

Community structure of fleas within and among populations of three closely related rodent hosts: nestedness and beta-diversity

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SUMMARY

We studied nestedness and its relationships with beta-diversity in flea communities harboured by three closely related rodent species (*Rhabdomys pumilio*, *Rhabdomys intermedius*, *Rhabdomys dilectus*) at two spatial scales (within and among host populations) in South Africa and asked (a) whether variation in species composition of flea communities within and among host populations follows a non-random pattern; if yes, (b) what are the contributions of nestedness and species turnover to dissimilarity (= beta-diversity) among flea communities at the two scales; and (c) do the degree of nestedness and its contribution to beta-diversity differ among host species (social *vs* solitary) and between scales. We found that nestedness in flea assemblages was more pronounced (a) in social than solitary host species and (b) at lower (among host individuals within populations) than at higher scale (among host populations). We also found that higher degree of nestedness was associated with its higher contribution to beta-diversity. Our findings support earlier ideas that parasite community structure results from the processes of parasite accumulation by hosts rather than from the processes acting within parasite communities.

Key words: Nestedness, beta-diversity, fleas, sociality, *Rhabdomys*.

INTRODUCTION

One of the main aims of community ecology is to understand mechanisms governing species composition of biological communities (Gotelli and Rohde, 2002). Numerous studies carried out on various taxa in various geographic regions and at different spatial scales demonstrated that communities of some taxa were structured, and their species composition conformed to one or another assembly rule being thus more or less predictable (Poulin and Valtonen, 2001; Valtonen *et al.* 2001; Dupont *et al.* 2003; Lewinsohn *et al.* 2006). On the contrary, communities of other taxa seemed to represent random species assemblages (Matthews, 1982; Gotelli and Rohde, 2002; Pitzalis *et al.* 2010). Moreover, the pattern of organization in many communities varies depending on the spatial scale being considered (Levin, 1992; Gotelli and Ellison, 2002; Sanders *et al.* 2007). For example, communities of some

taxa were found to be randomly assembled at lower spatial scales, but appeared to be structured at higher spatial scales (e.g. Korralo-Vinarskaya *et al.* 2013). This suggests that further investigation of the effect of spatial scale on community organization is crucially important (e.g. Krasnov *et al.* 2011, 2015; Andersson *et al.* 2014; Hoset *et al.* 2014; Kadowaki and Inouye, 2015) and may help future predictions of the response of biological communities to both stochastic and deterministic disturbance events such as climate change and habitat alteration at different scales.

Any study of spatial variation of community structure is inevitably confronted by a methodological problem of how to define community boundaries (Loreau, 2002). It is relatively easy for some free-living taxa such as freshwater species in isolated water bodies, but it is not self-evident for the majority of terrestrial or marine communities. On the contrary, parasitic animals represent a convenient model to study the spatial variation of community organization because the spatial distribution of these species is not continuous, but consists of an array of inhabited patches represented by their hosts, while the environment between these patches is

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unfavourable. An assemblage of parasites exploiting the same host species is thus fragmented, for example, among host individuals within a locality and among host populations across localities. Terminology commonly accepted in parasitological studies for distinguishing between a parasite community infesting an individual host (=infracommunity) and a parasite community infesting a set of conspecific hosts inhabiting the same locality (=component community) is well entrenched in the literature (Holmes and Price, 1986; Poulin, 2007).

Nestedness is one of the most common patterns of community organization of fragmented or island habitats (Patterson and Atmar, 1986; Wright and Reeves, 1992). A nested pattern of organization occurs when species-poor communities are composed of species that represent non-random subsets of progressively richer communities (Wright and Reeves, 1992; Rohde *et al.* 1998). This pattern proved to be a common feature in communities of free-living species (Dupont *et al.* 2003; Wethered and Lawes, 2005; Simaiakis and Martínez-Morales, 2010; Rodríguez and Ojeda, 2013). It is thus not surprising that significant nested patterns have been recorded in parasite communities as well (Poulin and Valtonen, 2001; Šimková *et al.* 2001; Timi and Poulin, 2003; González and Poulin, 2005; Krasnov *et al.* 2005, 2011). Nevertheless, inconsistencies have been reported for the manifestation of nestedness in parasite communities. For example, helminth communities of a fish seemed to be randomly assembled across host populations, but nestedness was found within host populations, albeit in some but not other seasons (Timi and Poulin, 2003). In contrast, monogenean assemblages on the roach (*Rutilus rutilus*) were randomly assembled within host populations, whereas nestedness was found among host populations (Šimková *et al.* 2001). Krasnov *et al.* (2011) presented evidence for nestedness in communities of two ectoparasite taxa (fleas and gamasid mites) among localities within a geographic region and among large geographic regions, although manifestation of nestedness was stronger at the former (i.e. lower) scale. Nevertheless, although nestedness has been repeatedly studied in helminth parasites of fish hosts (Rohde *et al.* 1998; Poulin and Valtonen, 2001; Šimková *et al.* 2001; Timi and Poulin, 2003; González and Poulin, 2005; González and Oliva, 2009), nestedness of ectoparasite communities of terrestrial hosts have received less attention (Goüy de Bellocq *et al.* 2003; Presley, 2007; Patterson *et al.* 2009; Krasnov *et al.* 2005, 2011) and deserves further investigation for the sake of elucidating general patterns.

An important aspect of nestedness is that it can affect dissimilarity among communities, in particular patterns of beta-diversity (Harrison *et al.* 1992; Baselga *et al.* 2007). Beta-diversity (Whittaker, 1972) is a measure of dissimilarity in species

composition of biological communities among sampling sites or localities and is a useful tool that facilitates a better understanding of spatial variation in biological communities (e.g. Fargione and Tilman, 2002; Legendre *et al.* 2005; Seidler and Plotkin, 2006). In fact, it is commonly accepted that the total amount of dissimilarity in species composition among communities (i.e. beta-diversity) is a net result of the actions of two opposing processes, namely nestedness and spatial species turnover (i.e. the replacement of one species by another across space as a consequence of environmental and historical differences among localities; Qian *et al.* 2005) (Baselga, 2010). It is difficult to understand mechanisms underlying spatial variation in community structure without disentangling these two processes.

Despite the suitability of parasites as model organisms for investigations of spatial variation in community structure, only a few studies examined nestedness and its contribution to beta-diversity of their assemblages simultaneously (e.g. Krasnov *et al.* 2011), although this was done for many free-living taxa (Baselga *et al.* 2012; Carvalho *et al.* 2012; Baselga, 2013; Si *et al.* 2015; Xu *et al.* 2015). Moreover, community ecology of ectoparasites of terrestrial animals has mainly been studied in the Palearctic realm (e.g. Goüy de Bellocq *et al.* 2003; Korallo-Vinarskaya *et al.* 2009; Krasnov *et al.* 2010b, 2011), whereas ectoparasites and their hosts in other biogeographic realms received less attention (but see Matthee and Krasnov, 2009; Lareschi and Krasnov, 2010). Here, we studied nestedness and its relationships with beta-diversity in flea communities harboured by three closely related rodent species (*Rhabdomys pumilio*, *Rhabdomys intermedius*, *Rhabdomys dilectus*; Du Toit *et al.* 2012) at two spatial scales (within and among host populations) in South Africa. Fleas are obligatory haematophagous ectoparasites that are most abundant and diverse on small- and medium-sized burrowing mammals. In most flea species, pre-imaginal stages are spent off the host, whereas adults feed intermittently on the host (Marshall, 1981; Krasnov, 2008). *Rhabdomys* is one of the most common and broadly distributed rodent genera in South Africa. More recently, it has been found that animals considered earlier as a single species (*R. pumilio sensu lato*) that demonstrates astoundingly flexible and diverse social organization (Schradin, 2005; Schradin and Pillay, 2005; Schoepf *et al.* 2015) in reality belong to at least four allopatric species inhabiting different biomes in South Africa (Du Toit *et al.* 2012). Apart from the ecological differences between the species, the taxon also display distinct social organization ranging from group-living in the western more xeric regions of the country (e.g. *R. pumilio*) to being strictly solitary in the more mesic regions (e.g. *R. dilectus*). We asked (a) whether variation in species composition of flea

infra- (i.e. among host individuals within the same host population) and component (i.e. among host populations across populations of the same host) communities harboured by different *Rhabdomys* species follows a non-random pattern; and, if yes, (b) what are the contributions of nestedness and species turnover to dissimilarity (=beta-diversity) of flea communities and (c) do the degree of nestedness and its contribution to beta-diversity differ among host species and between scales (within- vs among host populations)?.

We expected among-host species differences in the manifestation of flea community structure and beta-diversity of these communities because *R. pumilio* and *R. intermedius* are social and have smaller geographic and home range sizes, whereas *R. dilectus*, is solitary and has larger geographic and home range sizes (Schradin and Pillay, 2004, 2005; Schradin, 2005; Schradin *et al.* 2010; but see Du Toit *et al.* 2012). Social organization should have a direct influence on host density and inter-individual contact rates within a host population (i.e. increased contact rates with increased sociality) with profound consequences for parasite transmission (Altizer *et al.* 2003). Moreover, spatial distribution of individual hosts belonging to social species, in contrast to solitary species, is likely non-random. Consequently, we predicted that structure of flea communities will be more pronounced in social *R. pumilio* and *R. intermedius* than in solitary *R. dilectus*. As a result, infra- and component communities of fleas harboured by the former will be more dissimilar than those harboured by the latter.

We expected between-spatial scale differences because parasite assemblages of the same host species are thought to be governed by epidemiological processes acting at the level of parasite individuals (Morand *et al.* 2002), whereas parasite assemblages across host populations are mainly affected by biogeographic and historical processes (Brooks *et al.* 2006). According to the original ideas of the nested subset pattern (Patterson and Atmar, 1986), its main drivers are biogeographic rather than epidemiological processes. Therefore, when parasite communities were considered, the component community level has been argued to be more relevant for the search of this pattern than the infracommunity level (González and Poulin, 2005). Consequently, we predicted that (a) nestedness of flea infracommunities (i.e. within host populations) will be less pronounced than nestedness of flea component communities, (b) contribution of nestedness to beta-diversity of flea infracommunities within host populations will be lower than that of the spatial species turnover, whereas the opposite would be the case for flea component communities and (c) beta-diversity of flea infracommunities will be lower than that of component communities.

MATERIALS AND METHODS

Study design

Rodents were trapped at 25 localities across South Africa during austral spring and summer (warm-dry period) in 2010–2013. In each locality, Sherman-type live-traps were placed in five trap lines 25 m apart and within lines spaced 10 m apart. Trap sessions lasted 4–7 days per locality. Adult rodents (body mass >30 g) were targeted and once trapped, placed in labelled plastic bags and euthanized with sodium pentobarbital (200 mg kg⁻¹; ethical approval reference number SU-ACUM11-00004). This study was part of a much larger project in which all trapped animals were fully parasitologically examined. Fleas were removed by brushing each rodent body over a white plastic tray. Brushing continued until no additional fleas were removed for 2–3 consecutive brushes. A total of 1047 rodents were examined for fleas. Fleas collected for each individual host were stored in separate labelled tubes filled with 96% ethanol. All fleas were mounted on slides (see details in Van der Mescht *et al.* 2013) and a thorough morphological identification was done using a light microscope (Leica DM 3000, Leica Microsystems, Wetzlar, Germany) and the taxonomic identification keys by Segerman (1995).

Data organization

We included in the analyses only localities in which at least two flea species were recorded and at least nine rodents belonging to the same *Rhabdomys* species were captured (Fig. 1; Table 1). For each of the three *Rhabdomys* species, presence/absence data matrices were constructed for: (a) each host population (16 matrices in total) with flea species as rows and rodent individuals as columns and (b) total set of host populations separately for each of the three host species with flea species as rows and host populations (=localities) as columns. In addition, we calculated mean infra- and component community species richness as well as flea prevalence (proportion of infested individuals).

Measuring community structure and beta-diversity components

We estimated the degree of nestedness for each matrix. Various measures have been proposed to measure nestedness and each of them has certain merits and shortcomings (reviewed by Almeida-Neto *et al.* 2008). Almeida-Neto *et al.* (2008) proposed a nestedness metric based on overlap and decreasing fill of a matrix (NODF). Although absolute values and *Z*-transformed scores of NODF are not sensitive to matrix shape and size, it was found to be sensitive to matrix fill, except for *Z*-scores under some (fixed–fixed) null models (see Almeida-Neto

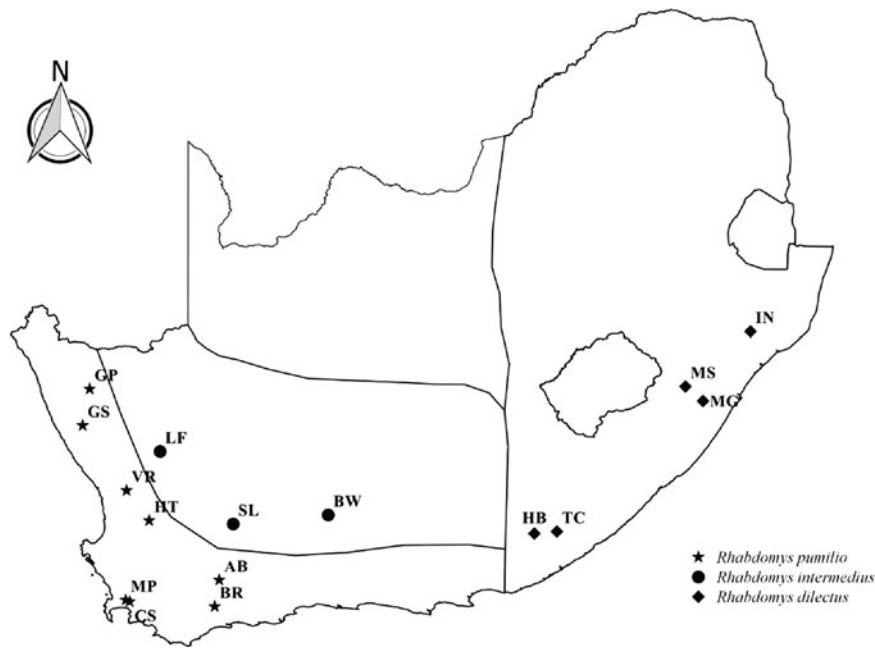


Fig. 1. A map of sampling localities sampled within the distribution range of *R. pumilio*, *R. intermedius* and *R. dilectus* in South Africa. Distribution for each species redrawn after Du Toit *et al.* (2012).

Table 1. Localities sampled, geographical coordinates, host sample size and flea prevalence (%) at each locality for the three *Rhabdomys* species. See Fig. 1 for spatial distribution of sampled locations throughout South Africa

Host species	Locality	Abbreviation	Latitude	Longitude	Host sample size	Prevalence (%)
<i>R. pumilio</i>	Springbok	GP	-29.70	18.03	32	56.25
	Garies	GS	-30.43	17.89	27	40.74
	Vanrhynsdorp	VR	-31.73	18.77	25	60.00
	Hottentotsholland	HT	-32.33	19.22	9	55.56
	Anysberg	AB	-33.52	20.62	33	48.48
	Kanu	CS	-33.95	18.83	67	38.80
	Mooiplaas	MP	-33.92	18.75	35	37.14
	Buffeljagsrivier	BR	-34.05	20.53	27	70.37
<i>R. intermedius</i>	Loeriesfontein	LF	-30.95	19.44	31	77.42
	Sutherland	SL	-32.40	20.90	25	56.00
	Beaufort West	BW	-32.22	22.80	33	36.36
<i>R. dilectus</i>	Inkunzi Lodge	IN	-28.56	31.24	9	55.56
	Mt Shannon	MS	-29.65	29.94	30	53.33
	Mt Gilboa	MG	-29.94	30.29	27	74.07
	The Croft	TC	-32.55	27.37	25	80.00
	Hogsback	HB	-32.59	26.92	10	50.00

et al. 2008 for details). We investigated the correlation between matrix fill and absolute values of NODF in our data and found a significant correlation for infracommunity data sets; Spearman’s correlation coefficient 0.52 ($P < 0.05$). Visual examination of the scatterplot indicated that the correlation between absolute values of NODF and matrix fill was due to one locality for *R. dilectus* (DE, Dohne). After the removal of this locality, the correlation between absolute values of NODF and matrix fill was not significant; Spearman’s correlation coefficient 0.46 ($P > 0.05$).

One of the vital features of the NODF metric is its ability to calculate nestedness among columns (N_{COL}) and rows (N_{ROW}) independently (Almeida-Neto *et al.* 2008). We evaluated N_{COL} for flea infracommunities within host population and for component communities within each of the three *Rhabdomys* species. N_{COL} were calculated using *nestednodf* function of the package ‘vegan’ (Oksanen *et al.* 2015) in R v3.1.3 (R Development Core Team, 2015). We assessed the statistical significance of each matrix against a series of simulated random

matrices by implementing function *oecosimu* of the package ‘vegan’. This function evaluates significance of metric (i.e. NODF) calculated for an observed community matrix using a series of simulated random community matrices based on the specific null model chosen. Standardized effect sizes (SES) were calculated as a *Z*-transformed score for each observed matrix and then the observed index was compared with the distribution of indices generated by 1000 randomly assembled null matrices.

Choosing a null model is one of the most controversial topics in nestedness analysis and it is important to choose a model that is biologically realistic for a taxon of interest (Ulrich *et al.* 2009). Presence of a flea species on a given host within a locality/region may be caused by horizontal transmission between co-occurring hosts (Krasnov and Khokhlova, 2001; Krasnov *et al.* 2004), whereas presence of a flea species on a given host among localities/regions seems to be determined by environmental preferences (Krasnov *et al.* 2006a; Vinarski *et al.* 2007). In our study, we evaluated the presence of flea species, within populations among host individuals (i.e. infracommunity scale) and among host populations (i.e. component community scale). Thus, for the sake of biological realism, flea species presences were (a) randomly assigned within columns (within an individual host) and within rows (among individual hosts) of simulated matrices at the infracommunity scale and (b) randomly assigned within columns (within a host population) and fixed within rows (among host populations) of simulated matrices at the component community scale. In other words, we chose to use equiprobable–equiprobable (EE) algorithm for constructing null matrices at infracommunity scale and fixed–equiprobable (FE) algorithm for constructing null matrices at component community scale (see Ulrich *et al.* 2009 for a review of null models). To make the results of the analyses comparable between scales, we then re-tested significance of nestedness in component communities of fleas using EE algorithm.

A Mantel test was performed to investigate the role of spatial distance on pairwise dissimilarity between sites by implementing function *mantel* of the package ‘vegan’. Then, we calculated beta-diversity and the contributions of nestedness and species turnover to it: (a) among host individuals within each population (infracommunity scale) and (b) among host populations (component community scale). Several different measurements have been proposed to measure beta-diversity of which pairwise dissimilarity have been most commonly used (Koleff *et al.* 2003). This method has been applied to assess multiple-site dissimilarity by calculating the average dissimilarity across all sites (e.g. Izsak and Price, 2001; Gaston *et al.* 2007; McKnight *et al.* 2007; Melo *et al.* 2009; Leprieur *et al.* 2011), but is constrained in its ability to observe the

extent of change in shared species between pairs of sites (Diserud and Ødegaard, 2007; Baselga, 2013; Ricotta and Pavoine, 2015). Given that infra- and component flea communities are collections of interacting units (due to host movement and contact between individuals and populations) we chose to use the multiple-site dissimilarity measure as proposed by Ricotta and Pavoine (2015). The contribution of nestedness (β_N) and turnover (β_T) to beta-diversity (β) was estimated for each matrix by implementing the multiple-site metric based on Jaccard similarity recently proposed by Ricotta and Pavoine (2015). These measures are invariant to any matrix ordering, but are intrinsically correlated with matrix size. We investigated the correlation between matrix size and β_N , and matrix size and β_T in our data and found a significant correlation for β_T but not for β_N in the infracommunity data sets (Spearman’s correlation coefficients 0.50, $P=0.05$ and 0.45, $P>0.05$, respectively). Then, we compared independent variables (a) the log-transformed degree of nestedness (N_{COL}), (b) β_N , (c) β_T and (d) β separately to a single dependent variable, among host species, within the infracommunity scale using Tukey–Kramer tests for unequal sample sizes.

RESULTS

Flea infestation rate, diversity and species composition

A total of 374 flea individuals were recorded, representing 11 species, from *R. pumilio*, 284 individuals, representing five species, from *R. intermedius* and 639 individuals, representing, eight species from *R. dilectus*. Flea prevalence varied between host species with the highest mean prevalence in *R. dilectus* (65.35%), followed by *R. intermedius* (56.18%) and *R. pumilio* (48.24%) (Table 1). Mean infracommunity richness varied between host species (Table 2). Mean component community richness was the highest in *R. pumilio*, followed by *R. dilectus* and then *R. intermedius* (Table 2). The two most common flea species on *R. pumilio* were *Chiastopsylla rossi* (occurred on all eight populations) and *Listropsylla agrippinae* (occurred on seven of the eight populations; Supplementary Table S1). The same two flea species were also recorded from all three *R. intermedius* populations (Supplementary Table S2). The most common flea species on *R. dilectus* were *Ctenophthalmus calceatus* (occurred on all five populations) and *Dinopsyllus ellobius* (occurred on four of the five populations) (Supplementary Table S3).

Degree of nestedness and beta-diversity in infra- and component flea communities

The degree of nestedness, estimation of beta-diversity and the contribution of nestedness and species turnover to beta-diversity of flea species composition

Table 2. Multi-site measurements of mean flea species richness, the degree of nestedness (N_{COL}) (with corresponding standardized effect size (SES) and lower (LCL) and upper critical limits (UCL)), beta-diversity (β), contribution of turnover to beta-diversity (β_T), and contribution of nestedness to beta-diversity (β_N) within (across infracommunities) and among (across component communities) populations of *Rhabdomys* species

Scale	Host	Mean species richness (\pm S.E.)	N_{COL}	SES	LCL	UCL	β	β_T	β_N
Within populations	<i>R. pumilio</i>								
	GP	1.33 \pm 0.18	24.18 ^{ns}	1.56	12.42	25.16	0.92	0.18	0.74
	GS	1.73 \pm 0.27	50.00 ^{ns}	1.77	20.91	50.02	0.76	0.21	0.55
	VR	1.20 \pm 0.11	32.38 ^{ns+}	1.70	17.14	32.38	0.90	0.17	0.73
	HT	1.40 \pm 0.24	30.00 ^{ns}	0.34	0.00	50.00	0.87	0.27	0.60
	AB	1.50 \pm 0.20	48.75 ^{***}	7.96	12.92	27.22	0.90	0.16	0.74
	CS	1.35 \pm 0.11	41.54 ^{***}	6.57	17.85	28.46	0.89	0.08	0.81
	MP	1.38 \pm 0.14	43.59 ^{***}	3.65	15.37	34.62	0.87	0.15	0.72
	BR	1.32 \pm 0.11	38.60 [*]	2.08	21.04	36.84	0.84	0.37	0.47
	<i>R. intermedius</i>								
	LF	1.58 \pm 0.16	53.26 ^{***}	2.51	30.07	48.55	0.71	0.21	0.50
	SL	1.71 \pm 0.22	53.85 ^{ns}	0.99	28.57	58.24	0.64	0.25	0.39
	BW	1.58 \pm 0.19	59.85 ^{***}	4.23	18.18	43.94	0.81	0.14	0.67
	<i>R. dilectus</i>								
	IN	1.20 \pm 0.20	30.00 ^{ns}	0.46	0.00	40.00	0.90	0.30	0.60
	MS	1.25 \pm 0.11	26.67 ^{ns}	-0.28	18.33	34.17	0.87	0.31	0.56
	MG	1.55 \pm 0.15	55.79 ^{***}	3.07	26.32	47.90	0.73	0.15	0.58
	TC	1.85 \pm 0.13	50.53 ^{ns}	0.11	32.63	60.00	0.58	0.08	0.50
	HB	1.60 \pm 0.24	20.00 ^{ns}	-0.83	0.00	60.00	0.80	0.40	0.40
Among populations	<i>R. pumilio</i>	4.13 \pm 0.35	47.20 ^{ns}	3.51	27.02	41.73	0.69	0.30	0.39
	<i>R. intermedius</i>	3.33 \pm 0.33	55.56 ^{ns}	0.24	44.44	66.67	0.42	0.25	0.17
	<i>R. dilectus</i>	3.50 \pm 0.34	26.67 ^{ns}	0.77	13.33	33.33	0.63	0.33	0.30

See Table 1 for location information and Fig. 1 for spatial distribution of sampled locations throughout South Africa. ns – non-significant.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

+ marginally significant $P = 0.053$.

within and among host populations of each host species are presented in Table 2. Significant or marginally significant nestedness of flea infracommunities was found in five of eight, two of three and one of five populations of *R. pumilio*, *R. intermedius* and *R. dilectus*, respectively (Table 2). On average, the degree of infracommunity nestedness did not differ among host species (Tukey–Kramer test for unequal sample sizes, $P = 0.083$ – 0.945 ; Fig. 2). No significant nestedness in component communities of fleas was found in any host species, even when we tested it against the more liberal EE algorithm for constructing null matrices.

There was no significant correlation between spatial distance and pairwise dissimilarity between sites for any of the three *Rhabdomys* species (*R. pumilio*: $r = 0.342$, $P = 0.068$; *R. intermedius*: $r = -0.615$, $P = 0.833$; *R. dilectus*: $r = 0.182$, $P = 0.333$). Beta-diversity of flea infracommunities was generally higher in *R. pumilio* and lower in both *R. intermedius* and *R. dilectus* (Table 2). Although no significant differences in beta-diversity were found among host species, flea infracommunities of *R. pumilio* tended to be more dissimilar than those of *R. intermedius* (Tukey–Kramer tests for unequal sample sizes, $P = 0.061$). However, this was not the

case for differences between *R. pumilio* and *R. dilectus* (Tukey–Kramer tests for unequal sample sizes, $P = 0.180$) and *R. intermedius* and *R. dilectus* (Tukey–Kramer tests for unequal sample sizes, $P = 0.671$). Beta-diversity of flea component communities was the highest in *R. pumilio*, followed by *R. dilectus* and the lowest in *R. intermedius* (Table 2). Furthermore, beta-diversity of flea infracommunities was higher than that of component communities in *R. pumilio* (0.87 ± 0.02 vs 0.69 , respectively) and almost twice higher in *R. intermedius* (0.72 ± 0.05 vs 0.42 , respectively), whereas infra- and component communities of fleas harboured by *R. dilectus* did not differ in the degree of dissimilarity (beta-diversity = 0.77 ± 0.06 and beta-diversity = 0.77 , respectively).

Nestedness contributed more than spatial species turnover to beta-diversity of flea infracommunities in all populations of the three host species (except one population of *R. dilectus* in which nestedness and species turnover contributed equally to beta-diversity) (Table 2). Contribution of nestedness or species turnover to beta-diversity of infracommunities did not differ among *Rhabdomys* species (Tukey–Kramer tests for unequal sample sizes, $P = 0.672$ – 0.999 and $P = 0.098$ – 0.995 , respectively; Fig. 3).

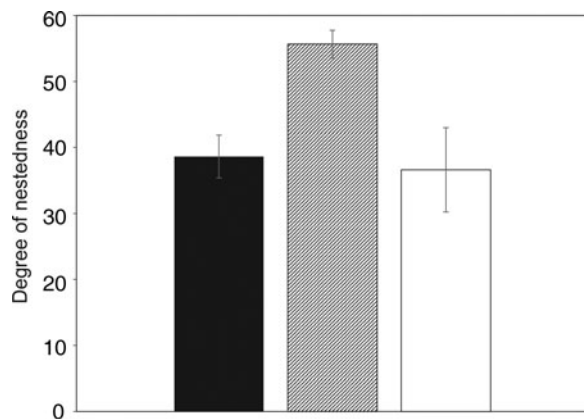


Fig. 2. The degree of nestedness (means \pm S.E.) of flea infracommunities within populations of *R. pumilio* (black bar), *R. intermedius* (pattern bar) and *R. dilectus* (white bar).

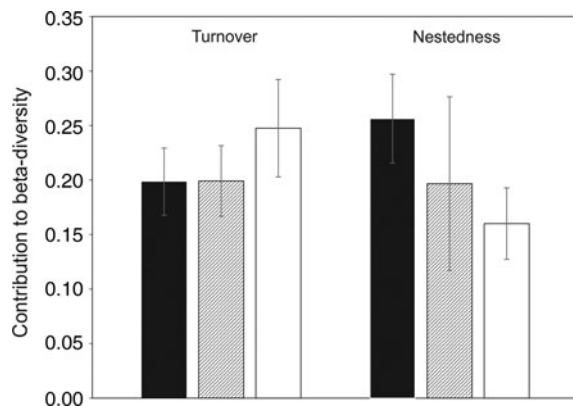


Fig. 3. The contribution of turnover (β_T) and nestedness (β_N) to the spatial variation in flea community composition within populations of *R. pumilio* (black bar), *R. intermedius* (pattern bar) and *R. dilectus* (white bar) in South Africa during 2010–2013.

DISCUSSION

Results of this study partly supported our predictions. As we expected, (a) non-randomness in flea species composition was more pronounced in social than in the solitary species, and (b) dissimilarity among flea infracommunities was higher in social hosts than in the solitary host, although this was not the case for component communities. Contrary to our expectation, we found non-random patterns in flea species composition at lower (i.e. infracommunities) but not higher (i.e. component communities) scale. As a result, dissimilarity among flea infracommunities was higher than that among component communities in two of the three host species.

Host sociality and parasite community structure

Host-related factors often play an important role in shaping parasite community structure (Poulin, 2011). Indeed, nestedness in helminth communities

of fish appeared to be affected, albeit indirectly, by host body size (Poulin and Valtonen, 2001; Timi and Poulin, 2003). Community structure of ecto- and endoparasites of a benthic marine fish (*Sebastes capensis*) was found to be associated with host's territorial behaviour (González and Poulin, 2005). In flea communities harboured by Palearctic small mammals, nestedness increased with a decrease in latitude of host's geographic range (Krasnov *et al.* 2005). Nevertheless, studies that investigated the relationship between host traits and parasite community structure revealed a variety of patterns. For example, nestedness of ecto- and endoparasite communities of a benthic marine fish (*S. capensis*) was pronounced differently as a result of differences in parasite life history (endoparasites prey on intermediate hosts, whereas ectoparasites do not) (González and Poulin, 2005). In another study, nested patterns in endoparasite infracommunities of fish was only revealed when fish size co-varied with parasite richness (Poulin and Valtonen, 2001). In ectoparasite communities of small mammals, host sheltering habits did not affect the degree of their nestedness, whereas the effect of the size of a host's geographic range on the degree of nestedness was found for communities of gamasid mites, but not fleas (Krasnov *et al.* 2011). This suggests that host-related effects on parasite community structure may be pronounced differently for different host traits and depend on either host or parasite taxon or both.

In our study, we found different patterns of flea community structure in different host species, which could perhaps be attributed to differences in social behaviour. Social organization could have a direct influence on host density (or local group size) and contact rates among individuals with profound consequences for parasite transmission and consequently nestedness (Altizer *et al.* 2003). In particular, increased contact between host individuals may lead to replacements (e.g. turnover) of flea species but not to the dynamics of species losses/gains (nestedness) and will unlikely result in well pronounced community structure. Social hosts live in aggregated groups with weak or no overlap in home ranges between groups. This may promote high between-individual contact rate within a group (i.e. over shorter distances), but precludes contact between individuals belonging to different groups (over longer distances). In our study, social species, *R. pumilio* and *R. intermedius*, live in aggregated groups (up to 30 individuals), have small home ranges and demonstrate limited mobility (Schradin, 2005; Schradin and Pillay, 2005, but see Du Toit *et al.* 2012), so that the entire population of these rodents in a given locality is fragmented. The nested pattern found in flea infracommunities harboured by social hosts may, thus, be generated by fragmented spatial distribution of host individuals

(Almeida-Neto *et al.* 2008; Meyer and Kalko, 2008). In contrast, solitary hosts do not form groups and individual rodents are usually highly mobile and homogeneously distributed across large areas with their home ranges broadly overlapping with those of not only conspecifics but also individuals belonging to different species (see Schradin, 2005; Schradin and Pillay, 2005; Du Toit *et al.* 2012 for *R. dilectus*). High mobility and broad home ranges result in high rates of both intraspecific and interspecific between-individual contact as well as contacts with burrows belonging to other con- or heterospecific individuals. These contacts facilitate frequent and substantial horizontal transfer of fleas (Krasnov and Khokhlova, 2001), so that a nested pattern of flea assemblages becomes unlikely. Furthermore, social *R. pumilio* and *R. intermedius* tended to harbour richer flea assemblages (at least, across all individuals within a population) than solitary *R. dilectus*. This is despite generally negative relationships between parasite diversity and sociality in rodent hosts found in meta-analysis of species richness for eight parasite taxa harboured by 46 rodent species (Bordes *et al.* 2007). One of the reasons for higher species richness of fleas in social as compared to solitary *Rhabdomys* could be related to difference in their sheltering habits. Indeed, burrows and nests (which are regarded as main habitats of immature fleas) of group-living and less mobile rodents are usually active for longer periods compared to shelters of solitary and highly mobile species (Kucheruk, 1983). Another reason for higher flea species richness in *R. pumilio* and *R. intermedius* compared to *R. dilectus* might be the higher density of the former associated with dynamics in their distribution ranges during repeated glacial-interglacial cycles (see Rymer *et al.* 2013; Engelbrecht *et al.* 2016). Hosts with higher density are usually characterized by richer parasite assemblages (Stanko *et al.* 2002). Therefore, *R. pumilio* and *R. intermedius* can accumulate most of the parasite species that occur in a given locality, whereas *R. dilectus* likely encounters only common parasites. This may result in the deviation of infracommunity structure of *R. pumilio* and *R. intermedius* from randomness (Poulin and Valtonen, 2001; Krasnov *et al.* 2010a, but see Krasnov *et al.* 2011).

Scale-dependence of parasite community structure

Scale-dependence of parasite community structure has been repeatedly demonstrated. For example, helminth communities of Argentinian anchovy (*Engraulis anchoita*) seemed to be randomly assembled at a higher scale (across host populations), but structure was found at a lower scale (within host populations), albeit in some but not other seasons (Timi and Poulin, 2003). Monogenean assemblages on the roach (*R. rutilus*) were randomly assembled at a lower scale (host individuals), whereas

non-random structure was found at a higher scale (host population) (Šimková *et al.* 2001). Scale differences in the manifestation of parasite community structure (e.g. the occurrence and/or degree of nestedness) have been attributed to different processes acting at different spatial scales with biogeographic and historical processes that predominate at component community scale being more relevant to the original concept of nestedness as formulated by Patterson and Atmar (1986) (González and Poulin, 2005). Nevertheless, our results contradict this idea since nestedness of flea assemblages in *Rhabdomys* hosts appeared to be pronounced in infra- but not component communities. The reason behind this might be due to the complex relationships between nestedness and the pattern of species co-occurrences (Ulrich and Gotelli, 2007). Although these relationships strongly depend on the nature of null models used to detect nestedness, a higher degree of nestedness is expected in communities with a lower degree of species segregation (Ulrich and Gotelli, 2007, but see Heino, 2009). In particular, this is true for low-fill matrices (Ulrich and Gotelli, 2007) which was the case in our study (on average, matrix fill was 0.42 ± 0.03 for infracommunities and 0.50 ± 0.09 for component communities). Species co-occurrences in flea infracommunities are characterized by aggregation rather than segregation (Krasnov *et al.* 2006b). This is generally not the case for helminth infracommunities of fish hosts (Gotelli and Rohde, 2002) for which nestedness was mainly not detected. Positive ectoparasite co-occurrences were found in a variety of small mammalian hosts including *R. pumilio*, habitats and geographic areas (Krasnov *et al.* 2010a) and might contribute to the nested pattern in flea infracommunities found in this study. Furthermore, Krasnov *et al.* (2011) presented evidence for structure of communities of two ectoparasite taxa (fleas and gamasid mites) (a) among localities within a geographic region and (b) among large geographic regions, although manifestation of this structure was stronger at the former scale. The results of this study together with those of Krasnov *et al.* (2011) show that structure of ectoparasite communities may occur at all hierarchical levels.

Beta-diversity

Beta-diversity measures dissimilarity in species composition of communities between sites or localities and it has become a fundamental topic to elucidate the ecological processes involved in shaping the dissimilarity in species composition (Baselga, 2010). In our study, beta-diversity was higher at a lower spatial scale whereas the opposite was observed at a higher scale. In other words, infracommunities were more dissimilar than component communities. Infra- and component communities of parasites differ in infestation status and variability in species composition through space

and time. Infracommunities are short-lived by definition and are largely shaped by stochastic processes such as transmission and demography (Morand *et al.* 2002). Parasite species composition of an individual host can vary with regard to the longevity of the host and due to the life history characteristics of parasites. For example, the flea infestation status of a host individual has been shown to change rapidly (e.g. daily) from being highly infested to non-infested and vice versa (Krasnov *et al.* 2006c). Fleas are characterized by alternating periods on and off host individuals and may thus not always be present on host individuals when sampled. In contrast, component communities persist much longer than infracommunities and their species composition is mainly determined by host species composition and environmental conditions of a location (Krasnov *et al.* 2015). For example, Krasnov *et al.* (2005) found that similarity in flea assemblages among populations of the same host species decrease with an increase in geographic distance and similarity of co-occurring host composition (or both). As a consequence, component communities of parasites harboured by the same host could be more similar than their infracommunities. This is especially true for parasite communities of a host within the same geographic region (which was the case in our study), whereas parasite communities considered across multiple distinct regions may demonstrate the reversed pattern.

Beta-diversity, nestedness and spatial species turnover

Disentangling of nestedness and spatial species turnover components of beta-diversity is essential to our understanding of ecological and biogeographic processes involved in structuring communities (Baselga, 2008). Baselga (2008, 2010) proposed a method to calculate nestedness-resultant dissimilarity (β_{NES}) as difference between a metric based on Sørensen dissimilarity measure (that encompasses both spatial turnover and differences in species richness; β_{SOR}) and a metric based on Simpson dissimilarity measure (that is measure multi-site spatial turnover free from the influence of species richness; β_{SIM}). Baselga (2008, 2010) recognised that β_{NES} was not an absolute measure of nestedness but rather a measure of community dissimilarity due to the effect of nestedness. Later, Almeida-Neto *et al.* (2012) argued that the metric proposed by Baselga (2010) was not a true measure of nestedness-resultant dissimilarity but actually measured how differences in species richness (that were not part of species replacements) contributed to dissimilarity. In addition, Almeida-Neto *et al.* (2012) demonstrated that Baselga's (2010) metrics were influenced by matrix size and fill, and might increase or decrease even when nestedness remained constant. In other words, positive relationships between contribution of nestedness to total amount of beta-diversity and the degree of nestedness could not be a priori

expected. Indeed, Krasnov *et al.* (2011) found no relationship between nestedness-resultant dissimilarity measured using β_{NES} and degree of nestedness (N_{COL}) for two parasite taxa, fleas and gamasid mites. In this study, we used new measures of multi-site beta-diversity and its nestedness/species turnover components proposed by Ricotta and Pavoine (2015) and based on information on species absences from the species \times sites matrix. When these measures were applied to artificial matrices, higher nestedness was, in general, accompanied by its higher contribution to total amount of multi-site dissimilarity (that is, beta-diversity) (Ricotta and Pavoine, 2015). As a result, in our study, differences in manifestation of nestedness among species and between scales were translated into differences in contributions of nestedness and turnover to beta-diversity of flea assemblages. For example, when the degree of nestedness of flea infracommunities was relatively low, infracommunity dissimilarity was mainly due to species turnover (*R. dilectus*), whereas when the degree of nestedness was relatively high, infracommunity dissimilarity was mainly due to nestedness (*R. pumilio*). Our results confirm that the multiple-site measures proposed by Ricotta and Pavoine (2015) can successfully measure contribution of nestedness and species turnover as well as discriminate between situations where dissimilarity is caused by varying degrees of nestedness.

In conclusion, structure of flea assemblages harboured by the three South African rodent hosts was expressed differently in hosts with different social structure which, in turn, could have affected their spatial distribution differently. Although not surprising, we also found differences in flea assemblage structure between scales, with more dissimilarity at lower (i.e. among host individuals) but not at higher (i.e. among host populations) scale. Our findings thus support earlier ideas that parasite community structure results from the processes of parasite accumulation by hosts rather than from the processes acting within parasite communities (Timi and Poulin, 2003).

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <http://dx.doi.org/10.1017/S0031182016000664>.

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