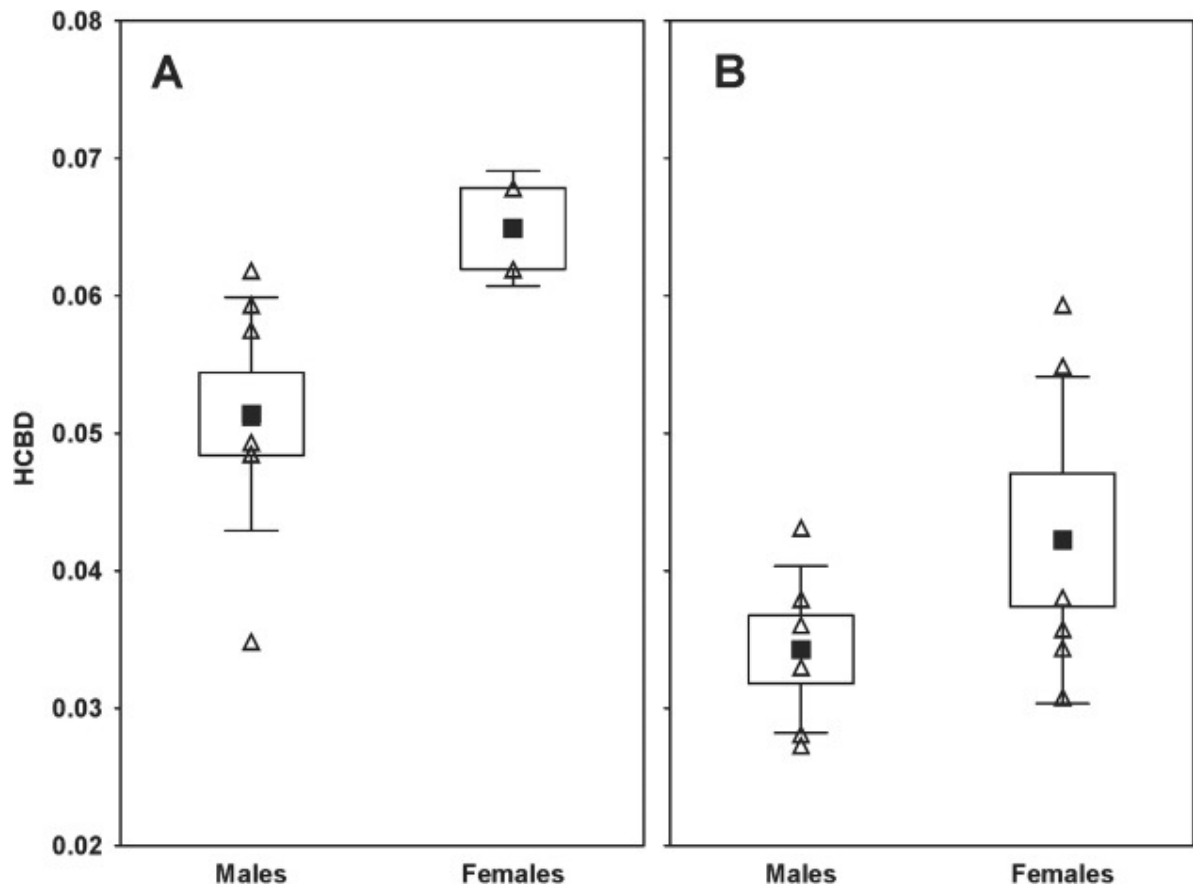


Fig. 5. Contribution of young (A) and adult (B) male and female *Reithrodon auritus* to the beta-diversity (HCBD) of flea infracommunities. Closed squares, means; boxes, \pm S.E.; whiskers, \pm S.D.; triangles, raw data.

4. Discussion

We found that parasite species' contributions to the total beta-diversity of helminth and flea infracommunities in different hosts were mainly associated with parasite prevalence or abundance. These patterns were similar across host species and independently of whether parasites were helminths in South Africa or fleas in South America. In contrast, SCBD did not differ between helminths with (i) either direct or indirect life cycles or (ii) different transmission modes, and (iii) varied in dependence on host specificity in one host species only. Similarly, flea SCBD did not depend on their attributes except microhabitat preference in two host species and possession of sclerotized combs in one host species. Differences in host contributions to infracommunities' beta-diversity between (i) young and adult or (ii) male and female hosts were detected in ungulates harbouring helminths (in two of the three host species), but only in two of the 11 rodent species parasitized by fleas.

Higher SCBDs in highly abundant and/or prevalent parasites were previously found for component helminth communities (Spickett et al., 2019) and compound flea communities (Krasnov et al., 2019) harboured by small mammals. In other words, highly abundant and/or prevalent parasites contribute more to the total beta-diversity of infra-, component, and compound communities than do scarce or less prevalent parasites. This suggests that the effect of prevalence or abundance on parasite SCBD is a common pattern governing parasite communities' beta-diversity, independently of parasite and host taxa, as well as the hierarchical

scale of parasite communities (in host individuals, host populations, or communities). Moreover, this pattern has also been recorded in free-living species (e.g., Heino and Grönroos, 2017, Vilmi et al., 2017). The most likely reason behind this is the positive relationship between abundance and occupancy when a species' average local abundance correlates with the number of sites it occupies (Lawton, 1993, Lawton, 1996, Gaston et al., 2000, Freckleton et al., 2006; but see Boeken and Shachak, 1998). In parasites, the abundance-occupancy relationship is manifested as the relationship between mean abundance and prevalence (Morand and Guégan, 2000, Simková et al., 2002, Krasnov et al., 2005a, Morand and Krasnov, 2008). Among multiple hypotheses explaining a positive abundance-occupancy pattern (see Gaston, 2003), the most popular ones are the sampling artifact (Ten Caten et al., 2022), core-satellite (Hanski, 1982), and ecological specialization (=niche-breadth) hypotheses (Brown, 1984, Hanski et al., 1993). The sampling artifact and core-satellite hypotheses were rejected for parasites (Poulin, 1998, Morand and Guégan, 2000, Simková et al., 2002). The ecological specialization hypothesis states that species with greater niche breadth attain higher abundance and distribution due to broad tolerance to environmental conditions. This was partly supported for parasites (Simková et al., 2002, Krasnov et al., 2004, Krasnov et al., 2005a; but see Poulin, 1998). However, the results of our study suggest that although common species, namely those more abundant and prevalent, contribute more to total beta-diversity (see also Vilmi et al., 2017), their level of specialization, in terms of host specificity, does not generally affect their SCBDs. The only exception is represented by helminths in *P. africanus*, which, in contrast to the above-mentioned relationships between niche breadth, abundance, occupancy, and SCBD, demonstrated higher SCBD in highly host-specific species. Moreover, neither mean abundance nor prevalence varied among parasites with different host specificity and exploiting the same host (ANOVAs; $F = 0.02\text{--}3.12$, $P > 0.12$ for all), except prevalence in helminths harboured by *P. africanus* (ANOVA; $F = 7.86$, $P = 0.005$).

In the majority of host species, the best models of the relationships between the SCBD of parasites and variables describing their population structure included either abundance or prevalence, whereas both variables were associated with SCBD in helminths of *R. arundinum*. This was the case despite the significant correlation between mean abundance and prevalence (Spearman $R = 0.72\text{--}0.98$, $P < 0.05$ for all), except in fleas of *A. iniscatus* (Spearman $R = 0.51$, $P > 0.05$). The most likely reasons behind this may be (i) the difference in the fit of the models between those containing abundance only and those containing prevalence only as explanatory variables and (ii) the curvilinearity of the abundance-prevalence relationship (prevalence, obviously, cannot attain values higher than unity) (Morand and Guégan, 2000). For example, the AIC values for the SCBD models testing the effect of mean abundance or prevalence of fleas parasitic on *G. griseoflavus* (the best model contained mean abundance) were -32.50 versus -26.10 , respectively, whereas the AIC values for these models on the data of fleas parasitic on *A. hirta* (the best model contained prevalence) were -59.30 versus -65.60 , respectively.

Although in the majority of host species, parasite species attributes did not affect their SCBD, these effects were found for helminths in *P. africanus* and fleas in *A. iniscatus*, *G. griseoflavus*, and *A. spegazzinii*. Detection of the host specificity effect in helminths in *P. africanus*, but not in the other two ungulate hosts, might be a consequence of the relatively high numbers of host-specific and host-opportunistic helminth species (six and nine species, respectively), whereas the number of helminths with an intermediate level of host specificity was low (two species only). In contrast, *T. angasii* and *R. arundinum* harboured mainly helminths with intermediate levels of host specificity (11 of 18 species and 16 of 21 species, respectively). Similarly, the majority of fleas harboured by *A. iniscatus* and *G. griseoflavus* preferred to spend most of their

time in a host's hair (seven of nine and 10 species, respectively), whereas in other rodents, the proportions of fleas with this microhabitat preference were lower (0.4–0.6). In other words, the effect of parasite species' attributes on SCBD might depend on the species composition of the assemblages, which, in turn, might influence a trait's distribution. However, the relative numbers of fleas possessing sclerotized combs or not were similar in all rodent hosts, whereas the effect of this attribute effect on SCBD was detected in *A. spegazzinii* only. This difference obviously has nothing to do with the composition of flea assemblages but might be related to some unknown features of this host's life history.

The difference in HCBD between young and adult host individuals was found in the helminth infracommunities of two ungulates and the flea infracommunities of one rodent, whereas the difference in HCBD between male and female hosts, was detected in the flea infracommunities of two rodents. Whenever the effects of these characteristics on HCBD were detected, HCBD appeared to be higher in young and/or female hosts. This suggests that, at least in some hosts, young animals or females drive dissimilarity between infracommunities. Young animals can be highly mobile (especially rodents during dispersal; Gaines and McClenaghan, 1980), and their anti-parasitic resistance (e.g., immunocompetence) is relatively low (Quinnell, 1992). This may result in a greater chance of being exposed to a larger number of parasite species (Krasnov et al., 2005b) and, consequently, higher HCBD. In South African ungulates, young animals, while having some innate knowledge of appropriate food items, also learn from observing adults and experimenting, causing them to consume a wide variety of vegetation (Frost, 1981). As a result, they may ingest parasite species that are not typically found in older hosts (Negovetich et al., 2006), causing between-age differences in HCBD. Higher HCBD values in female *R. auritus* and *A. spegazzinii* contradict the results of an earlier study that demonstrated male-driven flea infracommunity structure in Eurasian (but not African) rodents (Krasnov et al., 2011). However, the degree to which sex difference between hosts drives the beta-diversity of parasite infracommunities (or whether it drives this beta-diversity at all) may differ between host species, being dependent on the pattern of species-specific spatial behaviour and social structure (see Krasnov et al., 2011).

It is mostly unclear why the effects of parasite species' attributes on their SCBDs and host characteristics on their HCBDs were detected in some, but not other, host species. This could be associated with some differences in ecology, behaviour, and social structure between host species. For example, the effect of age on HCBD in *T. angasii* and *P. africanus*, but not in *R. arundinum*, might result from differences in these species' feeding preferences. *Tragelaphus angasii* are intermediate mixed feeders. While primarily browsers, feeding on the leaves, twigs, flowers, and fruits of a wide variety of plants, they will graze extensively when fresh green grass is available after good rain (Skinner and Chimimba, 2005). *Phacochoerus africanus* predominantly feed on annual and perennial grasses, but their diet also includes wild fruits, berries, the bark of trees or shrubs, and even carrion (Skinner and Chimimba, 2005). In contrast, *R. arundinum* are almost exclusively grazers (Skinner and Chimimba, 2005). As mentioned above, young animals experiment during the transition from suckling to an adult diet. Such experimentation would likely include a wider variety of food items in animals that naturally feed on a wider range of vegetation. This might lead to more pronounced dietary differences and, in turn, differences in exposure to infective parasite stages between young animals and adults in *T. angasii* and *P. phacochoerus* but not in *R. arundinum*. Furthermore, young *T. angasii*, due to their lack of height, tend to eat closer to the ground, and infective larvae of strongylids occur on low growing vegetation rather than trees. We recognize that this explanation is speculative and warrants further investigation. The life histories of large African ungulates are relatively well known, whereas this is not the case for South American rodents.

In many of the latter species, details of ecology, behaviour, and social structure remain to be studied. Consequently, the between-host differences in the occurrence of the effect of an individual's sex or age on the HCBD of its flea assemblages are difficult to explain, at least until details of these rodents' biological features become better known. We recognize that the data used in this study were collected from different geographic localities at different times. Although these differences appear unlikely to affect the results substantially, this has to be kept in mind.

Finally, the SCBD values of parasite species were higher than the HCBD values of host individuals. This suggests that parasite infracommunities' beta-diversity is mainly driven by variation in parasite species rather than the uniqueness of assemblages harboured by each individual host (Legendre and de Cáceres, 2013). This can be explained by the fact that hosts are conspecific and, thus, share multiple features. As a result, individual characteristics such as sex and age did not affect HCBD in the majority of hosts.

In conclusion, we found that the relationships between SCBD and parasite abundance/prevalence appear to be common and do not differ between different parasite-host associations in different geographic regions. However, the relationships between SCBD and parasite species' attributes, as well as HCBD and host characteristics, appeared to be contingent and depend on the parasite and host identities.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors did not use generative AI and AI-assisted technologies.

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Appendix A. Supplementary material

Supplementary Data 1. **Supplementary Fig. S1.** Map of sites where helminths of three ungulate species were sampled in South Africa. **Supplementary Fig. S2.** Map of sites where fleas of eight rodent species were sampled in Patagonia. **Supplementary Fig. S3.** Map of sites where fleas of three rodent species were sampled in northwestern Argentina.

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