Research Article

Compositional turnover in ecto- and endoparasite assemblages of an African bat, *Miniopterus natalensis* (Chiroptera, Miniopteridae): effects of hierarchical scale and host sex

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Abstract

We studied the compositional turnover in infracommunities and component communities of ecto- and endoparasites infesting a bat, *Miniopterus natalensis* (Chiroptera, Miniopteridae), across seven sampling sites using the zeta diversity metric (measuring similarity between multiple communities) and calculating zeta decline and retention rate (both scales) and zeta decay (component communities). We asked whether the patterns of zeta diversity differ between (a) infracommunities and component communities; (b) ecto- and endoparasites and (c) subsets of communities infecting male and female bats. The pattern of compositional turnover differed between infracommunities and component communities in endoparasites only. The shape of zeta decline for infracommunities indicated that there were approximately equal probabilities of ecto- and endoparasitic species to occur on/in any bat individual within a site. The shape of zeta decline for component communities suggested the stochasticity of ectoparasite turnover, whereas the turnover of endoparasites was driven by niche-based processes. Compositional turnover in component communities of ectoparasites was more spatially dependent than that of endoparasites. Spatial independence of compositional turnover in endoparasites was due to subcommunities harboured by female bats. We conclude that the patterns of compositional turnover in infracommunities were similar in ecto- and endoparasites, whereas the patterns of turnover in component communities differed between these groups.

Introduction

Recognition of parasites as an integral part of global biodiversity (Poulin and Morand, 2004; Gómez and Nichols, 2013) and their roles in structuring natural communities (e.g. Wood et al., 2007; Mellado and Zamora, 2017) and food webs (e.g. Lafferty et al., 2006; Sukhdeo, 2012) has led to a burst of studies of parasite community ecology during the last two decades (e.g. Matějusová et al., 2000; Gotelli and Rohde, 2002; Poulin and Luque, 2003; Krasnov et al., 2010; Dallas et al., 2019). In particular, patterns of variation in species composition (= compositional turnover) of parasite communities received much attention and were studied in a variety of parasite taxa exploiting various hosts in many geographic regions and in terrestrial, marine and freshwater environments (Perdiguero-Alonso et al., 2008; Quiroz-Martínez and Salgado-Maldonado, 2013; Krasnov et al., 2015, 2020; Spickett et al., 2017; Clark et al., 2018).

The main aim of many studies of variation in parasite species composition was a search for general laws, i.e. patterns repeatable in several parasites and host taxa. If a general pattern for parasite compositional turnover was found, it would indicate a certain level of predictability of parasite communities. This, in turn, would allow a better understanding of the rules governing these communities and facilitate the prevention of parasitic diseases in humans, livestock and wildlife. It is well known that parasite communities are complex entities that exist in a set of hierarchical scales and are fragmented between host individuals, populations of conspecific hosts (within a locality or between localities), as well as communities of hosts occurring at different localities. Parasite assemblages at these hierarchical scales are termed infracommunities, component communities, and compound communities, respectively (Holmes and Price, 1986; Poulin, 2007). Given that parasite communities at the lowest scale (infracommunities) are ephemeral and assembled mainly *via* demographic processes, whereas communities at the higher scales (component and compound communities) persist much longer and are shaped

via evolutionary and biogeographic processes (Morand *et al.*, 2002; Poulin, 2007), it is not surprising that patterns of compositional variation differ between communities of the same parasite taxon at different scales (e.g. van der Mescht *et al.*, 2016; Warburton *et al.*, 2016). In other words, these patterns should be considered separately for each scale.

Recently, Krasnov *et al.* (2020) studied compositional turnover in communities of fleas and gamasid mites harboured by small mammals in Western Siberia. They found that the patterns of turnover differed substantially between infracommunities and compound communities. However, the patterns of flea and mite turnover within these hierarchical scales were similar. In contrast, the patterns of turnover in component communities differed between fleas and mites. The study of Krasnov *et al.* (2020) dealt with two taxa with (a) similar strategies of parasitism (both haematophagous ectoparasites with alternating periods of staying on the host and being off-host, but remaining in the latter's burrow/nest) and (b) infesting multiple host species. It thus remained unclear whether (a) the patterns found in infracommunities are indeed parasite taxon-invariant and (b) the patterns found in component communities are indeed parasite taxon-dependent but are not affected by the identity of a host species. These questions can be answered by exploring compositional turnover in infracommunities and component communities of parasites with contrasting parasitism strategies (e.g. ectoparasites *vs* endoparasites) and infecting the same host species. Here, we attempted to fill this gap and studied compositional turnover in infracommunities and component communities of ecto- and endoparasites infesting the same host species, the insectivorous Natal long-fingered bat, *Miniopterus natalensis* (Chiroptera, Miniopteridae).

Several aspects of its biology make *M. natalensis* a convenient model for parasite community studies. The species has a wide geographic range in southern Africa, covering several of the South African biomes, and, being a gregarious cave dweller, occurs in large colonies (Skinner and Chimimba, 2005). The diet of *M. natalensis* is diverse and largely composed of dipterans, hemipterans, isopterans, lepidopterans and coleopterans, caught entirely on the wing, and with different insect groups being the dominant food items at different sites (Skinner and Chimimba, 2005; Schoeman and Jacobs, 2011). *Miniopterus natalensis* have adapted to a large range of vegetational associations, likely due to their migratory nature, and are limited in their distribution only by the availability of caves or similar extensive shelters as well as an adequate supply of food. Female bats migrate seasonally between wintering roosts where mating and hibernating colonies are formed, and summer maternity roosts where the young are born and raised; while many males undertake this migration as well, they usually only spend a short period of time in the maternity roosts, leaving soon upon the arrival of pregnant females (Skinner and Chimimba, 2005). There is little morphological variation between males and females (Miller-Butterworth *et al.*, 2003; Skinner and Chimimba, 2005), but morphological variation between the different subpopulations in South Africa might indicate that these bats have adapted to local environmental conditions, such as vegetation type, climate and/or prey differences (Jacobs, 1999; Miller-Butterworth *et al.*, 2003). The parasite fauna of bats in Africa is generally poorly known and the majority of studies are of a taxonomic nature (Ortlepp, 1932; Jobling, 1936; Zumpt, 1950; Dubois, 1956; Maa, 1965; Baruš, 1973; Saoud and Ramadan, 1976), with few parasite surveys having been conducted (Junker *et al.*, 2008). However, studies of bats in other parts of the world demonstrated that they are hosts to a variety of ecto- and endoparasites (Jameson, 1959; Blankespoor and Ulmer, 1970; Esteban *et al.*, 2001; Dick and Gettinger, 2005; Warburton *et al.*, 2016).

Following Krasnov *et al.* (2020), we investigated patterns of variation in species composition of parasite assemblages harboured by *M. natalensis*, using a novel metric, zeta diversity (Hui and McGeoch, 2014). Zeta diversity (denoted as ζ_i) measures the average number of species shared by i communities, where i is called the zeta order (Hui and McGeoch, 2014). The main advantage of zeta diversity is that, in contrast to traditional pairwise metrics of community dissimilarity (e.g. beta-diversity) that tend to overestimate the contribution of rare species and to underestimate the contribution of common species to compositional turnover (Latombe *et al.*, 2017), it takes into account the full spectrum of species, independent of the level of their rareness or commonness (McGeoch *et al.*, 2019). Furthermore, zeta diversity, by definition, represents compositional overlap across multiple (rather than only two) communities and thus expresses compositional change as similarity rather than dissimilarity. Obviously, zeta diversity values inevitably decline with zeta order. The shape of this decline indicates whether either stochastic or niche-based processes drive differentiation of species composition (McGeoch *et al.*, 2019; see details below).

The aims of this study were threefold. First, we asked whether the patterns of zeta diversity differ between hierarchical scales (i.e. infracommunities *vs* component communities) and expected predomination of stochastic processes in infracommunities and niche-based processes in component communities. This is because infracommunity dynamics are strongly affected by stochastic demographic processes (Poulin, 2007; see above), whereas the relationships between parasites and local environmental conditions play an important role in the dynamics of component communities (Krasnov *et al.*, 2005; Spickett *et al.*, 2017; but see Krasnov *et al.*, 2020). Second, we asked whether the patterns of (a) zeta diversity in infracommunities and component communities and (b) variation in zeta diversity over space (= zeta decay; see details below) in component communities differ between ecto- and endoparasites. We expected a more rapid zeta diversity decline for ecto- than for endoparasites, indicating fewer species shared by many assemblages in the former than in the latter. We also expected higher spatial stability in endo- as compared to ectoparasite communities. This is because the majority (albeit not all) of ectoparasites use their host intermittently, whereas the majority of endoparasites persist in a host individual or population for a much longer period. Third, we asked whether the patterns of zeta diversity and zeta decay differ between subsets of parasite communities harboured by male and female hosts. Earlier, Krasnov *et al.* (2011) reported that community structure in ectoparasites of rodents was mainly driven by male hosts and that the same factors (e.g. differences in the level of immunocompetence and mobility between male and female rodents) are responsible for both male-biased infection patterns and the male-biased manifestation of parasite community structure. Here, we expected that the patterns of zeta decline and zeta decay would be more pronounced (i.e. steeper zeta decline and zeta decay) in communities harboured by female bats because of female-biased parasitism often reported for ecto- and endoparasites of chiropterans (see Krasnov *et al.*, 2012 and references therein).

Materials and methods

Study sites

A total of 96 *M. natalensis* were captured at seven sites across South Africa during a single summer season (mid-September 2009 to early January 2010), in order to minimize the possible impacts of seasonal migration and/or hibernation. Sampling sites were situated in six of the eight South African Biomes (see Supplementary Material, Appendix 1, Fig. S1, Tables S1 and S2)

and included representatives of the three major-subpopulations of this bat species in South Africa: De Hoop Guano Cave in the south; Steenkampskraal Mine, Koegelbeen Sinkhole and Vanderkloof Dam in the west; Sudwala Caves and Shongweni Dam in the northeast, as well as Table Farm in the southeast regions of the country (Miller-Butterworth et al., 2003).

Bat sampling and parasite collection

Bats were caught as they emerged from their roosts at dusk using mist nets and/or harp-traps placed close to the entrance of the roost. Immediately upon capture, bats were temporarily placed into individual cloth bags for later identification of species (following Stoffberg et al., 2004), sex and age (adult or juvenile following Anthony, 1988). Any non-target species, pregnant females and juveniles were subsequently released. Pregnancy was determined by palpation and examination of nipples following Racey (1969). Specimens of M. natalensis were placed into sealable glass jars, together with the contents of their holding bags and euthanized using halothane (Leach et al., 2004).

Following euthanasia, the gastrointestinal tracts (GITs) were removed from the bats and placed into individual glass jars. GITs were fixed using boiling water and subsequently transferred into 70% ethanol. Similarly, the dissected bats, as well as ectoparasites, were placed into separate vials containing 70% ethanol. In the laboratory, any endoparasites present were collected from the abdominal cavity of each bat as well as from the various sections of the GIT (stomach, small and large intestine) and stored in 70% ethanol. Identification of endo- and ectoparasites was done following standard procedures and using the relevant taxonomic keys, descriptions and/or re-descriptions. Parasite specimens that could not be identified to species level, but which differed morphologically from each other and all known congeners, were designated as 'sp. A, B, etc.' (Supplementary Material, Appendix 2, Tables S2 and S3). Cestodes (Hymenolepididae) and some nematodes (Capillariidae) could only be identified to the family level. The latter two families were each included in the counts for species richness as a single taxon.

Data analyses

The analyses of compositional turnover of ecto- and endoparasites were carried out at two scales. At the scale of infracommunities, we analysed the turnover of parasite species across individual bats within a sampling site. For these analyses, we selected three sampling sites at which 19–20 bat individuals were captured and found infested. These sites were the Sudwala Caves, Koegelbeen Sinkhole and Table Farm (Supplementary Material, Appendix 1, Fig. S1, Table S1). At the scale of component communities, we analysed compositional turnover of parasites across bat populations inhabiting the seven sampling sites (see above).

For each parasite group (i.e. ecto- and endoparasites separately) at each scale (i.e. infracommunities at each of the three sampling sites and component communities), we constructed incidence matrices with bat individuals (for infracommunities) or sampling sites (for component communities) as rows and parasite species as columns. Then, we calculated the zeta decline and retention rate for each of these matrices (Hui and McGeoch, 2014; McGeoch et al., 2019). Zeta decline represents a decrease in the average number of shared species with an increase in the number of sampling units (= zeta order), that is the number of individual bats for infracommunities and the number of sampling sites for component communities. The steepness of the zeta decline indicates whether compositional turnover is mostly due to rare (steeper decline) or common (shallower decline) species.

Given that zeta diversity at ever-increasing orders reflects the relative contribution of species with an ever-increasing degree of commonness (see details in Hui and McGeoch, 2014; Latombe et al., 2017; McGeoch et al., 2019), the difference between zeta values at successive zeta orders demonstrates the relative difference in the number of rare as compared with that of common species. The shape of zeta decline is most often approximated by either a negative exponential or a power-law function (McGeoch et al., 2019). Each of these fits indicates the process most likely governing the differentiation of species composition. An exponential or a power-law fit suggests either equal or unequal chances, respectively, for species to occur in a given host individual or at a locality and, thus, indicates whether stochastic or niche-based processes, respectively, are the main mechanism of species turnover (Hui and McGeoch, 2014; McGeoch et al., 2019).

The zeta ratio is a quotient of two consecutive zeta values with a preceding zeta order as a denominator and a subsequent zeta order as a numerator. This ratio measures the proportion of species that remain (= retained) if more host individuals or sampling sites are added for calculating zeta values (Hui and McGeoch, 2014). A plot of zeta ratios against the denominator zeta orders is called a retention rate curve. The shape of a retention rate curve (increasing, asymptotic, modal, decreasing) indicates the rate and pattern at which common species remain across host individuals or sampling sites from low to high zeta orders (see McGeoch et al., 2019). For example, a modal curve indicates a complete turnover in the species composition beyond a certain zeta order. An asymptotic curve suggests the presence of certain species in all hosts or at all sampling sites. An ascending curve shows that common but not rare species are retained in additional samples and that the community is likely under-sampled.

To quantify variation in the number of shared species with an increase in distance between sampling sites, Hui and McGeoch (2014) adapted the concept of the distance decay of similarity (Nekola and White, 1999) to zeta diversity. This adaptation is called zeta decay and is represented by a series of plots of zeta values for samples distributed at different distances across zeta orders, visualizing thus the variation in the number of species shared by communities in dependence of spatial distance between them. The differences between slopes of zeta decay of different zeta orders allow the differentiation of spatial trends between rare and common species (low zeta orders and high zeta orders, respectively). Obviously, zeta decay was analysed for component communities only.

All calculations were carried out using the package 'zetadiv' (Latombe et al., 2018a) implemented in R (R Core Team, 2019). Initially, we analysed patterns of zeta diversity (zeta decline, retention rate, zeta decay), pooling data on parasites harboured by both male and female bats. To understand whether these patterns are affected by host sex, we then repeated all analyses for parasites infecting only male or only female hosts. Calculations of the values of zeta diversity and zeta ratio were done for all orders of zeta available for a given matrix, whereas zeta decay was calculated for orders 2–5 or 2–4 (because no female bats were captured at the Steenkampskraal Mine).

Results

Parasite assemblages

Miniopterus natalensis harboured diverse parasite assemblages, comprising ectoparasites, including flies, mites, ticks and fleas as well as endoparasites, represented by nematodes, cestodes and trematodes (Supplementary Material, Appendix 2, Table S1). Of the 15 species of ectoparasites, mites were the most speciose ($n = 9$), whereas ticks and fleas were represented by a single species each,

Table 1. Zeta diversity decline and retention rate for ecto- and endoparasite infracommunities harboured by *Miniopterus natalensis* at three sampling sites

Site	Parasites (N)	Sex (N)	ζ = 0	ΔAIC	E/P	Coefficient	Shape	OrderMax
SC	Ect (11)	Both (20)	18	23.80	E	−0.18	Modal	5
	Ect (8)	M (10)	10	6.78	E	−0.16	Modal	5
	Ect (8)	F (10)	9	12.60	E	−0.26	Modal	4
	End (9)	Both (18)	13	23.00	E	−0.38	Modal	4
	End (8)	M (8)	7	12.40	E	−0.35	Modal	2
	End (8)	F (10)	9	12.60	E	−0.26	Modal	4
KGBS	Ect (11)	Both (19)	15	24.70	E	−0.25	Modal	5
	Ect (10)	M (11)	9	18.20	E	−0.36	Modal	3
	Ect (7)	F (8)	8	12.30	E	−0.19	Modal	3
	End (4)	Both (19)	16	22.30	E	−0.29	Modal	2
	End (4)	M (11)	10	15.00	E	−0.24	Modal	2
	End (3)	F (8)	7	8.91	E	−0.29	Modal	1
TF	Ect (9)	Both (19)	16	28.40	E	−0.26	Modal	4
	Ect (8)	M (9)	9	21.00	E	−0.19	Modal	5
	Ect (9)	F (10)	10	16.00	E	−0.18	Modal	5
	End (8)	Both (20)	20	18.40	E	−0.07	Modal	6
	End (8)	M (10)	10	6.86	E	−0.14	Modal	4
	End (5)	F (10)	10	14.40	E	−0.15	Modal	4

Site (N): SC, Sudwala Caves; KGBS, Koegelbeen Sinkhole; TF, Table Farm; Parasites (N): Ect, ectoparasites; End, Endoparasites; N, number of species. Sex (N): Both, both male and female hosts; M, male hosts; F, female hosts; N, number of individuals. $\zeta = 0$: zeta order at which zeta diversity attains zero, ΔAIC: difference in Akaike Information Criterion between the negative exponential and the power-law regression of zeta diversity values against zeta order, E/P: whether the negative exponential (E) or the power-law (P) fit was found to be the best; Shape, shape of zeta retention curve; OrderMax: zeta order at which zeta ratio attains maximal value.

namely *Ixodes simplex* (Ixodidae) and *Oxyparius isomalus* (Ischnopsyllidae), respectively. Only three bat individuals were not infested by any ectoparasites at all and prevalence (proportion of infested individuals) of the various ectoparasite species ranged from 0.01 to 0.75. The highest prevalence was seen in the nycteribiid bat fly *Nycteribia schmidlii* (0.75), followed by two species of mites, *Spinturnix semilunaris* (0.406) and *Macronyssus* sp. C (0.344). Mean abundance (mean number of parasites per individual bat) was generally low, ranging from 0.01 ± 0.01 (recorded in four species) to 2.09 ± 0.23 in *N. schmidlii*.

Among the 11 endoparasite taxa, the onchocercid nematode *Litomosa chiropterorum* had by far the highest prevalence (0.667) as well as the second-highest mean abundance (7.32 ± 1.16); the latter only exceeded by that of the lecithodendriid trematode *Paralecithodendrium khalili* (14.95 ± 8.11), which also had the highest prevalence (0.146) among the trematodes. Hymenolepidid cestodes had a prevalence of 0.156, with a mean abundance of 0.24 ± 0.07. Mean abundance of the remaining taxa ranged from 0.01 ± 0.01 to 1.57 ± 1.01. Similar to the ectoparasites, only five hosts remained uninfected. Mean ectoparasite and endoparasite species richness on/in an individual bat across all sampling sites were 2.87 ± 0.14 and 1.89 ± 0.10, respectively, with no significant differences between male and female bats (ANOVAs; $F_{1,91} = 0.67$ for ectoparasites and $F_{1,94} = 0.08$ for endoparasites, respectively, $P > 0.40$ for both) (see Supplementary Material, Appendix 1, Table S1 for parasite species richness per site).

Compositional turnover in infracommunities

The average number of shared ecto- and endoparasite species declined as the number of bat individuals included in the calculations increased and attained zero at zeta orders smaller than or equal to the total number of bats (Table 1, Fig. 1). The rate of this decline for ectoparasites was either steeper (at Table Farm) or equal (at Koegelbeen Sinkhole) or else shallower (at Sudwala Caves) than that for endoparasites (Fig. 1). The shape of the zeta decline was consistently best fitted by the negative exponential function (Table 1). Retention curves for infracommunities of both ecto- and endoparasites were modal, attaining zero at higher zeta orders (Fig. 1). Initially, all curves increased, and then, the zeta ratios dropped beyond zeta orders 4–5 for ectoparasites and 4–6 for endoparasites (Table 1). The difference in the probabilities of retaining common species between ecto- and endoparasite infracommunities varied between sampling sites with the probability of retaining common ectoparasites being higher than that of endoparasites at Sudwala Caves and Koegelbeen Sinkhole, whereas the opposite was the case for Table Farm (Figs 1 and 2).

The shape of a decrease in the number of ecto- or endoparasite species with an increase in the number of bats was similar in infracommunities harboured by male or female bats (Figs 2–4, Table 1); except the zeta decline of ectoparasites was shallower in male than in female hosts at Sudwala Caves. However, the probability of retaining common ecto- or endoparasites differed between male- and female-harboured infracommunities with the pattern of this difference varying both between parasite groups and between sampling sites (Figs 2–4). Nevertheless, the shape of zeta decline for both ecto- and endoparasites harboured by both male and female hosts and in the three sampling sites was consistently best fitted by the negative exponential function (Table 1).

Compositional turnover in component communities

Values of zeta diversity of component communities of ecto- and endoparasites harboured by both males and females declined with
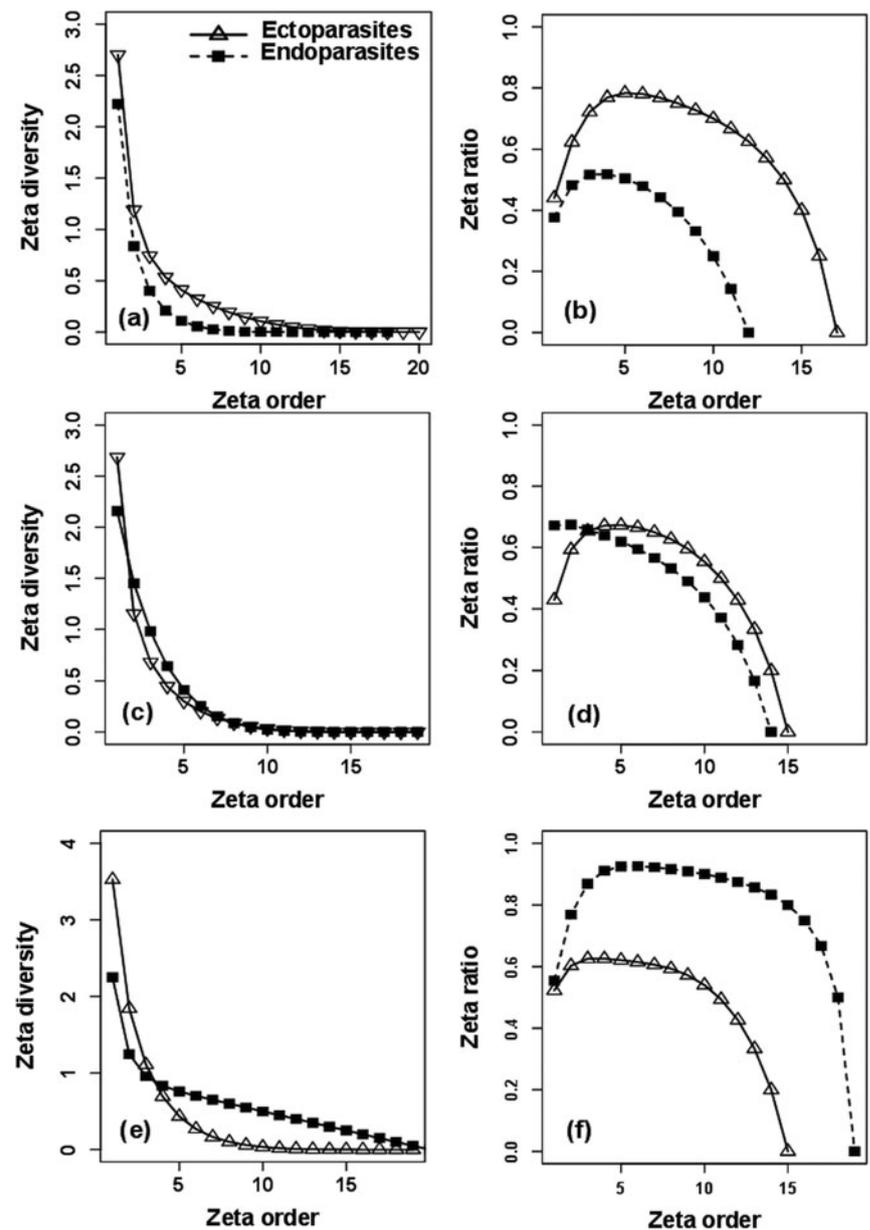
Fig. 1. Zeta diversity decline and retention rate curves for ecto- and endoparasite infracommunities harboured by *Miniopterus natalensis* at the Sudwala Caves (a, b), Koegelbeen Sinkhole (c, d) and Table Farm (e, f). The legend on the plot (a) also applies to other plots.

an increase in the number of sampling sites and did not attain zero at high zeta orders with two ectoparasites (the nycteribiid *N. schmidlii* and the spinturnicid *S. semilunaris*) and one endoparasite (the onchocercid *L. chiropterorum*) infecting bats at every sampling site (Fig. 5). The best fit of zeta decline for ectoparasites was found to be negative exponential (although the difference between power and exponential fit was small), whereas zeta decline for endoparasites was best described by the power-law function (Table 2). The rate of the zeta decline in component communities of ectoparasites was slightly slower than that for endoparasites (Fig. 5). The retention rate curve for ectoparasite component communities tended to be modal with a slow increase to zeta order 5 and then a slow decrease to zeta order 6 (Fig. 5). In endoparasites, the retention rate curve was ascending, attaining the highest zeta ratio of 0.875 (Table 2, Fig. 5).

Patterns of compositional turnover in component communities of ectoparasites harboured by either male or female hosts did not substantially differ from patterns found when data on ectoparasites were pooled for both host sexes, except that the modal shape of the retention rate curves was distinctly more pronounced (Fig. 6). The shape of zeta decline was fitted by the

negative exponential function with the absolute value of the coefficient of the fit being about 30% higher for male- than female-harboured communities (Table 2), indicating a faster decrease in the average number of shared species with an increasing number of sites for the latter as compared with the former. Similar to turnover in component communities of endoparasites pooled for all host individuals within a site, zeta decline of both male- and female-harboured endoparasites was best described by the power-law function (Table 2, Fig. 6) and the retention rate curves were ascending.

The rates of distance decay in the number of shared species were low and pronounced mainly for rare species (i.e. low zeta orders) for ectoparasites and moderately common species for endoparasites (zeta orders 3–4) (Table 3, Fig. 7). There was more ubiquitous ectoparasite than endoparasite species. For example, over distances of 100 km, there were, on average, 4–7 shared ectoparasites and 1–3 endoparasites (across zeta orders). Nevertheless, the number of shared endoparasites declined more slowly with distance than the number of shared ectoparasites did. In addition, there was no distance-associated trend in endoparasite zeta diversity beyond zeta order 4 (Table 3, Fig. 7). When
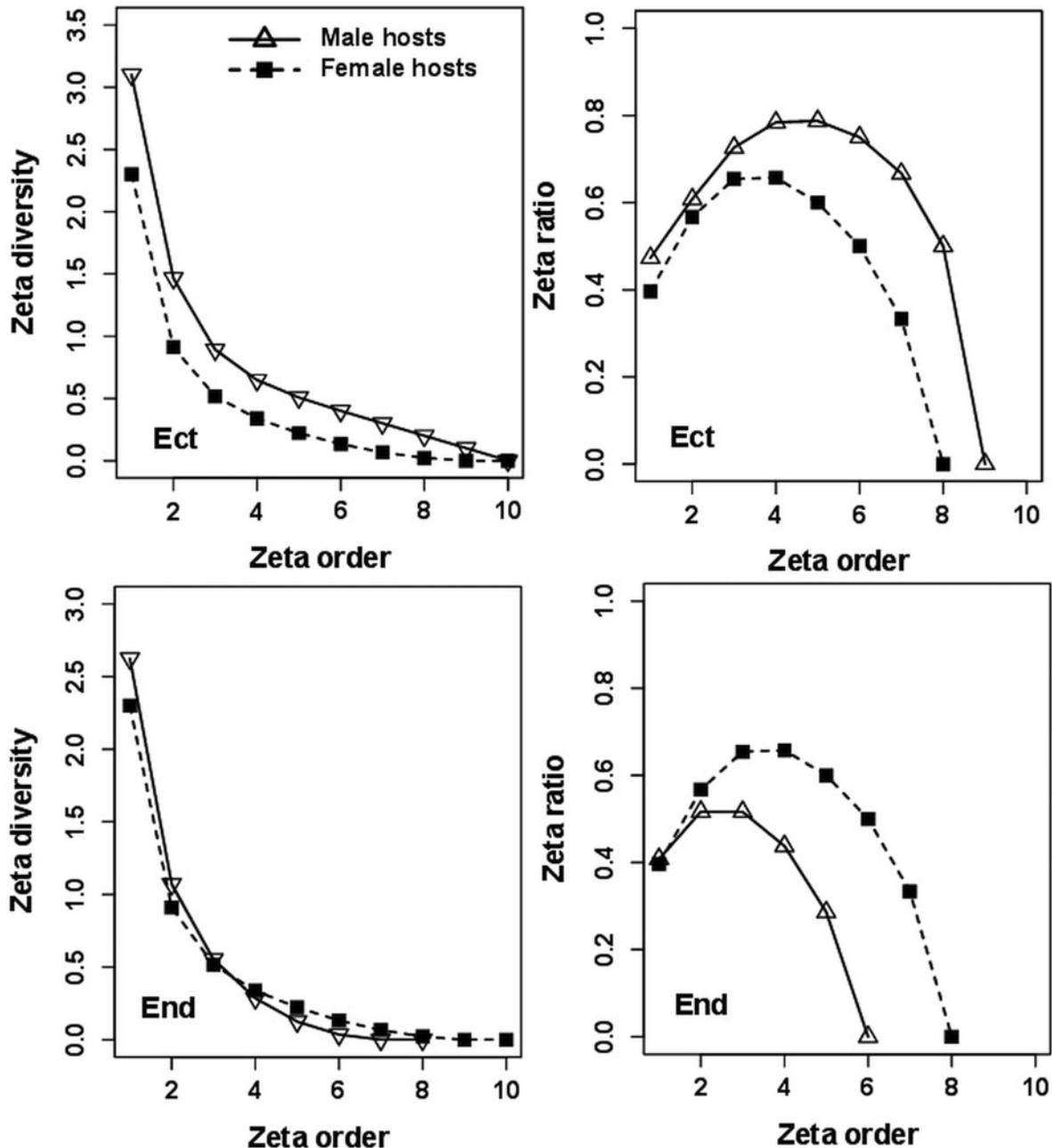
Fig. 2. Zeta diversity decline and retention rate curves for ecto- (Ect) and endoparasite (End) infracommunities harboured by male and female *Miniopterus natalensis* at the Sudwala Caves. The legend on the zeta decline plot for ectoparasites also applies to other plots.

the zeta decay was calculated for parasites infecting male and female bats separately, the rate of the decay for ectoparasites appeared to be slightly higher for male than female hosts (Table 3, Fig. 7). In endoparasites, the number of species shared by male bats across 2–4 sampling sites demonstrated a weak decay with the distance between these sites, whereas no zeta decay with distance was found in species shared by female bats for any zeta order (Table 3, Fig. 7).

Discussion

Our expectations were partly supported. We found that the pattern of compositional turnover differed between infracommunities and component communities in endoparasites, but not ectoparasites. As we expected, (a) the shape of zeta decline for infracommunities indicated that there were approximately equal probabilities of ecto- and endoparasitic species to occur in any

bat individual within a sampling site and (b) distribution of endoparasite species across component communities was likely driven by niche-based processes. Contrary to our expectations, the shape of zeta decline for component communities of ectoparasites suggested the lack of structure in these communities and stochasticity of ectoparasite turnover. Our prediction regarding the rate of zeta decline in ecto- and endoparasites has not been supported. In general, the direction of difference in the rate of zeta decline between ecto- and endoparasites in infracommunities varied across sampling sites, whereas zeta diversity for ectoparasites declined more rapidly than that for endoparasites in component communities. Turnover in the component community composition of ectoparasites appeared to be more spatially dependent than that of endoparasites. Furthermore, the spatial independence of compositional turnover in endoparasites was mainly due to subcommunities harboured by female bats. In other words, patterns of zeta decay in female as compared to male bats
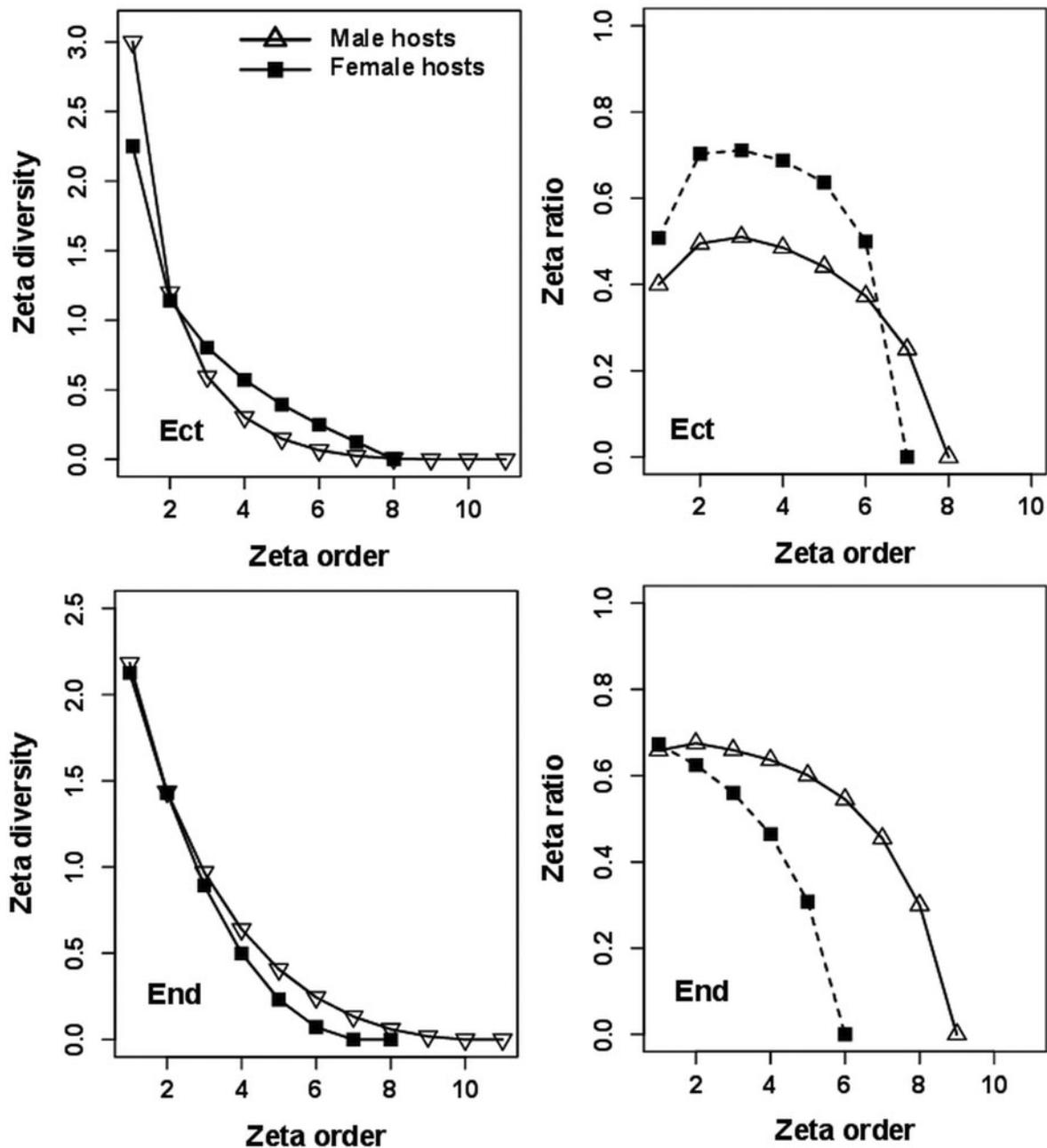
Fig. 3. Zeta diversity decline and retention rate curves for ecto- (Ect) and endoparasite (End) infracommunities harboured by male and female *Miniopterus nata-lensis* at the Koegelbeen Sinkhole. The legend on the zeta decline plot for ectoparasites also applies to other plots.

contradicted our prediction, whereas our prediction regarding host sex-specific patterns of zeta decline of parasites was supported. In particular, the average number of shared parasite species declined faster in female bats, although this was true for component communities only. In infracommunities, the rates of zeta decline of parasites did not differ substantially between male and female hosts.

Ectoparasites and endoparasites

Compositional turnover of both ecto- and endoparasites among individual bats was characterized by a decline of zeta diversity to zero at zeta orders smaller than the total number of infected bats (except for endoparasites at Table Farm; Table 1). This means that (a) no parasite species infected all bats at a given locality and (b) the entire parasite community was well represented by

parasitological examination at each site. The modal shape of the retention rate curves supported these conclusions. Indeed, zeta ratios attained their highest values at low and median zeta orders (from the lowest zeta order 2 in endoparasites at Koegelbeen Sinkhole to the highest zeta order 6 for endoparasites at Table Farm) and dropped to zero at high zeta orders. The modal shape of the retention rate curve indicating fast loss of rare species (the fastest for endoparasites at Koegelbeen Sinkhole), and either medium (ecto- and endoparasites at Koegelbeen Sinkhole) or slow (ectoparasites at Sudwala Caves and endoparasites at Table Farm) loss of widespread species (McGeoch *et al.*, 2019). The form of zeta decline for both ecto- and endoparasites in infracommunities consistently indicated a lack of structure. The main reason for this is the ephemerality of an infracommunity with its lifespan limited by the lifespan of an individual host (Poulin, 2007), although the longevity of
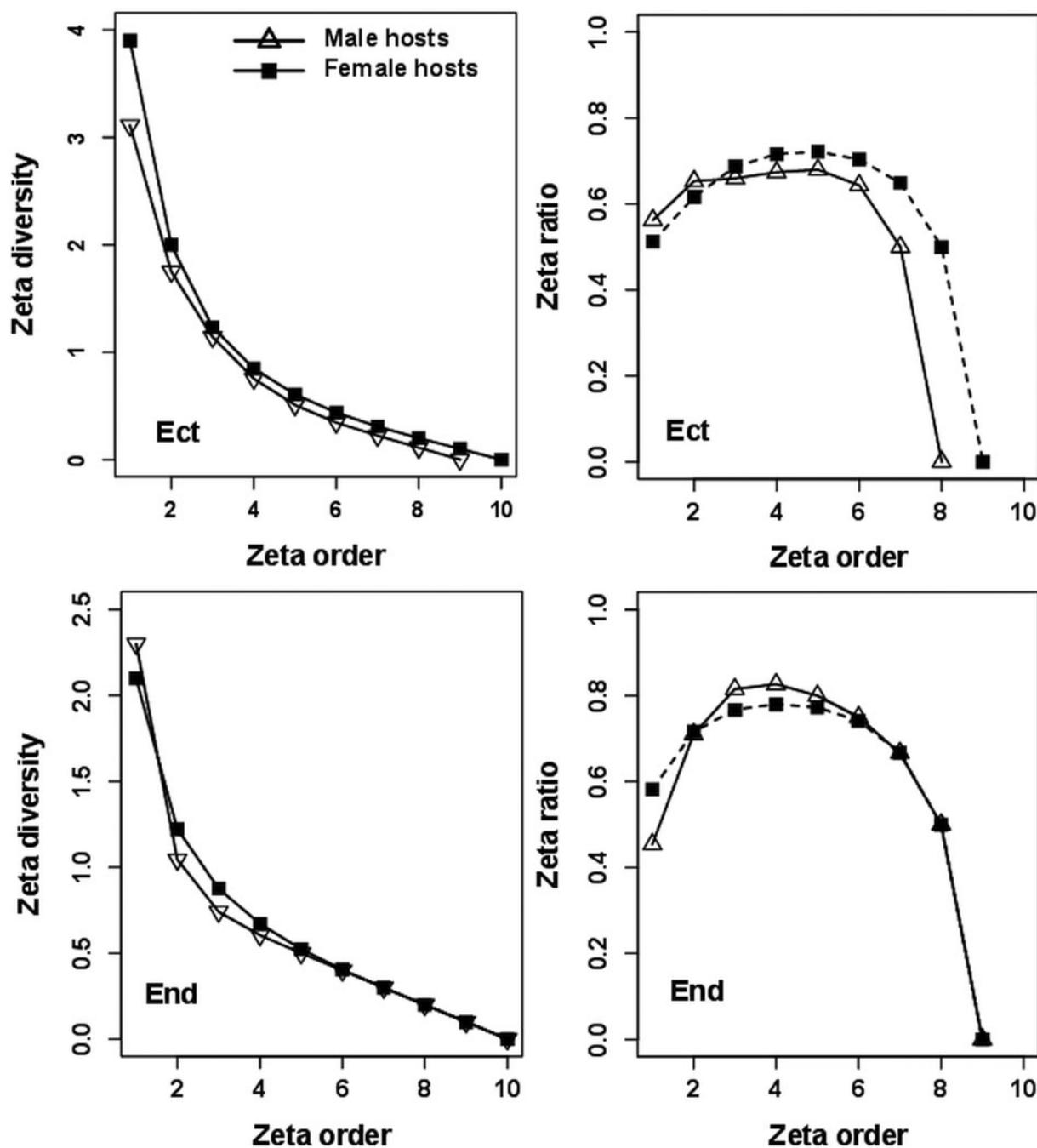
Fig. 4. Zeta diversity decline and retention rate curves for ecto- (Ect) and endoparasite (End) infracommunities harboured by male and female *Miniopterus natalensis* at the Table Farm. The legend on the zeta decline plot for ectoparasites also applies to other plots.

bats is much greater than that of non-flying mammals of similar size (e.g. Wilkinson and South, 2002). This is especially true for ectoparasites because many of them infest the host only for the time needed to engorge and then fall off (Lehane, 2005). For example, the ectoparasite assemblages of *M. natalensis* are dominated by macronyssid mites and nycteribiid bat flies. Adults of the former come into contact with their hosts only when a bloodmeal is due, are fast feeders, engorge within minutes and subsequently leave the host (Radovsky, 1994; Dowling, 2006), whereas the latter readily disperse among bat individuals (Dick and Patterson, 2006).

The lack of structure in endoparasite assemblages may be associated with species that can be easily exchanged between individual bats inhabiting the same roost, such as directly transmitted nematodes or the vector-transmitted filarial nematode

L. chiropterorum. Little is known about the life cycle of any of the monoxenous nematodes of bats. According to Moravec *et al.* (1987), some species of *Aonchotheca* are monoxenous whereas others are heteroxenous, with oligochaetes as typical intermediate hosts. Given the prey spectrum of *M. natalensis* and that prey is caught on the wing (Skinner and Chimimba, 2005; Schoeman and Jacobs, 2011), we consider it more likely that specimens of *Aonchotheca* collected in the present study, are monoxenous. It follows that the majority of nematodes collected from the bats in the present study, except for *Physaloptera* sp. and *L. chiropterorum*, have a direct life cycle. Junker *et al.* (2008) attributed the high prevalence of the molineid *Molinostrongylus ornatus* in *M. natalensis* to host density-induced accumulation of infective stages in the environment at De Hoop Guano Cave. *Miniopterus natalensis* form tightly packed clusters
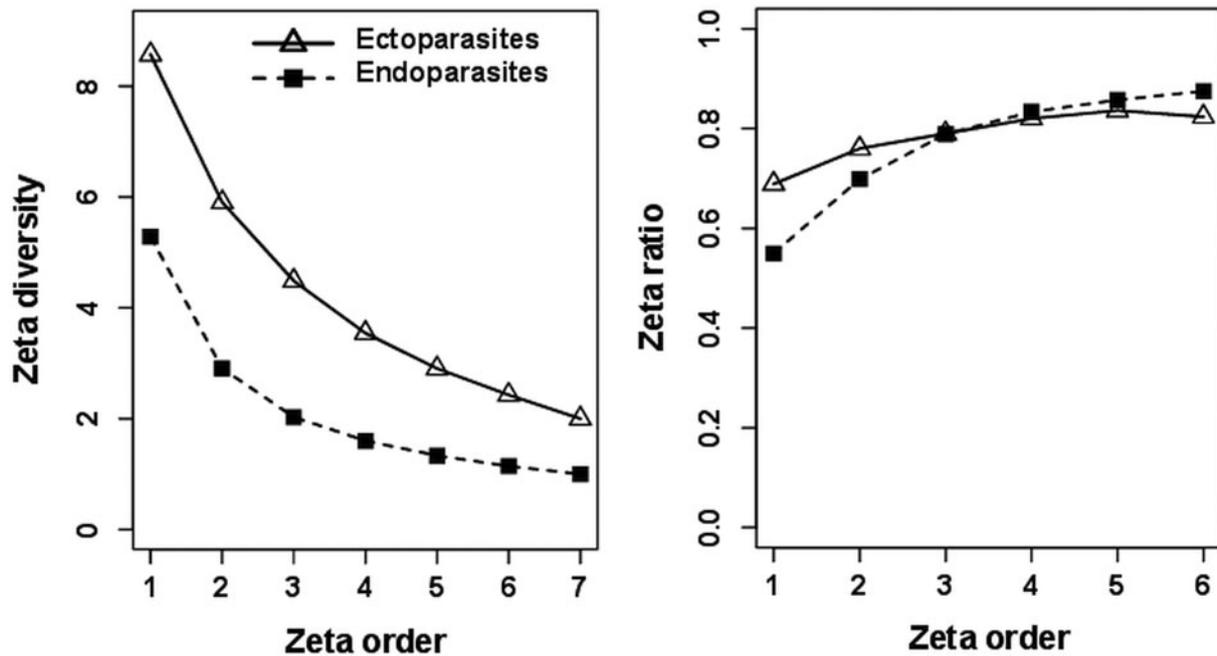
Fig. 5. Zeta diversity decline and retention rate curves for ecto- and endoparasite component communities harboured by *Miniopterus natalensis*. The legend on the zeta decline plot also applies to the retention rate plot.

Table 2. Zeta diversity decline and retention rate for ecto- and endoparasite component communities harboured by *Miniopterus natalensis* across sampling sites

Parasites (*S*, *N*)	Sex	$\zeta = 0$	ΔAIC	E/P	Coefficient	Shape	OrderMax
Ect (7, 15)	Both	–	0.75	E	−0.10	Modal	5
Ect (7, 12)	M	7	12.56	E	−0.22	Modal	2
Ect (6, 13)	F	6	16.52	E	−0.36	Modal	3
End (7, 12)	Both	–	44.37	P	−0.85	Ascending	6
End (7, 11)	M	–	47.85	P	−0.83	Ascending	6
End (5, 9)	F	–	8.51	P	−0.95	Ascending	4

Parasites (S, N): Ect, ectoparasites; End, Endoparasites; S, number of sites; N, number of species. Sex: Both, both male and female hosts; M, male hosts; F, female hosts. $\zeta = 0$: zeta order at which zeta diversity attains zero, ΔAIC: difference in Akaike Information Criterion between the negative exponential and the power-law regression of zeta diversity values against zeta order, E/P: whether the negative exponential (E) or the power-law (P) fit was found to be the best; Shape: shape of zeta retention curve; OrderMax: zeta order at which zeta ratio attains maximal value.

in their roosts (Skinner and Chimimba, 2005), and it is likely that this proximity facilitates parasite transmission. To date, the life cycle of *L. chiropterorum* or any of its congeners is unknown, but filariae, in general, are transmitted by haematophagous arthropods. The genus *Litomosa* is closely related to another onchocercid genus parasitic in bats, *Litomosoides* (Junker *et al.*, 2009), which is transmitted by haematophagous macronyssids (Guerrero *et al.*, 2006). It thus seems likely that *L. chiropterorum* is freely transmitted between individuals of *M. natalensis* by their macronyssid parasites during blood feeding, contributing to the observed lack of structure in the endoparasite assemblages of *M. natalensis*.

In contrast to infracommunities, the patterns of species turnover in component communities differed between ecto- and endoparasites. The shape of the zeta decline for ectoparasites was exponential. However, there was little difference between power and exponential fit (ΔAIC = 0.75). This suggests that both stochastic and deterministic (niche-driven) processes play a role in ectoparasite species assembly. In other words, turnover of some ectoparasite species among sampling sites was stochastic, whereas the distribution of other ectoparasite species among these sites was affected by their environmental preferences. For

example, streblid bat flies of the genus *Ascodipteron* spend their entire life on a bat, with females embedded in the skin of their hosts (Maa, 1965), whereas spinturnicid mites do not leave the wing membrane of their host (Dick and Patterson, 2006). The strong dependence of these species on an individual bat host is presumably accompanied by their low dependence on external environmental conditions so that their distribution across sampling sites is stochastic. On the other hand, *I. simplex* is a tick with a three-host life cycle: each active stage attaches to a host for a period of several days, engorges and falls off; moulting takes place in the roost substrate and each emerging stage has to find a new host to further continue its development (Durden, 2006; Sándor *et al.*, 2019). Obviously, once detached from their bat hosts, these ticks are strongly influenced by external conditions. Given the strong environmental preferences (i.e. distinct environmental niche) reported for many ixodid species, *I. simplex* may be responsible for the niche-associated component in the parametric form of the zeta decline for ectoparasites.

The shape of the zeta decline across component communities of endoparasites clearly demonstrated unequal probabilities among helminth species to occur across compound communities. In other words, the most likely assembly processes of component
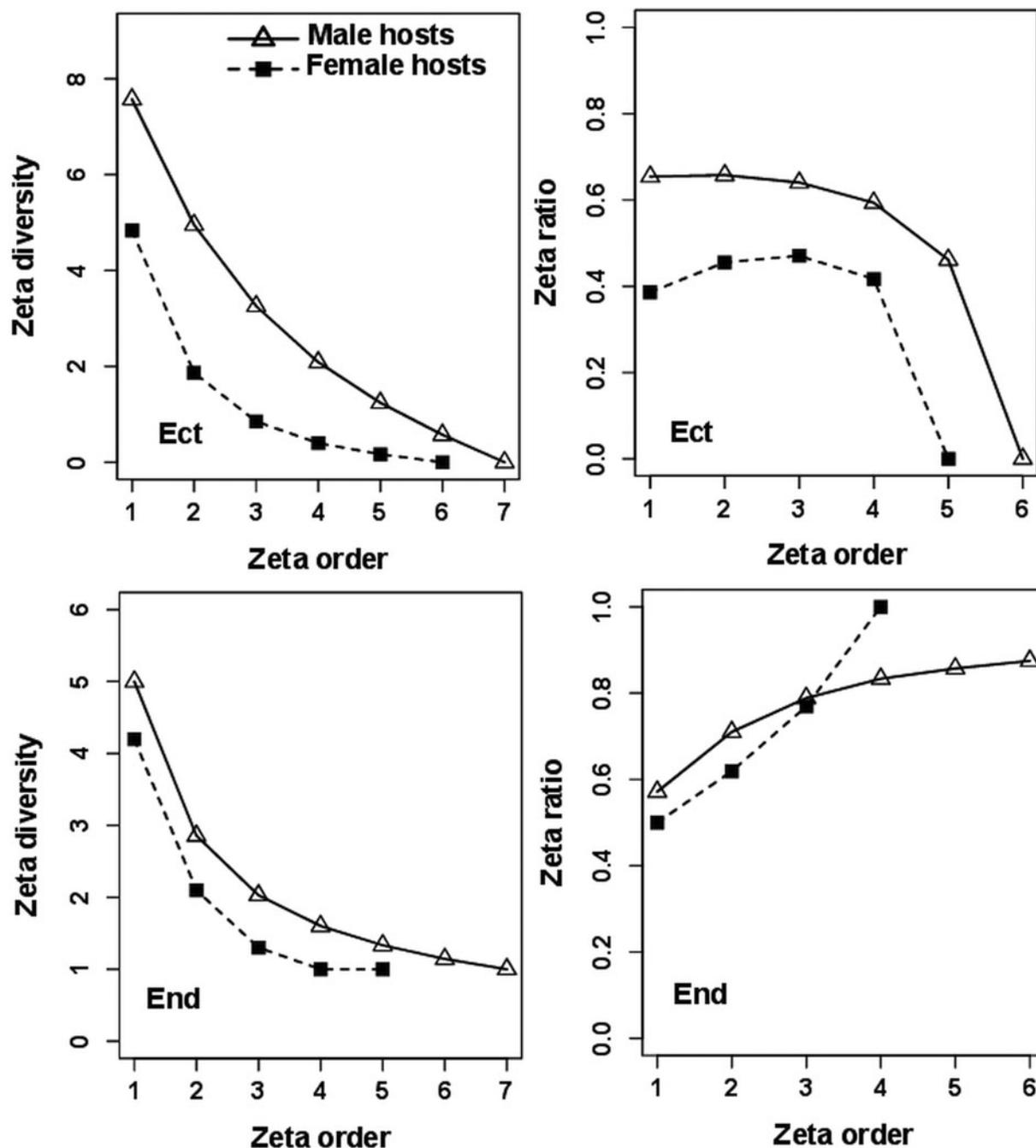
Fig. 6. Zeta diversity decline and retention rate curves for ecto- (Ect) and endoparasite (End) component communities harboured by male and female *Miniopterus natalensis*. The legend on the zeta decline plot for ectoparasites also applies to other plots.

communities of endoparasites are niche-based. The two main components of a niche for any parasite species are the component associated with its hosts (see Poulin *et al.*, 2011 for review) and another associated with the external environment. Evidently, the host-associated niche component does not play any role when parasite communities harboured by the same host species are considered, as in the present study. Consequently, the pattern of compositional change of endoparasite communities was most likely determined by (a) differences in the degree of environmental tolerance/environmental preferences of immature stages among both monoxenous and heteroxenous taxa and (b) differences in the availability of intermediate hosts among sampling localities for heteroxenous endoparasites. For example, variation in air temperature and vegetation structure among sites may affect the occurrence of nematodes with direct life cycles because they

require suitable environments for egg survival and larval development (e.g. Hulbert and Boag, 2001). The abundance of various terrestrial arthropods that serve as intermediate hosts for many hymenolepidid cestodes (Georgiev *et al.*, 2006) and nematodes such as *Physaloptera* species (Anderson, 2000) as well as terrestrial molluscs and aquatic insects that serve as intermediate hosts for trematodes such as *Paralecithodendrium* species (Kudlai *et al.*, 2015), is most certainly affected by environmental conditions and will thus vary among localities. This, in turn, leads to variation in the species composition of endoparasite communities harboured by the same host species at these localities (e.g. Dybing *et al.*, 2013; Spickett *et al.*, 2017).

Spatial decay of zeta diversity for both ecto- and endoparasites, respectively, was pronounced at lower zeta orders only, indicating that changes in species composition over space were due to rare

Table 3. Zeta diversity decay across space for ecto- and endoparasite component communities harboured by *Miniopterus natalensis* across sampling sites

Parasites	Sex	Zeta order	Intercept	Coefficient	% of deviance explained
Ect	Both	2	7.35	−0.02	0.11
		3	6.74	−0.002	0.17
		4	5.78	−0.002	0.13
		5	5.23	−0.002	0.08
	M	2	6.28	−0.002	0.15
		3	5.10	−0.002	0.20
		4	3.55	−0.001	0.10
		5	2.22	−0.0007	0.03
	F	2	3.89	−0.001	0.06
		3	3.47	−0.001	0.32
		4	1.58	−0.0003	0.02
End	Both	2	3.07	−0.0002	0.003
		3	2.32	−0.0003	0.01
		4	1.95	−0.0003	0.01
		5	1.33	0.00	0.00
	M	2	3.05	−0.0002	0.00
		3	2.32	−0.0003	0.01
		4	1.95	−0.0003	0.01
		5	1.33	0.00	0.00
	F	2	2.10	0.00	0.00
		3	1.30	0.00	0.00
		4	1.00	0.00	0.00

Parasites: Ect, ectoparasites; End, endoparasites. Sex: Both, both male and female hosts; M, male hosts; F, female hosts.

species (e.g. Latombe *et al.*, 2018*b*). Furthermore, the number of shared ectoparasite species decreased with the distance between localities faster than the number of shared endoparasites for the same zeta order. This suggests that endoparasite turnover was much less dependent on the distance between sites than that of ectoparasites. At first glance, this contradicts our results on mainly random (i.e. stochastic) ectoparasite *vs* structured (i.e. deterministic) endoparasite communities. However, it is still unclear whether the distance decay in community similarity arises from random and dispersal-related (i.e. neutral; Hubbell, 2001) or niche-related processes (Cottenie, 2005), with numerous empirical studies supporting either the former or the latter hypothesis (e.g. Carola and Baselga, 2018 *vs* Bahram *et al.*, 2013, respectively). In other words, stochastic *vs* niche-based assembly processes may not necessarily be associated with the relationship between the average number of shared species and the average distance between communities. In indirect support of this, distance explained only a small part of the variation in bat gene flow between these sites, suggesting that other factors, besides distance, determine bat movement between sites (Miller-Butterworth *et al.*, 2003).

Male hosts and female hosts

In contrast to the majority of small mammals, parasitism in chiropterans is mainly female- rather than male-biased (see Krasnov *et al.*, 2012 for review). The reason behind this difference is that, for example, rodent males are characterized by higher mobility and lower immunocompetence (due to the immunosuppressive effect of testosterone) and thus have a higher chance to encounter

parasites, combined with a reduced ability to cope with parasitism (see Krasnov *et al.*, 2012 and references therein). In bats, female-biased parasitism has also been attributed to reduced resistance to parasites (in terms of, for example, immunocompetence) in reproducing females at early stages of pregnancy (McLean and Speakman, 1997; Christe *et al.*, 2000) or increased survival of parasites due to presumably better nutrition status in non-reproductive females (Christe *et al.*, 2003, 2007). However, in this study, we examined parasite assemblages in adult male and adult non-reproductive female bats only; consequently, behavioural (in terms of mobility) and hormonal differences between the sexes were likely minor, which resulted in similar parasite species richness in male and female *M. natalensis*. Nevertheless, the shape of zeta decline was steeper for parasites harboured by the female as compared to male bats. Furthermore, the retention rate curves suggested that common ectoparasites are more likely retained across sites in male-harboured subcommunities than in female-harboured subcommunities. This may be the result of differential survival of ectoparasites on males and females but in an opposite manner to that found by Christe *et al.* (2007).

Another explanation for the observed difference in retention rates of ectoparasites between male and female bats might be associated with the increased mobility of male *M. natalensis* within their natal area (van der Merwe, 1975), exposing them to ectoparasites from other caves. Like female *M. natalensis*, male *M. natalensis* bats return to their natal caves (van der Merwe, 1973; Miller-Butterworth *et al.*, 2003) and occupy the same maternity caves with females and pups, after mating has occurred in hibernacula (van der Merwe, 1973). However, males then leave the maternity caves for other as yet unknown caves
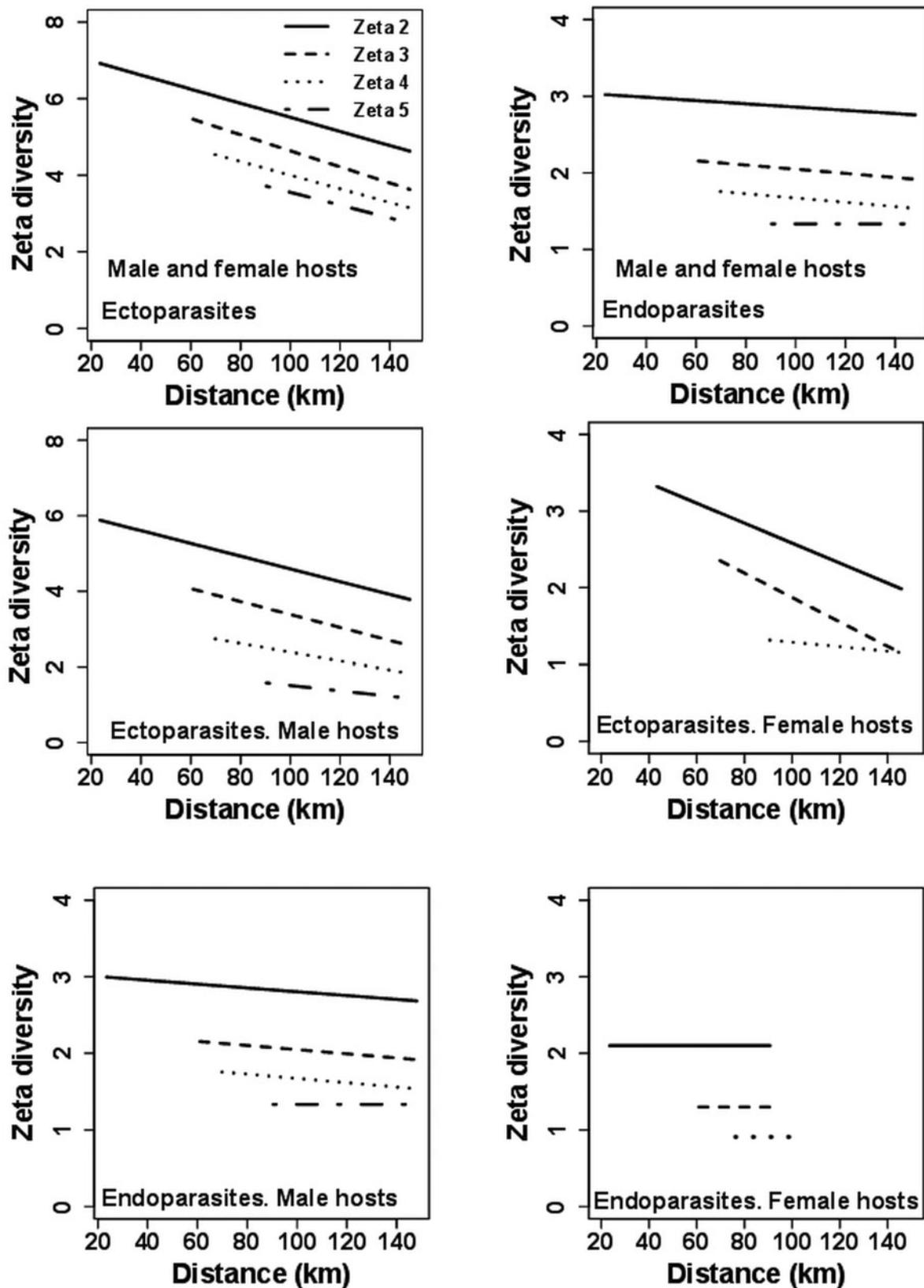
Fig. 7. Distance decay of zeta diversity for ecto- and endoparasite component communities harboured by *Miniopterus natalensis* for zeta orders 2–5 (separately for both sexes, male hosts only and female hosts only).

(van der Merwe, 1975), where they may be exposed to other ecto-parasites either from the caves or other species of bats with whom they share these caves.

In addition, the ascending retention rate curve of endopara-sites in subcommunities of female bats hinted that the sampling

extent was, perhaps, smaller than the entire female-associated hel-minth metacommunity (McGeoch *et al.*, 2019). Indeed, no female bats were captured at the Steenkampskraal Mine, while the only three females captured at De Hoop Guano Cave were not infected with any helminths.

Patterns of zeta decay for ectoparasites did not reveal any substantial differences between subcommunities on male and female bats in the association between ectoparasite zeta diversity and distance. However, the compositional similarity in endoparasite subcommunities harboured by female bats did not differ between sampling sites situated at either short or long distances. In other words, the dependence of endoparasite turnover among localities on the distance between these localities was due to parasites residing in male but not female hosts. Here, too, these differences might be associated with differences in mobility between males and females. Although nuclear and mitochondrial DNA supports strong philopatry in both sexes of *M. natalensis*, additional movement of males within their natal area compared to females is reflected in a weak but significant correlation between genetic variation and distance for females suggesting that females may move less than males (Miller-Butterworth *et al.*, 2003; see also van der Merwe, 1973, 1975). This additional movement by males may also be accompanied by additional parasite exchange between males. Mark-recapture studies support the notion that movement of both males and females within the natal area is more complex and involves the use of more caves, at least by males, than just those associated with hibernation or the rearing of pups. Females, and some males, form pre-maternity colonies in different caves used for maternity colonies but tended to use the same set of caves each year. Males from different maternity colonies may disperse from these colonies, leaving females and pups behind, and move to, as yet, unknown caves. Some males return to the hibernacula and the maternity caves before the females and will leave the maternity caves as more females arrive from the pre-maternity caves for other unknown caves (van der Merwe, 1973, 1975). One of the consequences of these complex movement patterns to caves not used by females but shared with other males may be higher chances for parasite exchange between males from different localities, as well as exposure to a wider variety of possible intermediate hosts.

In conclusion, our results support the results of Krasnov *et al.* (2020) that the rules governing compositional turnover in parasite communities for the lowest hierarchical scale (infracommunities) are taxon-invariant. The patterns of compositional turnover in infracommunities were similar in ecto- and endoparasites, whereas the patterns of turnover in component communities differed between these parasite groups.

Conflict of interest. None.

Ethical standards. Ethical clearance for this research was obtained from the Science Faculty Animal Ethics Committee, University of Cape Town (ethics clearance number 2009\V16\SW). Permits to capture and handle bats were obtained from the relevant provincial authorities of the KwaZulu-Natal, Mpumalanga, Northern Cape, Eastern Cape and Western Cape Provinces, South Africa.

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