

## ORIGINAL ARTICLE

# Seasonal and habitat dependence of fleas parasitic on small mammals in Tanzania

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## Abstract

We investigated host and flea species composition across different habitats during dry and rainy seasons in the Western Usambara Mountains in Tanzania. During both seasons, similarity in flea species composition increased with an increase in the similarity in host species composition. Nevertheless, between-season within-habitat as well as within-season between-habitat similarity in host species composition was higher than similarity in flea species composition. Ordination of habitats according to their host and flea species composition demonstrated that the pattern of between-habitat similarity in both host and flea species composition varied seasonally. Despite the relatively rich mammal and flea fauna of the study region, the major contribution to variation in species composition between seasons and among habitats was due to a few species only. Flea assemblages on *Lophuromys kilonzoï* Verheyen *et al.*, 2007 and *Praomys delectorum* Thomas, 1910 in different habitats were equally similar in either season. In contrast, flea assemblages on *Mastomys natalensis* (Smith, 1834) occurring in different habitats were more similar in the dry than in the rainy season, whereas the opposite was the case for fleas on *Grammomys sp.* In different hosts, the main differences in species composition of flea assemblages between seasons as well as among habitats were due to different flea species. Although our results support the earlier idea that parasite species composition is determined by both host species composition and habitat properties, the former appears to explain variance in flea species composition between localities in the tropics better than between localities in temperate and arid zones.

**Key words:** Africa, flea assemblages, rodents, seasonal, tropical habitats.

## INTRODUCTION

Biological communities vary in space and time even

within the same geographic region. Indeed, spatial variation in the composition of plant and animal communities has been shown for a variety of taxa, at various scales and across various regions (Gentry 1988; McCoy 1990; Davidson 1993; Jorgensen & Demarais 1999; Orrock *et al.* 2000; Mortelliti & Boitani 2007). One of the most important reasons for spatial variation in community composition is variation in the environmental conditions. Surprisingly, spatial variation in the composition of com-

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munities of parasites has been given less attention than spatial variation in the composition of communities of free-living organisms. Parasites form a large proportion of the diversity of life on earth and parasitism is suggested to be more common than all other feeding strategies combined (Bansemir & Sukdheo 1996). The lack of studies on spatial variation in parasite communities might be, at least partly, explained by the dual nature of parasites' environment. One component of the parasite environment is represented by the hosts, whereas another component is the environment of the hosts, which influences parasites both directly (e.g. affecting their free-living transmission stages; Chiejina *et al.* 1989; McSorley 2003; Carrillo *et al.* 2007) and indirectly (Morand *et al.* 2006). In other words, the complicated nature of the environment of a parasite is determined by the fact that it has to deal with the host itself as well as with the host's biotic and abiotic environment. The latter component is especially important for ectoparasites, which, in contrast to endoparasites, are strongly affected by the off-host environment.

The diversity of the host's biotic and abiotic environment seems to be the main cause of the variation of parasite communities across host individuals, populations, species and communities (Calvete *et al.* 2004). Therefore, some part of a parasite community encountered in a host is due to host identity, whereas another part is due to the host's environment (Kennedy & Bush 1994). However, the relative importance of spatially variable factors in the dynamics of community composition is poorly known for most parasite taxa.

Several recent studies on spatial and temporal variation in the composition of communities of fleas (Siphonaptera) parasitic on small mammals demonstrate that host-habitat relationships are important determinants of flea community structure (Krasnov *et al.* 1997, 2005). Species composition of a flea community and relative abundances of flea species in a habitat appear to be affected not only by species composition and relative abundances of their hosts, but also by some properties of the habitat itself. Interestingly, the linkage between flea communities, host communities and habitat types appears to be manifested differently in different geographic regions. For example, among-habitat differences in flea assemblages within a host species in temperate zones appear to be less pronounced than those in desert habitats. This is explained by the low predictability of environmental conditions and predominating pattern of mammal sheltering in deep burrows in deserts, which might lead to more pronounced among-habitat differences in the environmental conditions for pre-imaginal fleas. Furthermore, the between-region

difference in the effect of a host's habitat on ectoparasite community composition does not answer explicitly the question about the relative importance of host identity versus habitat identity in structuring flea assemblages both within host species and host communities. Consequently, further studies in more geographic regions are needed.

Here, we study seasonal and habitat variation in the composition of flea assemblages parasitic on small mammals in the Western Usambara Mountains in Tanzania. Although several studies have dealt with fleas parasitic on mammals in tropical Africa (Devignat 1949; Heisch 1952; Schwan 1983; Njunwa *et al.* 1989; Makundi & Kilonzo 1994), habitat variation of flea assemblages has never been documented. Species diversity in the tropics is much higher than in other biogeographic zones (Klopfer *et al.* 1974; Chapman & Reiss 1992; Kozak & Wiens 2007) and specific niche breadth is generally narrow (Pagel *et al.* 1991) as a result of either increased interspecific competition due to higher numbers of co-occurring species (Brown 1975) or relative stability of environmental conditions, which allows the persistence of specialized species (Chesson & Huntly 1997), or both. In addition, tropical rainforests are characterized by a stable temperature with relatively constant humidity, which allows most rainforest trees to be evergreen, whereas in disturbed forest and agricultural areas, microclimatic variations (especially humidity) are more variable. Consequently, bearing in mind the influence of abiotic factors on flea preimaginal stages, we expect that the composition of flea assemblages in the first habitat will be primarily determined by host species composition rather than by some properties of the habitat. In the other habitat types, we expected environmental factors to be of greater importance.

In particular, we ask whether and how the distribution of small mammals and fleas varies within and among five major habitat types, and within and between the dry and the rainy season. We also ask which species contribute most to between-season and among-habitat dissimilarity in host and flea species composition. In addition, we examine whether between-location similarity in flea species composition is associated with similarity in host species composition. Finally, we examine the composition of flea assemblages in the most common rodent species (*Lophuromys kilonzo* (Verheyen *et al.* 2007), *Mastomys natalensis* (Smith, 1834), *Praomys delectorum* Thomas, 1910 and a 'non-determined' species of the genus *Grammomys* Thomas, 1915) in different habitats to understand the role of habitat in determining the composition of flea assemblages exploiting the same host.

## MATERIAL AND METHODS

### Study area and habitat types

Small mammals were sampled and fleas collected between May 2005 and January 2008 in four locations in the West Usambara Mountains of Tanzania (Lushoto district, Tanga region; 04°22'–05°08'S, 38°05'–38°38'E). The area of the district is approximately 3500 km<sup>2</sup> at elevations ranging from 900 to 2250 m above sea level. Land use in the study area includes dry land farming (58% of the area), tree crops and irrigated areas (11%), forest reserves (16%) and grazing areas (15%) (Halperin 2002; Shemdoe 2002). The climate is characterized by a bimodal rainfall distribution with wet seasons in October–December and March–mid May. A rainfall gradient occurs from west-facing to east-facing slopes and from lower (1200 mm per annum) to higher altitudes (2200 mm per annum). Mean annual temperatures vary with altitude from a maximum of 25–27°C at 800 m above sea level to a minimum of 17–18°C at 1500–1800 m above sea level (Shemdoe 2004).

We distinguished five habitat types based on their physiognomy as follows: (i) natural forests occur in submontane and montane areas and are dominated by *Prunus africana* Kalkman, *Newtonia buchananii* Baker, *Parinari excelsa* Sabine, *Albizia gummifera* Smith and *Allanblackia stuhlmannii* Engler; (ii) shrubs in forested zones (further referred to as closed shrubbery) are dominated by *Rubus steudneri* Schweinfurth and ferns of the genus *Dryopteris* Adanson; (iii) shrubs in open habitats and grassland (further referred to as open shrubbery) represent dense low to middle height vegetation (up to 1.5 m) dominated by *Rumex usambarensis* Dammer, *Vernonia myriantha* Hooker, *Vernonia brachycalyx* Hoffmann and *Kalanchoe crenata* Raymond-Hamet; (iv) crop fields are situated mainly on the mountain slopes and major cash crops are represented by maize (*Zea mays* Linnaeus), beans (*Phaseolus spp.* Linnaeus) and potatoes (*Solanum tuberosum* Linnaeus), while vegetables are planted in irrigated valley bottoms; and (v) commercial plantations of timber or fruit trees (further referred to as commercial plantations) are represented by introduced *Grevillea robusta* Cunningham, *Eucalyptus saligna* Smith, *Cupressus lusitanica* Miller, *Acacia mearnsii* De Wildeman, *Pinus patula* Schiede & Deppe, *Pyrus communis* Linnaeus and *Juniperus procera* Hochstetter, and native *Albizia schimperiana* Oliver and *Croton megalocarpus* Hutchinson, often surrounded by fences of *Agava sisalana* Perrine.

### Mammal sampling and flea collection

Small mammals were captured mainly using Sherman traps (model LFA, 3 in × 3 in, 5 in × 9 in, Sherman Traps, Tallahassee, USA) baited with peanut butter and maize. Occasionally, Tomahawk collapsible traps (model 202, 6 × 6 × 19 inches, Tomahawk Live Traps, USA), pitfall traps with a drift fence, and snaptraps were also used. However, trapping success of the three latter trap types was extremely low (no more than 3.4%). On average, 108 Sherman traps (ranging from 86 to 118) were set per trapping session (= samples). Each trapping session lasted 4 to 5 nights. Between May 2005 and January 2008, seven sites were surveyed and each habitat was, on average, visited 2 times at 16 month intervals. On average, there were 12 replicated trapping sessions (= samples) per habitat type, ranging from a minimum of 7 in closed shrubbery to a maximum of 21 in open shrubbery. Each captured animal was transferred to the laboratory in a white tissue bag and killed using ether. The animals were weighed, sexed and morphological measurements (length of body, tail, ear and hind foot) were recorded. Tissue samples were taken from heart, lung, kidney, liver and spleen and stored in 70% ethanol. Each mammal was initially identified at genus level in the field. Species identification was confirmed in the laboratory (University of Antwerp and Natural Science Institute in Brussels) by combining craniometric measurements and mitochondrial DNA cytochrome-b sequencing. We combed the fur of each mammal with a lice comb above a white plastic pan filled with water until all fleas were recovered. Fleas were stored in 70% ethanol in individual vials for each host specimen and transferred to the laboratory for identification.

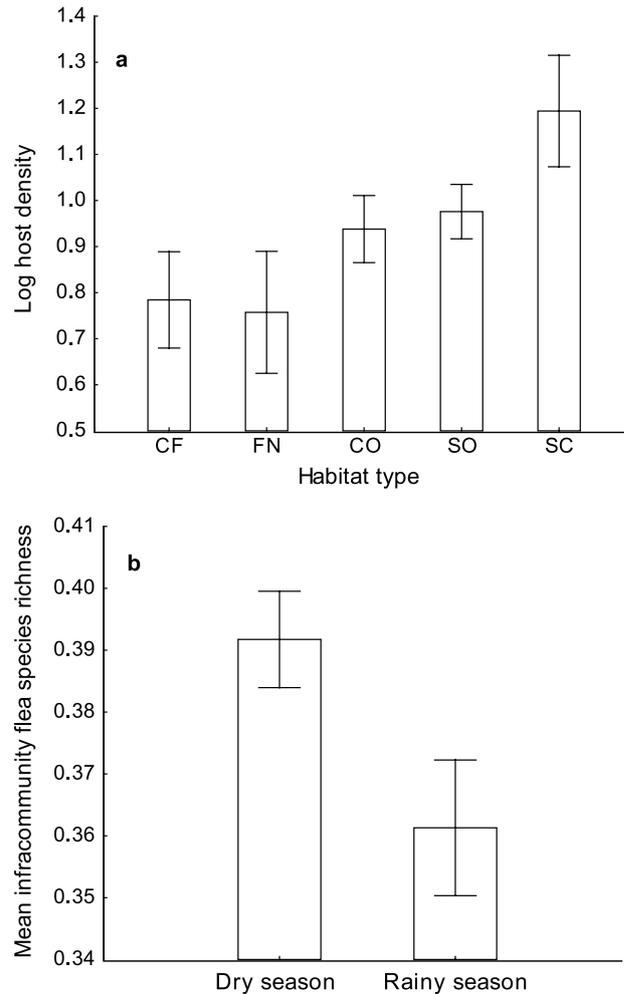
### Data analysis

In the analyses, we used data from those trapping sessions (samples) in which at least 3 host individuals were captured and at least 3 flea individuals were collected. First, for each sample we calculated: (i) pooled density of all hosts (number of individual mammals captured per 100 trap/nights); (ii) pooled mean abundance of all fleas (number of flea individuals per individual mammal); (iii) total host species richness; (iv) total flea species richness; (v) mean infracommunity flea species richness (mean number of flea species per infested host individual); and (vi) mean component community flea species richness (mean number of flea species per host species). Prior to analysis, these data were log-transformed. The only variable that was affected by sampling effort was total flea species richness, being positively correlated with the number of captured mammals ( $R^2 = 0.31$ ,  $F_{1,59} = 26.8$ ,  $P < 0.001$ ).

Consequently, this variable was controlled for the differences in sampling effort by substitution of the original data values to their residual deviations of the regressions against sampling effort in log-log space. We compared the six variables describing abundance and species richness of host and flea communities using 2-way ANOVA with habitat type and season as independent variables.

Second, we calculated: (i) density of each host species; and (ii) mean abundance of each flea species on all host species for each sample. To test for the matching between rodent species composition and flea species composition of a set of samples, we calculated the Bray–Curtis similarity (Bray & Curtis 1957) in both host and flea species composition between each pair of samples from standardized log-transformed abundance data (see details in Clarke & Warwick 2001). We tested whether and how closely the two sets of host and flea distribution are related by calculating rank correlation coefficients ( $\tilde{r}$ ) between all elements of the two resulting among-sample similarity matrices (for hosts and for fleas) (Clarke & Warwick 2001). The coefficient  $\tilde{r}$  can vary between 0 (no relation between two similarity matrices) and 1 (perfect match between two matrices). Statistical significance of  $\tilde{r}$  was estimated by permutation procedure with 999 permutations. These calculations were performed using the RELATE routine implemented in the program Primer-5 (Clarke & Gorley 2001). In addition, we tested for the relationship between similarities in host and flea composition by regressing similarity in flea composition against similarity in host composition across all pairs of habitats. Because the pairwise similarity values were not truly independent in a statistical sense, the significance of each regression model was tested using a randomization approach (Manly 1997) implemented in the RT 2.1 software (Western EcoSystems Technology, Cheyenne, Wyoming). All regression probabilities were based on 10 000 permutations.

Third, to understand how host and flea species composition changes among habitats and between seasons, we applied multidimensional non-parametric scaling to ordinate host and flea assemblages across habitats and seasons. For these analyses, we averaged densities of hosts and abundances of fleas across trapping sessions within habitat types and seasons. A matrix of Bray–Curtis similarities between each pair of habitats was used as input data. In a first step, we identified those host and flea species that primarily accounted for the observed assemblage differences (Clarke & Gorley 2001). This was carried out by decomposition of Bray–Curtis similarity into contribution of each species using the routine SIMPER implemented in the program Primer-5 (Clarke & Gorley 2001).



**Figure 1** (a) Effects of habitat type on host density (mean number of individuals captured per 100 trap-nights) in Lushoto district, Tanzania. (b) Effects of habitat type on mean infracommunity flea species richness (controlled for sampling effort; see text for explanations). CF, crop fields; CO, commercial plantations; FN, natural forest; SC, closed shrubbery; SO, open shrubbery.

We carried out pair-wise comparisons between habitats within a season and between seasons within a habitat. In a second step, to understand how the composition of flea assemblages varies between seasons and among habitats within a host species, we repeated the aforementioned analyses for fleas collected from the 4 most common hosts (*L. kilonzoii*, *M. natalensis*, *P. delectorum* and *Grammomys* sp.).

**Table 1** Effect of season and habitat type on host and flea abundance and species richness

Dependent variable	Factor	Degrees of freedom	<i>F</i> -value	<i>P</i> -value
Host density	S	4	0.53	0.46
	H	1	2.93	0.03
	H × S	4	1.69	0.16
Flea abundance	S	4	1.99	0.16
	H	1	1.84	0.13
	H × S	4	0.21	0.93
Total host species richness	S	4	0.24	0.52
	H	1	1.38	0.25
	H × S	4	1.05	0.39
Total flea species richness	S	4	0.04	0.84
	H	1	0.83	0.51
	H × S	4	0.84	0.50
Mean infracommunity flea species richness	S	4	4.83	0.03
	H	1	0.47	0.76
	H × S	4	0.79	0.53
Mean component community flea species richness	S	4	0.75	0.39
	H	1	0.88	0.48
	H × S	4	1.44	0.23

Summary of the ANOVA for the effect of season (S) and habitat type (H) on host and flea abundance and species richness in Lushoto district, Tanzania (error degrees of freedom = 51 for all ANOVA).

## RESULTS

A total of 1021 (on 12 811 trap nights) mammal individuals belonging to 19 species were trapped, from which 2075 fleas belonging to 22 species were collected (see Table 5).

### Seasonal and habitat-dependent patterns in host and flea abundance and species richness

The results of 2-way ANOVA of the effect of season and habitat type on host and flea abundance and species richness are presented in Table 1. The only host and flea community parameters affected by either season or habitat type were host density and mean infracommunity flea species richness. In particular, host density was lowest in crop fields and natural forest, higher in commercial plantations and open shrubbery, and highest in closed shrubbery (Fig. 1a). Host individuals harbored, on average, significantly more flea species during the dry season than during the rainy season (Fig. 1b).

### Seasonal patterns in host and flea species composition

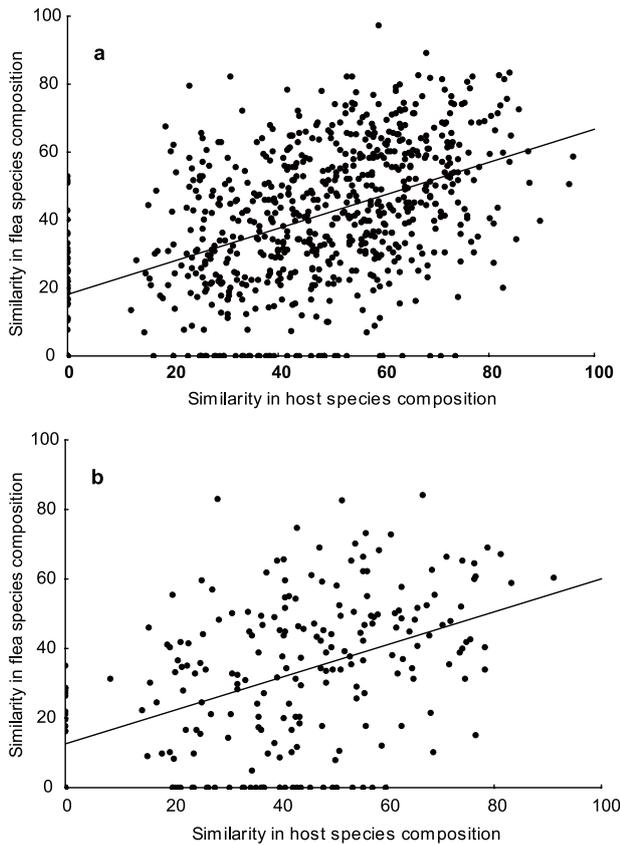
Similarity in species composition varied greatly among

pairs of samples. During the dry season, it varied from 0 to 96.0% for hosts and from 0 to 97.5% for fleas, whereas during the rainy season it varied from 0 to 91.0% for hosts and from 0 to 84.2% for fleas. Nevertheless, values of average similarities among samples in host and flea species composition within a season were rather close to each other (46.3 and 40.6%, respectively, during the dry season and 47.4 and 31.9%, respectively, during the rainy season).

In general, during both seasons, among-sample similarity in flea species composition was reflected by among-sample similarity in host species composition ( $\bar{n} = 0.48$  during both dry and rainy seasons,  $P < 0.001$  for both). The among-sample similarity in flea species composition increased with an increase in the among-sample similarity in host species composition ( $R^2 = 0.23$ ,  $F_{1,739} = 223.2$  for the dry season and  $R^2 = 0.21$ ,  $F_{1,229} = 61.7$  for the rainy season,  $P < 0.001$  for both) (Fig. 2).

### Seasonal and habitat-dependent patterns in host and flea species composition

Between-season within-habitat similarity in host species composition averaged 50.1% and ranged from a minimum of 44.5% in closed shrubbery to a maximum of 55.1%



**Figure 2** Relationship between similarity in flea species composition and similarity in host species composition across pairs of samples during (a) the dry or (b) the rainy season in Lushoto district, Tanzania.

in natural forest. Between-season similarity in flea species composition averaged 37.3% and ranged from a minimum of 31.8% in commercial plantations to a maximum of 46.4% in open shrubbery. Among-habitat similarity in species composition during the dry season averaged 43.1% for hosts (ranging from 25.3 to 54.8% between crop fields and natural forest and closed shrubbery, respectively) and 37.9% for fleas (ranging from 34.7% between commercial plantations and closed shrubbery to 46.7% between crop fields and open shrubbery). Analogously, during the rainy season, similarity in host species composition was, on average, 47.9%, and ranged from 36.9 to 56.0% between natural forest and crop fields and commercial plantations, respectively. For fleas, the average among-habitat similarity in species composition was 30.7% and ranged from 22.4% between natural forest and open shrubbery to 37.0% between two shrubbery habitats.

The distribution of habitats according to their host and flea species composition in the ordination space constructed using non-parametric multidimensional scaling is shown in Fig. 3. Comparison of the diagrams allows us to distinguish groups of habitats that are more similar to each other than to other habitats in both host and flea species composition. Furthermore, the pattern of between-habitat similarity in both host and flea species composition varies seasonally. For example, host assemblages between open shrubbery and commercial plantations were highly similar during the dry season, whereas this was not the case during the rainy season. Flea assemblages between open shrubbery and crop fields were much more

**Table 2** Variation in rodent and flea species composition between seasons

Taxon	Habitat	Species	Percentage of contribution	Density/abundance during	
				dry season	rainy season
H	CF	<i>Praomys delectorum</i>	16.73	1.39	2.02
	CO	<i>Grammomys sp.</i>	19.81	3.90	1.52
	FN	<i>Lophuromys kilonzo</i>	22.02	2.33	0.74
	SC	<i>Lophuromys kilonzo</i>	23.00	7.88	1.79
	SO	<i>Grammomys sp.</i>	15.34	2.03	4.77
F	CF	<i>Nosopsyllus incisus</i>	15.12	0.42	0.18
	CO	<i>Nosopsyllus incisus</i>	14.51	0.81	0.06
	FN	<i>Ctenophthalmus eximius</i>	12.03	0.12	0.00
	SC	<i>Nosopsyllus incisus</i>	13.33	0.68	0.25
	SO	<i>Dinopsyllus grypurus</i>	13.07	0.31	0.15

Host (H) and flea (F) species that contributed maximally to dissimilarity in species composition between seasonal assemblages within a habitat CF, crop fields; CO, commercial plantations; FN, natural forest; SC, closed shrubbery; SO, open shrubbery.

similar during the rainy season than during the dry season.

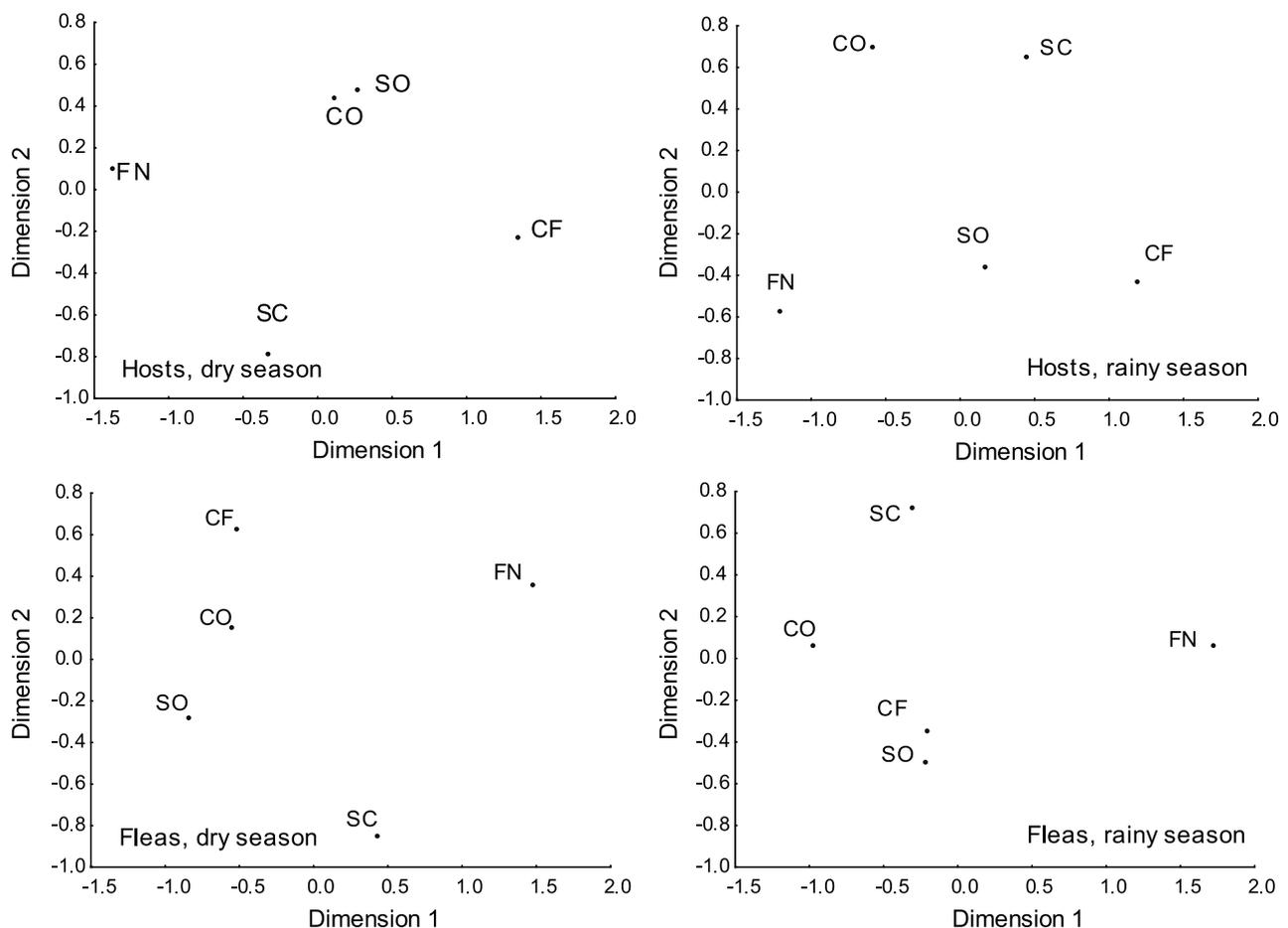
Despite the relatively rich mammal and flea fauna of the study region, the major contribution to variation in species composition between seasons and among habitats was due to a few species only (Tables 2 and 3). Indeed, seasonal differences in host species composition within a habitat were mainly due to changes in relative abundance of *L. kilonzo*, *Grammomys* sp. and *P. delectorum*. The density of *L. kilonzo* decreased and the density of *P. delectorum* increased in the rainy season, whereas the opposite trends occurred in seasonal density change of *Grammomys* sp. in common plantations and open shrubbery. Seasonal differences in flea species composition were mainly a result of a decrease in the abundance of *Nosopsyllus incisus* Jordan & Rothschild, 1913,

*Ctenophthalmus eximius* Jordan & Rothschild, 1913 and *Dinopsyllus grypurus* Jordan & Rothschild, 1913 in the rainy season.

Between-habitat within-season differences in host and flea species composition were determined by differences in abundance of almost the same species set that contributed strongly to between-season differences. In addition, species that contributed most to the majority of between-habitats pairwise dissimilarities were *Grammomys* sp. in both seasons and *M. natalensis* in the rainy season.

### Seasonal and habitat-dependent patterns in flea species composition within a host species

Plots of multidimensional scaling of flea assemblages within hosts and across seasons and habitats demon-



**Figure 3** Multidimensional scaling distribution of habitats based on Bray-Curtis similarity in host and flea species composition during the dry or the rainy season in Lushoto district, Tanzania. CF, crop fields; CO, commercial plantations; FN, natural forest; SC, closed shrubbery; SO, open shrubbery.

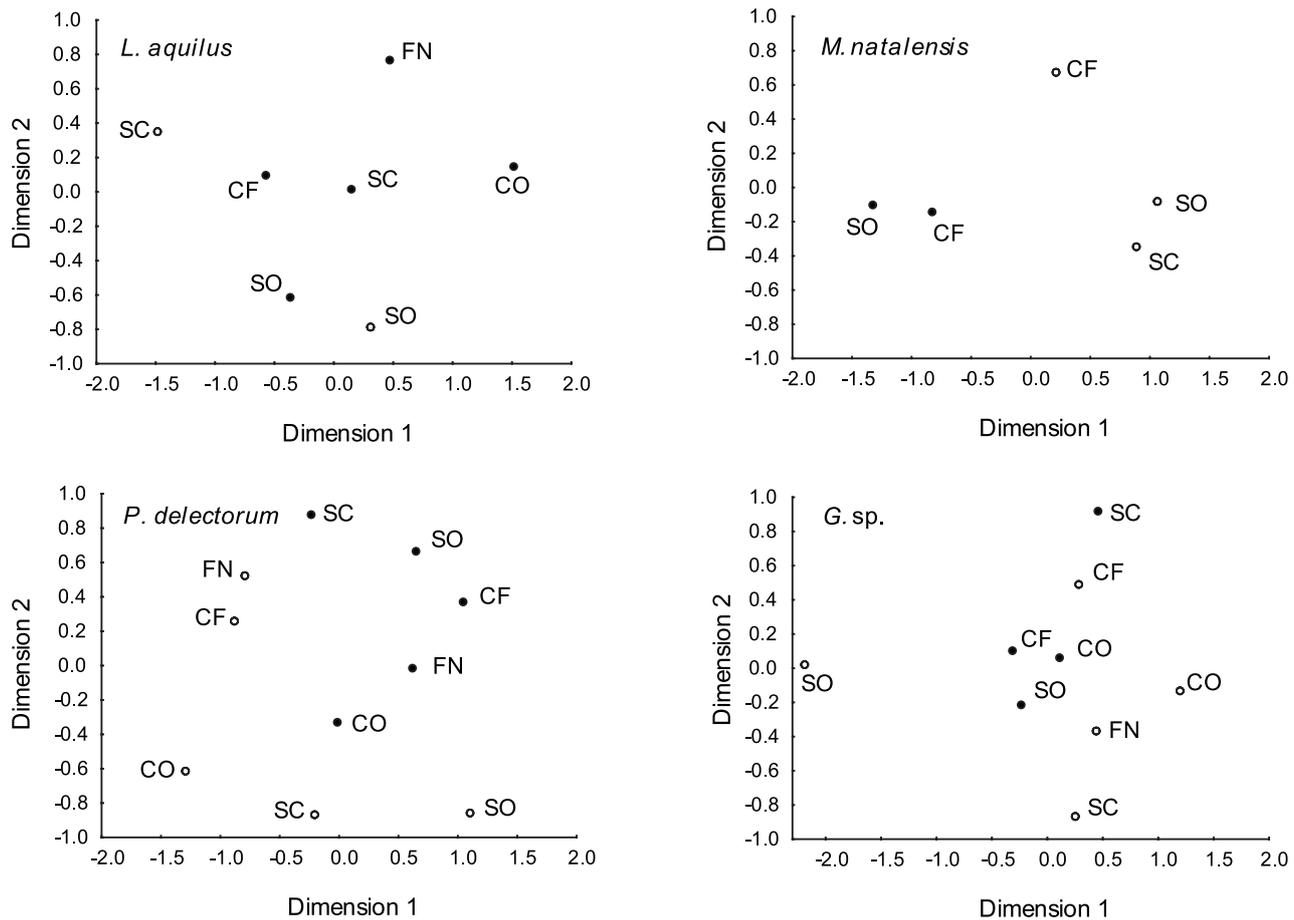
**Table 3** Variation in rodent and flea species composition among habitats

Taxon and season	Habitat 1– Habitat 2	Species	Percentage of contribution	Density/abundance in	
				Habitat 1	Habitat 2
H/DR	CF–CO	<i>Grammomys</i> sp.	16.47	1.31	3.90
	CF–FN	<i>Mastomys natalensis</i>	20.29	2.77	0.00
	CF–SC	<i>Mastomys natalensis</i>	21.03	2.77	0.00
	CF–SO	<i>Lophuromys kilonzoii</i>	20.44	0.37	2.60
	CO–FN	<i>Grammomys</i> sp.	21.40	3.90	0.13
	CO–SC	<i>Grammomys</i> sp.	18.53	3.90	1.67
	CO–SO	<i>Grammomys</i> sp.	15.80	3.90	2.60
	FN–SC	<i>Praomys delectorum</i>	18.31	4.40	2.21
	FN–SO	<i>Grammomys</i> sp.	19.41	0.13	2.60
	SO–SC	<i>Grammomys</i> sp.	16.59	2.60	1.67
H/RA	CF–CO	<i>Mastomys natalensis</i>	23.92	3.06	0.19
	CF–FN	<i>Mastomys natalensis</i>	25.59	3.06	0.00
	CF–SC	<i>Mastomys natalensis</i>	21.62	3.06	2.45
	CF–SO	<i>Mastomys natalensis</i>	19.47	3.06	0.50
	CO–FN	<i>Grammomys</i> sp.	25.61	1.52	0.97
	CO–SC	<i>Grammomys</i> sp.	21.42	1.52	5.29
	CO–SO	<i>Lophuromys kilonzoii</i>	20.90	0.39	2.76
	FN–SC	<i>Grammomys</i> sp.	18.34	0.97	5.29
	FN–SO	<i>Hylomyscus arcimontensis</i>	17.07	0.71	0.42
	SO–SC	<i>Lophuromys kilonzoii</i>	17.28	2.76	1.79
F/DR	CF–CO	<i>Dinopsyllus grypurus</i>	14.53	0.33	0.14
	CF–FN	<i>Dinopsyllus lypusus</i>	13.14	0.30	0.00
	CF–SC	<i>Nosopsyllus incisus</i>	13.01	0.42	0.68
	CF–SO	<i>Ctenophthalmus eximius</i>	15.74	0.22	0.76
	CO–FN	<i>Dinopsyllus grypurus</i>	19.78	0.14	0.55
	CO–SC	<i>Nosopsyllus incisus</i>	14.09	0.81	0.68
	CO–SO	<i>Dinopsyllus grypurus</i>	14.85	0.14	0.31
	FN–SC	<i>Nosopsyllus incisus</i>	13.65	0.17	0.68
	FN–SO	<i>Nosopsyllus incisus</i>	16.91	0.17	1.53
	SO–SC	<i>Ctenophthalmus eximius</i>	14.76	0.76	0.38
F/RA	CF–CO	<i>Ctenophthalmus eximius</i>	16.46	0.07	0.41
	CF–FN	<i>Nosopsyllus incisus</i>	14.76	0.18	0.25
	CF–SO	<i>Ctenophthalmus eximius</i>	13.89	0.07	0.38
	CF–SO	<i>Nosopsyllus incisus</i>	13.38	0.18	0.10
	CO–FN	<i>Ctenophthalmus eximius</i>	13.58	0.41	0.05
	CO–SC	<i>Nosopsyllus incisus</i>	13.79	0.07	0.94
	CO–SO	<i>Ctenophthalmus eximius</i>	14.65	0.41	0.00
	FN–SC	<i>Nosopsyllus incisus</i>	10.83	0.10	0.25
	FN–SO	<i>Nosopsyllus incisus</i>	12.74	0.10	0.94
	SO–SC	<i>Nosopsyllus incisus</i>	13.35	0.94	0.25

Host (H) and flea (F) species that contributed maximally to dissimilarity in species composition between each pair of habitat assemblages during either dry (DR) or rainy (RA) season. CF, crop fields; CO, commercial plantations; FN, natural forest; SC, closed shrubbery; SO, open shrubbery.

strated that seasonal and among-habitat variation in flea composition was manifested differently in different hosts

(Fig. 4). Flea assemblages on *L. kilonzoii* and *P. delectorum* in different habitats were equally similar in either season



**Figure 4** Multidimensional scaling distribution (based on Bray-Curtis similarity) of flea assemblages collected from three common host species in a particular habitat during the dry (closed circles) or the rainy (opened circles) season in Lushoto district, Tanzania. CF, crop fields; CO, commercial plantations; FN, natural forest; SC, closed shrubbery; SO, open shrubbery.

(Table 4). In contrast, flea assemblages on *M. natalensis* occurring in different habitats were more similar in the dry than in the rainy season, whereas the opposite was the case for fleas on *Grammomys* sp. Furthermore, in different hosts, the main differences in species composition of flea assemblages between seasons as well as among habitats were due to different flea species.

In particular, seasonal flea assemblages on *L. kilonzo* within a habitat differed mainly by relative abundance of *Ctenophthalmus calceatus* Waterston, 1912 (contribution of this species to seasonal dissimilarity was 19–28%). Seasonal changes in abundance of this flea species on this host lacked unidirectional trend. Instead, *C. calceatus* seemed to re-distribute among habitats in different seasons. Indeed, in open shrubbery this flea species was

more abundant in the dry season than in the rainy season (0.43 versus 0.23 fleas per individual host, respectively), whereas the opposite was the case in closed shrubbery (0.36 versus 2.67 fleas per individual host, respectively). In the dry season, flea assemblages on *L. kilonzo* in crop fields differed drastically from all other habitats by high abundance of *Dinopsyllus lypusus* Jordan et Rothschild, 1913 (contribution of this species to pairwise habitat dissimilarity was 20–26%), whereas the same host in commercial plantations carried a high abundance of *N. incisus* (18% contribution). *C. calceatus* was mainly responsible for the difference in flea composition among natural forest and two shrubbery habitats (16–22% of contribution) in the dry season as well as between the two shrubbery habitats in the rainy season (26% contribution).

In habitats where *M. natalensis* persisted in both seasons, its flea assemblages were mainly characterized by high abundance of *D. grypurus* in the dry season (26–29% contribution) and was absent in the rainy season. However, among-habitat differences in flea species composition of this host were due to *D. lypusus* in the dry season (18% contribution) and *Xenopsylla brasiliensis* Baker, 1904 in the rainy season (32% contribution).

In contrast with the 2 former hosts, seasonal differences in flea assemblages on *P. delectorum* and *Grammomys* sp. were determined by different fleas in different habitats. For *P. delectorum*, these were *Ctenophthalmus leptodactylus* Hubbard, 1963 in open shrubbery and natural forest (higher abundance in rainy season; 15–24% contribution), *Leptopsylla aethiopica* Rothschild, 1908 in crop fields and closed shrubbery (complete absence of this flea in either the dry or the rainy season, respectively; 19–27% contribution) and *D. grypurus* in commercial plantations (higher abundance in rainy season; 19% contribution). For *Grammomys* sp., seasonal difference in flea species composition in commercial plantations and crop fields were due to *L. aethiopica* (27–38% contribution, respectively). In the former habitat, this flea occurred during the dry season, but disappeared in the rainy season, whereas in the latter habitat its abundance in the dry season was lower than that in the rainy season. Seasonal flea assemblages on this host in commercial plantations and closed shrubs differed mainly due to *N. incisus*, which decreased its abundance in rainy season.

In the dry season, flea assemblages on *P. delectorum* occupying different habitats differed mainly by relative abundance of *C. leptodactylus* (relatively low abundance in open shrubbery, high in crop fields and intermediate in natural forest and closed shrubbery; 19–27% contribution) or *L. aethiopica* (relatively high abundance in closed shrubs, low in open shrubs and absence in both crop fields and natural forest; 21–26% contribution). The latter flea was responsible also for the main difference in flea species composition in some of the between-habitat comparisons in the rainy season (high abundance in crop fields compared to other habitats; 21–26% contribution). In addition, in the rainy season, flea assemblages on *P. delectorum* in commercial plantations differed from most other habitats by relatively low abundance of *D. grypurus* (14–24% contribution), whereas those in closed shrubbery were characterized by relatively high abundance of *D. lypusus* (17–32% contribution).

In the dry season, flea assemblages on *Grammomys* sp. differed between habitats mainly because of the differ-

**Table 4** Similarity of seasonal flea assemblages on main hosts.

Species	Similarity (%)	
	Dry season	Rainy season
<i>Lophuromys kilonzo</i>	46.4	42.5
<i>Mastomys natalensis</i>	45.5	78.8
<i>Praomys delectorum</i>	44.6	55.7
<i>Grammomys</i> sp.	75.7	23.4

Mean pairwise between-habitat similarity (Bray–Curtis) in four common rodent species in dry and rainy seasons

ential abundance of *L. aethiopica* (higher abundance in open shrubs, the lower abundance in crop fields and commercial plantations and the absence in the remaining habitats; 27–62% contribution). In the rainy season, the flea that contributed most to between-habitat dissimilarity in the majority of comparisons was *N. incisus* (higher abundance in open shrubbery, lower abundance in crop fields and the lowest abundance or absence in the remaining habitats; 19–31% contribution). In addition, open shrubbery was characterized by relatively high abundance of *L. aethiopica* (17–43% contribution), whereas natural forest was the only habitat type where *Grammomys* sp. harbored *Ctenophthalmus teucgae* Laudisoit & Beaucournu, 2007 (22% contribution).

## DISCUSSION

### General patterns of host and flea abundance and diversity

Despite substantial environmental differences between seasons and among habitats, general patterns of abundance and diversity of small mammals and their fleas appeared to be relatively stable both in temporal and spatial scale. Mammal diversity and abundance were surprisingly similar between seasons, although the amount of rainfall has been shown to strongly affect the abundance of small mammals in other areas of tropical Africa (Fleming & Loveridge 2003; Gebreselassie *et al.* 2004; Makundi *et al.* 2007; Odhiambo *et al.* 2008). The lack of seasonal effect on pooled mammal density in the present study might be related to asynchronous seasonal dynamics of individual species composing a community. For example, in the study area, abundance of *M. natalensis* usually peaks in August and declines between September and January, whereas *P. delectorum* attains highest abundance in March–June and



December–February (Makundi *et al.* 2007). The net results of this asynchrony might be relative seasonal stability of the pooled abundance of small mammals.

The habitat effect on mammal abundance (but not on diversity) was pronounced, mainly due to high mammal density in closed shrubbery. The latter might be explained by shrub structure and availability of resources. Indeed, shrubs not only provide nesting sites and diverse food sources, but also offer an effective shelter for ground-dwelling mammals from carnivores and avian predators (Tews *et al.* 2004), and, hence, there is lower predation risk in closed habitats (Morse 1980; Parmenter & Macmahon 1983). Indeed, total rodent abundance increased with increasing shrub cover in Kalahari (Blaum *et al.* 2007) and the Kibale Mountains of Uganda (Isabirye Basuta & Kasenene 1987).

The only seasonal effect on flea diversity was that each individual mammal harbored more flea species during the dry season than during the rainy season. An explanation for this might be that tropical small mammals increase their foraging ranges and activity in response to food scarcity during the dry season (Foster 1982; Glanz *et al.* 1982; Ray 1998). Therefore, higher mobility might increase the exposure to parasites as well as chances of exchanging parasites between different individuals both conspecific and heterospecific. In addition, many rodents in tropical Africa start their reproduction during the rainy season (Happold & Happold 1990), so that their peaks of abundance are mainly observed at the onset of the dry season. As a result, the proportion of dispersing individuals in this period is large (e.g. Steinmann *et al.* 2005). The probability of a dispersing individual to be exposed to a larger variety of parasites is likely high. In addition, dispersers often visit burrows and nests of sedentary individuals, where they can be attacked by a variety of fleas (Lareshi *et al.* 2004).

### Seasonal and habitat variation in host and flea species composition

The results of the present study support earlier observations that species composition of flea assemblages on a given host in a given habitat at a given time is determined by both host identity and habitat identity (Krasnov *et al.* 1997, 2006). Furthermore, seasonal and habitat variation in host and flea species composition were mainly due to variation in their relative abundances rather than due to their occurrence. Seasonal variation in host species composition within a habitat was mainly due to changes in relative abundances of *L. kilonzoii*, *Grammomys* sp. and *P. delectorum*, whereas seasonal differences in flea spe-

cies composition were mainly due to changes in relative abundances of *N. incisus*, *C. eximius* and *D. grypurus*. Interestingly, the direction of change of relative abundance from the dry to the rainy season differed between host species, whereas changes of fleas' relative abundances were unidirectional. Indeed, populations of *L. kilonzoii* declined from the dry to the rainy season, whereas the opposite was the case for *P. delectorum*. In contrast, abundances of the three flea species (*N. incisus*, *C. eximius* and *D. grypurus*) decreased in the rainy season.

Contrasting patterns of seasonal changes in abundance between host species might be associated with differences in seasonal availability of their preferred food as well as with differences in reproductive patterns (Genest-Villard 1980). In the tropics, the abundance of rainfall, fruits and insects are important factors that might act directly or indirectly to initiate breeding activity to ensure that lactation occurs during a period when food abundance is greatest (Nicolas *et al.* 2003). In the rainy season, the abundance of a frugivore-granivore forest specialist, *P. delectorum*, might increase as a result of an increase in fruit abundance and abundance and quality of the leaf litter on which this species relies (Waweru & Odanga 2004). An additional reason for the growth of *P. delectorum* populations might be earlier and greater recruitment of young and/or survival during the preceding short rains (Makundi *et al.* 2007). The low values of abundance of *L. kilonzoii* in the rainy season could be a result of lower trapping success. This species feeds mainly on soil-dwelling invertebrates, which are highly abundant during the wet season and, therefore, a seed bait might attract it only when its preferred food becomes scarce (i.e. in the dry season). Small invertebrates indeed decreased in the importance of the diet of *Lophuromys flavopunctatus* Thomas, 1888 in Uganda during the dry season (Clausnitzer *et al.* 2003). Seasonal and habitat-related abundance patterns of *Grammomys* sp. suggest that this species relocates from commercial plantations and open shrubbery in the dry season to closed shrubbery in the rainy season. *Grammomys* sp. constructs above-ground nests, which are less conspicuous in closed shrubbery, so the pups will be less prone to predation.

Seasonal changes in the abundance and reproductive patterns of fleas have been observed not only in areas with pronounced seasonality, but also in regions where seasonal climate variation is not prominent (Krasnov *et al.* 2008). For example, seasonal peaks in abundance have been reported for *D. lypusus*, *Ctenophthalmus calceatus cabirus* Jordan et Rothschild, 1913 and *Xenopsylla bantorum* Jordan, 1938 in Kenya (Schwan 1993).

Variation in host species composition in different habitats is mainly a result of between-habitat variation in environmental characters, whereas variation in flea species composition is a result of between-habitat variation in both host-related and environment-related factors. Effects of habitat characteristics on mammal species composition have been frequently reported (e.g. Shenbrot *et al.* 1999 for deserts; Mortelliti & Boitani 2006 for African tropical forest), whereas the effects of a habitat type on parasite species composition have attracted less attention. The results of the present study suggest that both habitat characteristics and host species composition are important determinants of the structure of flea assemblages. Indeed, whereas some hosts were heavily infested, other co-occurring host species (e.g. *Nannomys minutoides* Smith, 1834 and *Dendromus nyikae* Wroughton, 1909) harbored few or no fleas. It remains to be further investigated whether the between-host variation is due to differences in the environmental conditions of their shelter, body size, skin or fur structure, or is due to antiparasitic behavioral and/or immunological host defenses.

The importance of habitat identity was supported by habitat variation in flea assemblages exploiting the same host species. Flea assemblages on each of 4 studied rodents varied in different habitats. For example, in the dry season, flea assemblages on *P. delectorum* were dominated by *C. leptodactylus* in crop fields, *L. aethiopica* in closed shrubbery, and *D. grypus* in natural forest. Flea assemblages on *L. kilonzo* were dominated by *D. lypus* in crop fields, *C. eximius* in closed shrubbery, and *C. calceatus* in the other shrub habitat. *M. natalensis* was mainly infested by *Dinopsyllus* sp. in open shrubs and in crop fields during the dry season, whereas *X. brasiliensis* replaced them in crop fields during the rainy season. Finally, *Grammomys* sp. harbored mainly *L. aethiopica* in the dry season and was replaced by *N. incisus* everywhere except in the forest, where *C. teucqae* was abundant. The main reason for the habitat effect on flea species composition is the high sensitivity of fleas to environmental factors such as temperature and relative humidity. In particular, the effect of these factors is most important for pre-imaginal fleas because flea development occurs mainly off-host (Klein *et al.* 1975; Amin *et al.* 1993; Yao *et al.* 2006). One of the sharpest examples of habitat effect on flea species composition is a complete replacement of one flea species with another on the same rodent hosts between two different habitats situated at the opposite sides of a steep precipitation gradient in the Negev Desert (Krasnov *et al.* 1997, 1998). This replacement is a result of, to a great extent, abiotic properties of the habitat (air

temperature, relative humidity and substrate texture), which affect survival and rate of development of pre-imaginal fleas (Krasnov *et al.* 2001).

Ordination of habitats according to their host or flea species composition demonstrated that some habitat pairs were characterized by similar host and flea assemblages. However, there were also habitat pairs with similar flea assemblages but different host composition (compare host similarity and flea similarity between open shrubbery and crop fields during the rainy season; Fig. 3) and pairs with similar host communities but different flea composition (compare host similarity and flea similarity between open shrubbery and commercial plantations during the dry season; Fig. 3). For example, during the dry season, similarity in host species composition between closed shrubbery and crop fields was as low as 26% due to the complete absence of *M. natalensis* in the former. Nevertheless, similarity in flea assemblages of these habitats was approximately 45%, because among a total of 10 flea species recorded there, the 7 most common fleas occurred in both habitats. This suggests that the occurrence of *M. natalensis* in closed shrubbery was not a necessary prerequisite for occupation of this habitat by the majority of fleas exploiting this host in crop fields. They merely switched to other hosts in closed shrubbery. The ability to utilize a variety of different host species (i.e. relatively low host specificity, is characteristic of fleas (Krasnov *et al.* 2008). This could be another reason for the effect of habitat identity as opposed to the effect of host community on flea species composition.

The importance of host-related factors was nevertheless supported by positive correlation between similarity in host species composition and similarity in flea species composition as well as a significant agreement between sample  $\times$  abundance matrices constructed for hosts and fleas. In other words, some fleas always accompanied the same host whenever this host occurred. For example, *Lybiastus duratus* Jordan, 1931 was highly host-specific and was associated only with the squirrel *Paraxerus vexillarius* Kershaw, 1923 so this flea did not occur in habitats where this host was absent. This close association usually reflects a strong adaptation of a particular flea to ecological, behavioral, physiological and biochemical traits of a particular host (see Sarfati *et al.* 2005). Moreover, even a highly host-opportunistic flea performs differently in different host species (Krasnov *et al.* 2003). Such a flea is not equally dependent on all its host species, but rather the flea's population dynamics is determined by populations of some but not other hosts (Stanko *et al.* 2006).

## Host-related and habitat-related determinants of flea species composition: Geographic perspective

The relative importance of host community structure versus habitat properties as determinants of flea species composition has been studied previously for fleas parasitic on small mammals in the Negev Desert (Krasnov *et al.* 1997, 1998) and Slovakia (Krasnov *et al.* 2006). The results of the current study demonstrate that, despite a strong habitat effect, host species composition better explains variance in flea species composition between localities in a tropical setting than in temperate and arid zones. The differences between tropical, temperate and arid environments might be associated with differences in the sheltering pattern of host species. Imago fleas spend a considerable part of their lives in a host's shelter, which is also the crucial habitat for pre-imagos. Almost all small desert mammals construct deep below-ground burrows (e.g. Shenbrot *et al.* 2002). In contrast, only a few small temperate mammals dig deep burrows, whereas many species dig shallow burrows or construct above-ground nests (Kucheruk 1983). In tropical rainforest, the soil layer is very thin, but leaf litter is permanent and deep, with a humid layer of humus below. Consequently, many tropical mammals prefer to build above-ground nests or dig single galleries in the litter. Consequently, between-habitat differences in the environmental conditions of host shelters in terms of microclimate and, consequently, in terms of their effect on pre-imaginal fleas in the tropics, are likely less pronounced than those of temperate areas and deserts (Shenbrot *et al.* 2002).

In conclusion, our results suggest that the composition of a flea assemblage in a habitat is determined by both host-related and habitat-related factors. However, the relative importance of these two groups of factors might vary geographically.

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## REFERENCES

- Amin OM, Liu J, Li S, Zhang Y, Sun L (1993). Development and longevity of *Nosopsyllus laeviceps kuzenkovi* (Siphonaptera) from Inner Mongolia under laboratory conditions. *Journal of Parasitology* **79**, 193–7.
- Bansemir AD, Sukhdeo MV (1996). Critical resources that influence habitat selection decisions by gastrointestinal helminth parasites. *International Journal for Parasitology* **26**, 483–98.
- Blaum N, Rossmanith E, Jeltsch F (2007). Land use affects rodent communities in Kalahari savannah rangelands. *African Journal of Ecology* **45**, 189–95.
- Bray JR, Curtis JT (1957). An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* **27**, 325–49.
- Brown JH (1975). Geographical ecology of desert rodents. In: Cody ML, Diamond JM, eds. *Ecology and Evolution of Communities*. Belknap Press, Cambridge, pp. 315–41.
- Calvete C, Estrada R, Lucientes J, Estrada A, Telletxea I (2004). Spatial variation in helminth community structure in the red-legged partridge (*Alectoris rufa* L.): Effects of definitive host density. *Parasitology* **129**, 101–13.
- Carrillo CM, Valera F, Barbosa A, Moreno E (2007). Thriving in an arid environment: High prevalence of avian lice in low humidity conditions. *Ecoscience* **14**, 241–9.
- Chapman JL, Reiss MJ (1992). *Ecology: Principles and Applications*. Cambridge University Press, Cambridge.
- Chesson P, Huntly N (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* **150**, 519–53.
- Chiejina SN, Fakae BB, Eze PI (1989). Development and survival of free-living stages of gastrointestinal nematodes of sheep and goats on pasture in the Nigerian derived savanna. *Veterinary Research Communications* **13**, 103–12.
- Clarke KR, Gorley RN (2001). *PRIMER v 5: User Manual Tutorial*. PRIMER-E, Plymouth.
- Clarke KR, Warwick RM (2001). A further biodiversity index applicable to species lists: Variation in taxonomic distinctness. *Marine Ecology Progress Series* **216**, 265–78.
- Clausnitzer V, Churchfield S, Hutterer R (2003). Habitat occurrence and feeding ecology of *Crocidura montis* and *Lophuromys flavopunctatus* on Mt. Elgon,

- Uganda. *African Journal of Ecology* **41**, 1–8.
- Davidson DW (1993). The effects of herbivory and granivory on terrestrial plant succession. *Oikos* **68**, 23–35.
- Devignat R (1949). Epidémiologie de la peste au Lac Albert 1944–1945–1946. *Annales de la Société Belge de Médecine Tropicale* **29**, 277–305.
- Fleming PA, Loveridge JP (2003). Miombo woodland termite mounds: Resource islands for small vertebrates? *Journal of Zoology, London* **259**, 161–8.
- Foster RB (1982). The seasonal rhythm of fruitfall on Barro Colorado Island. In: Leigh EG Jr, Rand AS, Windsor DM, eds. *Ecology of a tropical forest*. Smithsonian Institution Press, Washington, DC, pp. 151–72.
- Gebreselassie W, Bekele A, Belay G, Balakrishnan M (2004). Microhabitat choice and diet of rodents in Maynugus irrigation field, northern Ethiopia. *The African Journal of Ecology* **42**, 315–21.
- Genest-Villard H (1980). Régime alimentaire des rongeurs myomorphes de forêt équatoriale (région de M'Baiki, République Centrafricaine). *Mammalia* **44**, 423–6.
- Gentry AH (1988). Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* **75**, 1–34.
- Glanz WE, Thorington Jr RW, Giacalone-Madden J, Heaney LR (1982). Seasonal food use and demographic trends in *Sciurus granatensis*. In: Leigh Jr EG, Rand AS, Windsor DM, eds. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*. Smithsonian Institution Press, Washington, DC, pp. 239–52.
- Halperin J (2002). Reforestation planning in the West Usambara Mountains of Tanzania (Masters thesis). North Carolina State University, Washington, DC.
- Happold, DCD, Happold M. (1990). An ecological study of small rodents in the woodland savanna of Liwonde National Park, Malawi. *Journal of Zoology, London* **221**, 219–35.
- Heisch RB (1952). Wild-rodent plague in Kenya. Transactions of the Royal Society of Tropical Medicine and Hygiene **46**, 547–9.
- Isabirye Basuta GM, Kasenene JM (1987). Small rodent populations in selectively felled and mature forest tracts of Kibale Forest, Uganda. *Biotropica* **19**, 260–6.
- Jorgensen EE, Demarais S (1999). Spatial scale dependence of rodent habitat use. *Journal of Mammalogy* **80**, 421–9.
- Kennedy CR, Bush AO (1994). The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* **109**, 187–96.
- Klein JM, Simonkovich E, Alonso JM, Baranton G (1975). Observations écologiques dans une zone enzootique de peste en Mauritanie. 2. Les puces de rongeurs (Insecta, Siphonaptera). *Cahiers O.R.S.T.O.M., série Entomologie Médicale et Parasitologie* **13**, 29–39.
- Klopfer PH, Rubenstein DI, Ridgely RS, Barnett RJ (1974). Migration and species diversity in the tropics. *Proceedings of the National Academy of Sciences* **71**, 339–40.
- Kozak KH, Wiens JJ (2007). Climatic zonation drives latitudinal variation in speciation mechanisms. *Proceedings of the Royal Society B: Biological Sciences* **274**, 2995–3003.
- Krasnov B, Shenbrot G, Medvedev S, Vatschenok V, Khokhlova I (1997). Host–habitat relation as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. *Parasitology* **114**, 159–73.
- Krasnov B, Shenbrot G, Khokhlova I, Medvedev S, Vatschenok V (1998). Habitat dependence of a parasite-host relationship: Flea (Siphonaptera) assemblage in two gerbil species of the Negev desert. *Journal of Medical Entomology* **35**, 303–13.
- Krasnov BR, Khokhlova IS, Fielden LJ, Burdelova NV (2001). Development rates of two *Xenopsylla* flea species in relation to air temperature and humidity. *Medical and Veterinary Entomology* **15**, 249–58.
- Krasnov BR, Sarfati M, Arakelyan MS, Khokhlova IS, Burdelova NV, Degen AA (2003). Host-specificity and foraging efficiency in blood-sucking parasite: Feeding patterns of a flea *Parapulex chephrenis* on two species of desert rodents. *Parasitology Research* **90**, 393–9.
- Krasnov BR, Mouillot D, Shenbrot GI, Khokhlova IS, Poulin R (2005). Abundance patterns and coexistence processes in communities of fleas parasitic on small mammals. *Ecography* **28**, 453–64.
- Krasnov BR, Stanko M, Khokhlova IS *et al.* (2006). Aggregation and species coexistence in fleas parasitic on small mammals. *Ecography* **29**, 159–68.
- Krasnov BR, Shenbrot GI, Khokhlova IS, Mouillot D, Poulin R (2008). Latitudinal gradients in niche breadth: Empirical evidence from hematophagous ectoparasites. *Journal of Biogeography* **35**, 592–601.

- Kucheruk VV (1983). Mammal burrows: Their structure, topology and use. *Fauna and Ecology of the Rodents* **15**, 5–54 (in Russian).
- Lareschi M, Ojeda R, Linardi PM (2004). Flea parasites of small mammals in the Monte Desert biome in Argentina with new host and locality records. *Acta Parasitologica* **49**, 1230–2821.
- Makundi RH, Kilonzo BS (1994). Seasonal dynamics of rodent fleas and its implication on control strategies in Lushoto district, North-Eastern Tanzania. *Journal of Applied Entomology – Zeitschrift für Angewandte Entomologie* **118**, 165–71.
- Makundi RH, Massawe AW, Mulungu LS (2006). Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *African Journal of Ecology* **45**, 17–21.
- McCoy ED (1990). The Distribution of Insects along Elevational Gradients. *Oikos* **58**, 313–22.
- McSorley R (2003). Adaptations of nematodes to environmental extremes. *Florida Entomologist* **86**, 138–42.
- Morand S, Krasnov BR, Poulin R (2006). *Micromammals and Macroparasites: From Evolutionary Ecology to Management*. Morand S, Krasnov B, Poulin R, ed. Springer-Verlag, Tokyo and Berlin, 647 pp.
- Morse DH (1980). The effect of nectar abundance on foraging patterns of bumble bees. *Ecological Entomology* **5**, 53–9.
- Mortelliti A, Boitani L (2007). Patterns of interspecific and intraspecific microhabitat segregation of two rodents *Praomys jacksoni* (De Winton, 1897) and *Hylomyscus stella* (Thomas 1911) (Rodentia) in an African rainforest subjected to various levels of anthropogenic disturbance. *Tropical Zoology* **20**, 163–86.
- Nicolas V, Wendelen W, Verheyen W, Colyn M (2003). Population structure and reproduction of *Heimyscus fumosus* (Muridae, Brosset *et al.* 1965). *Revue d'Ecologie (la Terre et la Vie)* **58**, 209–16.
- Njunwa KJ, Mwaiko GL, Kilonzo BS, Mhina JIK (1989). Seasonal patterns of rodents, fleas and plague status in the Western Usambara Mountains, Tanzania. *Medical and Veterinary Entomology* **3**, 17–22.
- Odhambo RO, Makundi RH, Leirs H, Verhagen R (2008). Demography, reproductive biology and diet of the bushveld gerbil *Tatera leucogaster* (Rodentia: Gerbillinae) in the Lake Rukwa valley, south-western Tanzania. *Integrative Zoology* **3**, 31–7.
- Orrock JL, Pagels JF, McShea WJ, Harper EK (2000). Predicting presence and abundance of a small mammal species: The effect of scale and resolution. *Ecological Applications* **10**, 1356–66.
- Pagel MD, May RM, Collie AR (1991). Ecological aspects of the geographical distribution and diversity of mammalian species. *American Naturalist* **137**, 791–815.
- Parmenter RR, MacMahon JA (1983). Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. *Oecologia* **59**, 145–56.
- Ray JC (1998). Temporal variation of predation on rodents and shrews by small African forest carnivores. *Journal of Zoology, London* **244**, 363–70.
- Sarfati M, Krasnov BR, Ghazaryan L, Khokhlova IS, Fielden LJ, Degen AA (2005). Energy costs of blood digestion in a host-specific haematophagous parasite. *Journal of Experimental Biology* **208**, 2489–96.
- Schwan TG (1983). Seasonal dynamics of fleas and flea-phoretic mites on the Nile grass rat (*Arvicanthis niloticus*) in Lake Nakuru National Park, Kenya (PhD thesis). University Of California, Berkeley.
- Shemdoe RS (2002). Socio-economic analysis of ecosystem conservation practices in West Usambaras: A case of plague infested areas in Lushoto District, Tanzania. Research Report Submitted to IDRC Ecosystem Approaches to Human Health Training Awards Scheme. Sokoine University of Agriculture, Tanzania.
- Shemdoe RS (2004). Local knowledge on ecosystem management practices and human Plague Problems in West Usambaras, Tanzania. International Institute for Applied Systems Analysis Interim Report IR-04-007. Laxenburg, Austria.
- Shenbrot GI, Krasnov BR, Rogovin KA (1999). *Spatial Ecology of Desert Rodent Communities*. Springer-Verlag, Berlin.
- Shenbrot G, Krasnov B, Khokhlova I, Demidova T, Fielden L (2002). Habitat-dependent differences in architecture and microclimate of Sundeval jird (*Meriones crassus*) burrows in the Negev Desert, Israel. *Journal of Arid Environments* **51**, 265–79.
- Stanko M, Krasnov BR, Morand, S (2006). Relationship between host density and parasite distribution: inferring regulating mechanisms from census data. *Journal of Animal Ecology* **75**, 575–83.
- Steinmann AR, Priotto JW, Castillo EA, Polop JJ (2005).

Size and overlap of home range in *Calomys musculinus* (Muridae: Sigmodontinae). *Acta Theriologica* **50**, 197–206.

Tews J, Blaum N, Jeltsch F (2004). Structural and animal species diversity in arid and semi-arid savannas of the southern Kalahari. *Annals of Arid Zone* **42**, 1–43.

Waweru CW, Odanga JE (2004). Demographic aspects of

sympatric *Praomys jacksoni* and *P. stella* in a tropical lowland forest in Kakamega, Kenya. *African Journal of Ecology* **42**, 93–9.

Yao KP, Ngoran KE, Franc M (2006). Etude de quelques paramètres écologiques de *Ctenopcephalides felis strongylus* (Jordan, 1925) (Siphonaptera: Pulicidae). *Parasite* **13**, 159–64.