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Relationships between local and regional species richness in flea communities of small mammalian hosts: saturation and spatial scale

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Abstract The number of species coexisting in a community may be regulated by local factors (e.g., competitive interactions), or by regional processes (e.g., dispersal from a regional species pool). The relative importance of local and regional processes can be inferred from the shape of the relationship between local and regional species richness. We investigated this relationship in communities of fleas parasitic on small mammals at two spatial scales: between the richness of fleas on individual hosts (infracommunities) and that of fleas on host populations (component communities), and between the richness of component communities and that of the entire regional species pool. We tested linearity (proportional sampling) versus curvilinearity with an asymptote (species saturation) by plotting "local" against "regional" species richness of fleas either among host species or within host species among populations. At the two spatial scales, we found consistent curvilinear relationships between species richness of the more "local" communities and richness of the more "regional" communities. This was true across all host species in the data set and for geographic subsets, even after controlling for the influence of sampling effort on estimates of species richness, and that of host phylogeny in interspecific analyses. We also tested for density compensation in species-poor communities. There was no strong evidence for density compensation at the infracommunity level, although its existence at the component community level appeared likely. Our results suggest that identical patterns in local-versus-regional species richness observed on two different spatial scales arise via different mechanisms: infracommunities appear saturated with flea species most likely because of local processes, such as host immune defenses, whereas component communities are saturated with species through interspecific competition, possibly among larval stages.

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Introduction

One of the most important paradigms of community ecology is that patterns in local communities are governed not only by local (such as competition, predation and habitat heterogeneity) but also by regional and historical processes (such as long distance migration and speciation) (Cornell and Lawton 1992; Gaston and Blackburn 2000). For example, a species has to either arrive there repeatedly by dispersal or originate there and maintain its population in the local environment to persist in a locality. The relative importance of local and regional processes in governing local species composition can be inferred from examination of the relationship between local and regional species richness and/or diversity (Srivastava 1999). For example, if regional processes strongly control local communities by dispersal that limits local species richness, then the relationship between local and regional species richness will be linear (Cornell and Lawton 1992). Local communities are thus unsaturated (species are often absent from suitable habitats) and exhibit “proportional sampling” of the available regional species pool. However, if local processes (e.g., competition) play the main role in structuring local communities and impose upper limits on the number of species that are able to coexist, then local species richness will approach an asymptote with an increase in regional richness (Terborgh and Faaborg 1980; Cornell and Lawton 1992). At higher regional species richness, local richness becomes independent of regional richness. Local communities demonstrating a curvilinear relationship of local-versus-regional species richness are considered to be saturated with species (Guégan et al. 2005, but see Rohde 1998).

Testing the relationship between local and regional species richness is rather straightforward at first glance and can be carried out using regression analysis (e.g., Oberdorff et al. 1998). However, some methodological problems arise (Cresswell et al. 1995; Caley and Schluter 1997; Griffiths 1999; Srivastava 1999; Fox et al. 2000; Loreau 2000; Shurin et al. 2000; Hillebrand 2005), and thus, the use of local–regional richness plots to test for saturation of diversity has been strongly criticized. The criticism was mainly related to statistical issues (Srivastava 1999), the definition of two spatial scales (Loreau 2000; Shurin et al. 2000; Hillebrand and Blenckner 2002), and the effects of different types of interactions (Shurin and Allen 2001). Nevertheless, the use of regional to local diversity regressions remains common (Valone and Hoffman 2002; Heino et al. 2003; Calvete et al. 2004; Karlson et al. 2004). The reason for this can be the methodological problems that arise when using some of recently suggested “unorthodox” approaches to compare between “local” and “regional” species richness. For example, an approach suggested by Loreau (2000) involves determination of the way the total diversity is partitioned between its α and β components. However, determining the β component of diversity for the real data is highly problematic.

One of the most important methodological issues is a definition of borders for local and regional communities. It is sometimes self-evident for freshwater organisms (e.g., a pond, Shurin and Allen 2001), but it is much more difficult for terrestrial or marine organisms. Furthermore, the terms “local” and “regional” can be misleading. Loreau (2000) consequently argued that consideration of species richness at multiple spatial scales should be favored instead, although this does not avoid the difficulty of definitions. For parasitic animals however, the definition of a community at the lowest hierarchical scale is relatively easy. This is the infracommunity, which includes all parasitic individuals of all species within an individual host. The measure of local parasite species richness is thus mean (e.g., Morand et al. 1999) or maximum (e.g., Calvete et al. 2004) infracommunity parasite species richness. The next hierarchical level is the component community of parasites, which is defined as all infracommunities within a give host population. Finally, all component parasite communities within a given host species represent either a regional parasite community or a parasite fauna. The latter is considered across the entire geographic range of a host species (Poulin 1998). Although Srivastava (1999) argued that in the case of parasites, an equivalent of “regional” species richness is the parasite fauna, we believe that component community richness can be considered as “regional” in relation to infracommunity richness. This is because the species pool of a component community contains all species than can colonize an infracommunity assuming the absence of competitive exclusion. Dispersal of species within a component community may be slow, nevertheless, it is more frequent than host-switching (equivalent to dispersal between regions, see Srivastava 1999).

Most studies of the relationship between species richness of communities of free-living organisms at different spatial scales have demonstrated that unsaturated communities are the norm (e.g., Lawton et al. 1993; Hugueny and Paugy 1995; Oberdorff et al. 1998; see Srivastava 1999 for review). However, analyses of local-versus-regional species richness in parasites have revealed that saturated and unsaturated communities are equally common (e.g., Poulin 1996; Morand et al. 1999; Kennedy and Guégan 1996; Calvete et al. 2004). Guégan et al. (2005) suggested that these contrasting results arise due to the fact that studies reporting linear relationships between the infracommunity and component community species richness tested this relationship among host species (e.g., Poulin 1996), whereas studies reporting curvilinear relationships between the two parameters compared different populations of the same host species (e.g., Calvete et al. 2004).

Testing the relationship between parasite infracommunity and parasite component community species richness among host species while simultaneously testing it among different populations within these same host species has never been done. In addition, no one, as far as we know, has considered component communities of parasites as entities at a lower hierarchical scale and tested for the relationship between species richness of component communities and species richness at a higher hierarchical scale, i.e., richness of the regional community or parasite fauna. Moreover, most previous studies of these patterns in parasites have involved gastrointestinal helminths of various host taxa and ectoparasites of marine fish; the relationship between local and regional species richness in ectoparasites of terrestrial hosts has never been studied.

We considered here species richness of flea communities in small mammalian hosts at different hierarchical levels, namely infracommunities, component communities and regional communities. We asked (1) whether species richness of infracommunities and component communities of fleas demonstrate linear or curvilinear relationships with flea species richness of communities at a higher hierarchical level (component community and regional species pool, respectively) and (2) whether the relationship between infracommunity and component community species richness varies among host species and/or among different geographic regions. Thus, we tested for linearity (proportional sampling) versus curvilinearity with an asymptote (species saturation) in the relationship between "local" and "regional" species richness at two spatial scales, namely, (1) between infracommunity and component community and (2) between component community and regional community. The relationship between infracommunity and component community flea species richness was tested among different host species and among different populations within these host species.

Demonstrating the existence or absence of saturation in parasite assemblages requires the additional investigation of interspecific interactions (Guégan et al. 2005). Therefore, we tested for the possible existence of density compensation in species-poor flea infracommunities and component communities by testing the relationships between mean abundance of fleas and "local" species richness. The occurrence of a linear trend between these two parameters would suggest the lack of density compensation in species-poor communities (Cornell 1993; Oberdorff et al. 1998). Density compensation is the phenomenon whereby the population density of each species is greater in species-poor than in species-rich communities. The increased densities thus compensate for the loss of some populations relative to species-rich communities. Density compensation is generally associated with intense competition for resources (McArthur et al. 1972; Tonn 1985). If complete compensation occurs, there will be no relation between mean flea abundance and "local" species richness.

Materials and methods

Infracommunity species richness versus component community species richness

We used data on fleas collected from 65 species of small mammals (Insectivora, Lagomorpha and Rodentia). Data on flea infracommunity and component community species richness were obtained from field surveys in the Negev desert (Israel) and Slovakia and from published studies performed in other regions, where number of examined hosts, maximal infracommunity species richness of fleas and number of flea species found on a given host species in a given study area were reported (Appendix 1). Sampling of small mammals for flea collection in the field was carried out using methods described in Krasnov et al. (1997) for the Negev Desert and Stanko et al. (2002) for Slovakia. For each host species, we calculated the maximum infracommunity species richness of fleas, hereafter MISR (maximum number of flea species found on an individual of a given host species in a study area), component community species richness of fleas, hereafter CSR (number of flea species found on a population of a given host species in a study area) and the mean flea abundance per individual host (mean number of flea individuals of all species found per individual of a given host species in a study area). These data were used for interspecific analysis (see below). We also carried out intraspecific analyses for 10 species (eight species from Slovakia and two species from the Negev Desert, see Appendix 1), for which a sufficient number of different populations (9–63) were sampled.

Component community species richness versus regional species richness

To test for the relationship between component and regional flea species richness, we used data obtained from published surveys that reported flea distribution and abundance on small mammals (Insectivora and Rodentia) in 38 different regions (Appendix 2). These sources provided data on the number of individuals of each flea species found on a given number of individuals of each particular host species. From these, we chose 28 small mammal species that occurred in at least four regions (Appendix 3). For each mammal species, we calculated (1) maximum and mean component community species richness of fleas, taken either as the maximum (MCSR) flea species richness in one region for that host species or the mean richness across all regions where that host species occurs, respectively; (2) regional flea species richness (RSR), taken as the total richness of the flea fauna for that host species, compiled across all regions where it occurs; and (3) mean abundance of fleas (all species combined) per individual host.

Data analyses

Estimates of parasite species richness may be biased if some hosts are studied more intensively than others (Morand and Poulin 1998). Indeed, log-transformed values of flea infracommunity and component community species richness were strongly affected by sampling effort (r^2=0.12–0.53, F=8.7–28.8, P<0.005 for all). Each value of flea species richness was then substituted by its residual deviation from a linear regression against the number of hosts examined using log-transformed values. This provided a measure of flea richness that is independent of sampling effort. Also, regional flea species richness is affected by the size of host geographic range (Krasnov et al. 2004a). Regional flea species richness was controlled both for sampling effort and the size of host geographic range using residual deviations from a multiple linear regression of log-transformed richness of the flea fauna for each host species, compiled across all regions where it occurs, against the number of regions where this host species was found and total number of hosts examined (r^2=0.65, F=23.7, P<0.001).

Two main methods have been used to test the shape of the relationship between local and regional species richness (Griffiths 1999), namely: (1) fitting a second-order polynomial regression (curvilinearity is indicated by the significance of the second-order term; e.g., Hawkins and Compton 1992) and (2) performing a linear regression on logarithmically transformed values (curvilinearity is indicated by the value of the slope; e.g. Griffiths 1997). There is no common agreement regarding which of these methods is preferable (Griffiths 1999). We chose to use the latter approach because of the necessity to control for the confounding effects of sampling effort and the size of the host geographic range. These corrections of the raw data are usually performed using residuals from the regressions on log-transformed data. We tested linearity (proportional sampling) versus curvilinearity with an asymptote (species saturation) by plotting "local" (either maximum infracommunity or component community) against "regional" (component community or regional, respectively) species richness of fleas either among host species (for maximum infracommunity versus component community and for maximum component community versus regional flea species richness), or within host species among populations (for maximum infracommunity versus component community flea species richness) for 10 host species for which at least nine populations were sampled. In a regression using log-transformed data, a slope of 1 indicates linearity or the proportional increase of local richness with regional richness, whereas a slope less than 1 indicates curvilinearity, i.e., local richness increasing at a decreasing rate with increasing regional richness. We analyzed relationships between flea density (mean abundance) and "local" species richness both inter- and intraspecifically (see above) using linear regressions to test for density compensation in flea communities. We also tested the relationship between maximum infracommunity flea richness and either component community flea richness or mean flea abundance for three separate geographic regions, for which a sufficient number of host species were sampled (Slovakia, the Negev Desert and central California).

All interspecific analyses were done using both conventional regressions and the method of independent contrasts (Felsenstein 1985) that allows to control for the confounding effect of phylogeny. A phylogenetic tree for hosts was constructed using various sources (see Krasnov et al. 2004b for details). We used the PDAP: PDTREE program (Midford et al. 2005) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2004) to compute independent contrasts. There was no need to force the regression of independent contrasts through the origin (Garland et al. 1992) for the analyses of the relationship between "local" versus "regional" flea species richness because the intercepts did not differ significantly from zero in all analyses. However, the regressions of independent contrasts were forced through the origin for the analysis of the relationship between mean flea abundance and either infracommunity or component community flea species richness.

Fox et al. (2000) recently pointed out that species that are shared between regional species pools create problems of nonindependence. In our analyses for instance, if some flea species occur on several species of mammalian hosts, then using these host species in interspecific analyses based on conventional regression techniques would be inappropriate. We have opted not to use the Monte Carlo test proposed by Fox et al. (2000) for three reasons. First, the test is very conservative and its robustness has not been demonstrated yet. Second, on average between any two host species in our data set, there were only about 12% shared species; this suggests that the nonindependence between species pools was very limited. Third, the patterns we found are remarkably consistent across all analyses (see below), suggesting that the ecological phenomena we have uncovered are unlikely to be artifacts of some limited nonindependence in the data.

Results

Infracommunity species richness versus component community species richness

Maximum infracommunity species richness of fleas in 65 host species ranged from 1 to 6 with a median value of 3,

Table 1 Summary of the conventional regression analyses (A) and regression analyses using independent contrasts (B) of maximum infracommunity flea species richness versus component community flea species richness (log-transformed values controlled for sampling effort) among host species for the entire data set and for three separate geographic regions

Data set		r^2	F	Intercept (SE)	Slope (SE)
Entire (65 hosts)	A	0.53	76.9	−0.01 (0.04)[a]	0.53 (0.06)**
	B	0.48	59.4	−0.03 (0.03)[a]	0.49 (0.06)**
Slovakia (18 hosts)	A	0.69	35.8	0.08 (0.08)[a]	0.66 (0.11)**
	B	0.57	21.6	−0.07 (0.06)[a]	0.64 (0.14)**
Negev (12 hosts)	A	0.55	12.1	0.11 (0.07)[a]	0.59 (0.17)**
	B	0.32	5.2	0.006 (0.05)[a]	0.49 (0.13)*
California (16 hosts)	A	0.28	5.4	−0.17 (0.13)[a]	0.48 (0.20)*
	B	0.39	7.8	−0.07 (0.07)[a]	0.62 (0.22)**

r^2 is not directly comparable between conventional and phylogenetically independent contrasts equations

*$P<0.05$

**$P<0.01$

[a] Nonsignificant

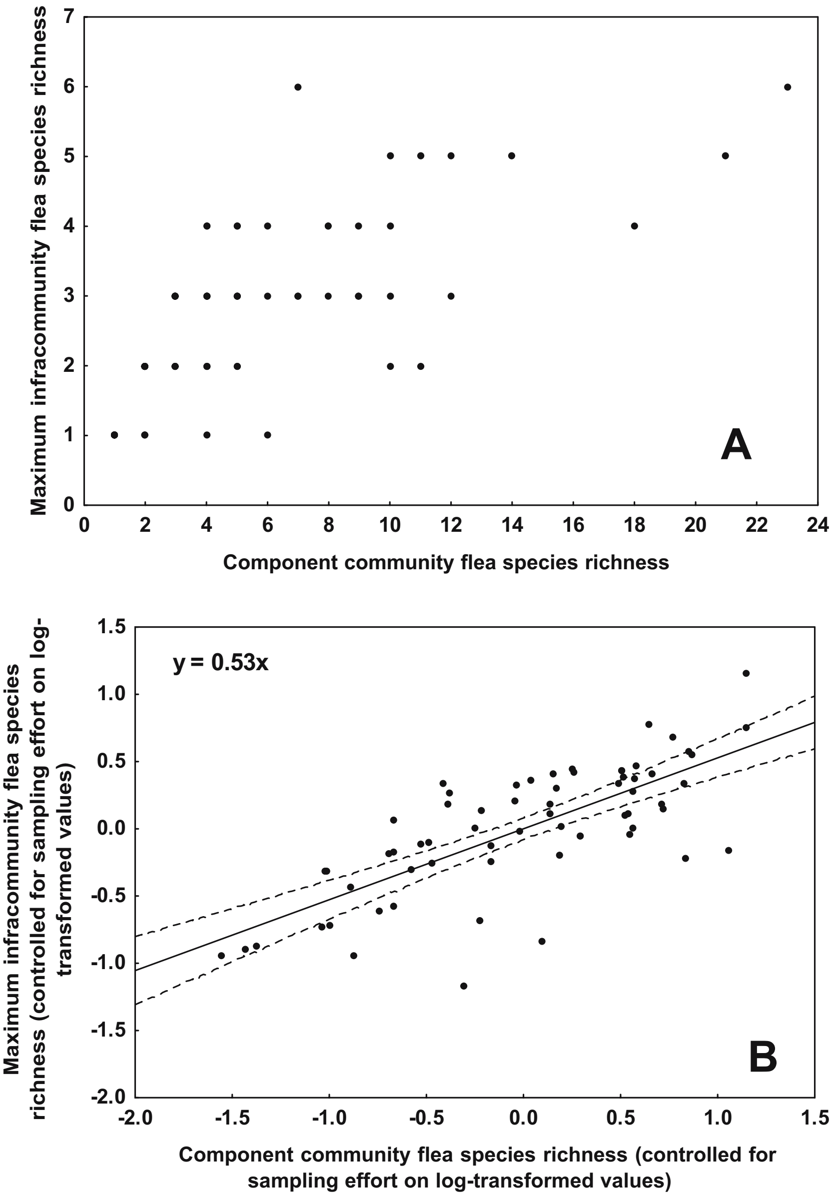


Fig. 1 Relationship between maximum infracommunity flea species richness and component community flea species richness for 65 small mammal hosts. **a** Raw data, **b** log-transformed values controlled for sampling effort. *Dotted lines* represent 95% confidence intervals

whereas the component community species richness for these hosts ranged from 1 to 23 with a median value of 4. We found a significant positive relationship between maximum infracommunity flea richness and component community flea richness with the slope of the relationship significantly lower than 1 and the intercept not significantly

Table 2 Summary of the regression analyses of maximum infracommunity flea species richness and component community flea species richness (log-transformed values controlled for sampling effort) among populations within host species

Host	r^2	F	Intercept (SE)	P	Slope (SE)	P
Apodemus agrarius	0.47	49.4	0.01 (0.04)	0.73	0.82 (0.11)	<0.001
Apodemus flavicollis	0.41	47.9	0.02 (0.03)	0.48	0.70 (0.10)	<0.001
Apodemus uralensis	0.37	24.2	−0.04 (0.04)	0.39	0.75 (0.15)	<0.001
Clethrionomys glareolus	0.34	31.8	−0.03 (0.04)	0.33	0.63 (0.11)	<0.001
Microtus arvalis	0.53	46.0	0.008 (0.04)	0.83	0.76 (0.11)	<0.001
Microtus subterraneus	0.87	125.0	0.03 (0.04)	0.20	0.93 (0.08)	<0.001
Neomys fodiens	0.83	33.8	−0.05 (0.07)	0.49	0.69 (0.12)	<0.001
Sorex araneus	0.66	62.8	−0.02 (0.03)	0.57	0.71 (0.08)	<0.001
Gerbillus dasyurus	0.13	6.8	0.02 (0.06)	0.72	0.76 (0.29)	<0.001
Meriones crassus	0.11	5.4	−0.02 (0.05)	0.74	0.57 (0.24)	<0.001

Fig. 2 Relationship between maximum infracommunity flea species richness and component community flea species richness (log-transformed values controlled for sampling effort) across host populations for *M. arvalis* (**a**) and *M. subterraneus* (**b**). *Dotted lines* represent 95% confidence intervals

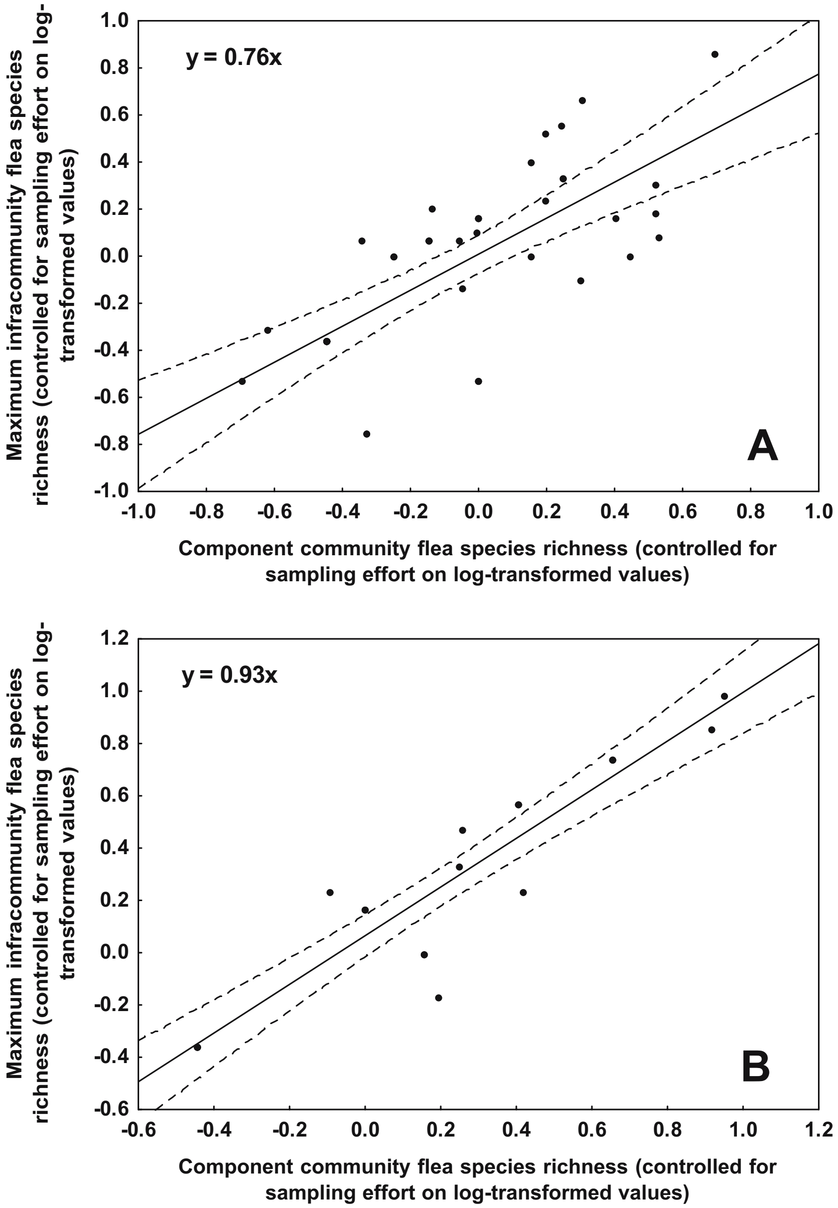


Table 3 Summary of the conventional regression analyses (A) and regression analyses using independent contrasts (B) of the relationship between mean abundance of fleas and maximum infracommunity flea richness among host species for the entire data set and for three separate geographic regions

Data set		r^2	*F*	Slope (SE)	*P*
Entire (65 hosts)	A	0.34	31.7	1.79 (0.32)	<0.0001
	B	0.27	22.5	1.82 (0.32)	<0.0001
Slovakia (18 hosts)	A	0.74	45.9	2.06 (0.30)	<0.0001
	B	0.60	24.1	1.70 (0.35)	<0.0001
Negev (12 hosts)	A	0.06	0.6	1.22 (1.53)	0.44
	B	0.23	2.6	2.66 (0.13)	0.14
California (16 hosts)	A	0.12	1.9	0.81 (0.58)	0.18
	B	0.54	14.5	0.71 (0.19)	<0.005

r^2 is not directly comparable between conventional and phylogenetically independent contrasts equations

Table 4 Summary of regression analyses of the relationship between mean abundance of fleas and maximum infracommunity flea richness among populations within host species

Host	r^2	*F*	Slope (SE)	*P*
A. agrarius	0.35	30.5	0.74 (0.13)	<0.001
A. flavicollis	0.39	43.4	0.90 (0.13)	<0.001
A. uralensis	0.39	25.2	0.73 (0.14)	<0.001
C. glareolus	0.51	64.0	0.98 (0.12)	<0.001
M. arvalis	0.49	39.1	1.15 (0.18)	<0.001
M. subterraneus	0.47	17.2	1.14 (0.27)	<0.001
N. fodiens	0.86	44.2	2.11 (0.31)	<0.001
S. araneus	0.24	10.4	1.08 (0.34)	<0.002
G. dasyurus	0.27	17.2	0.70 (0.17)	<0.001
M. crassus	0.01	0.6	0.18 (0.23)	0.44

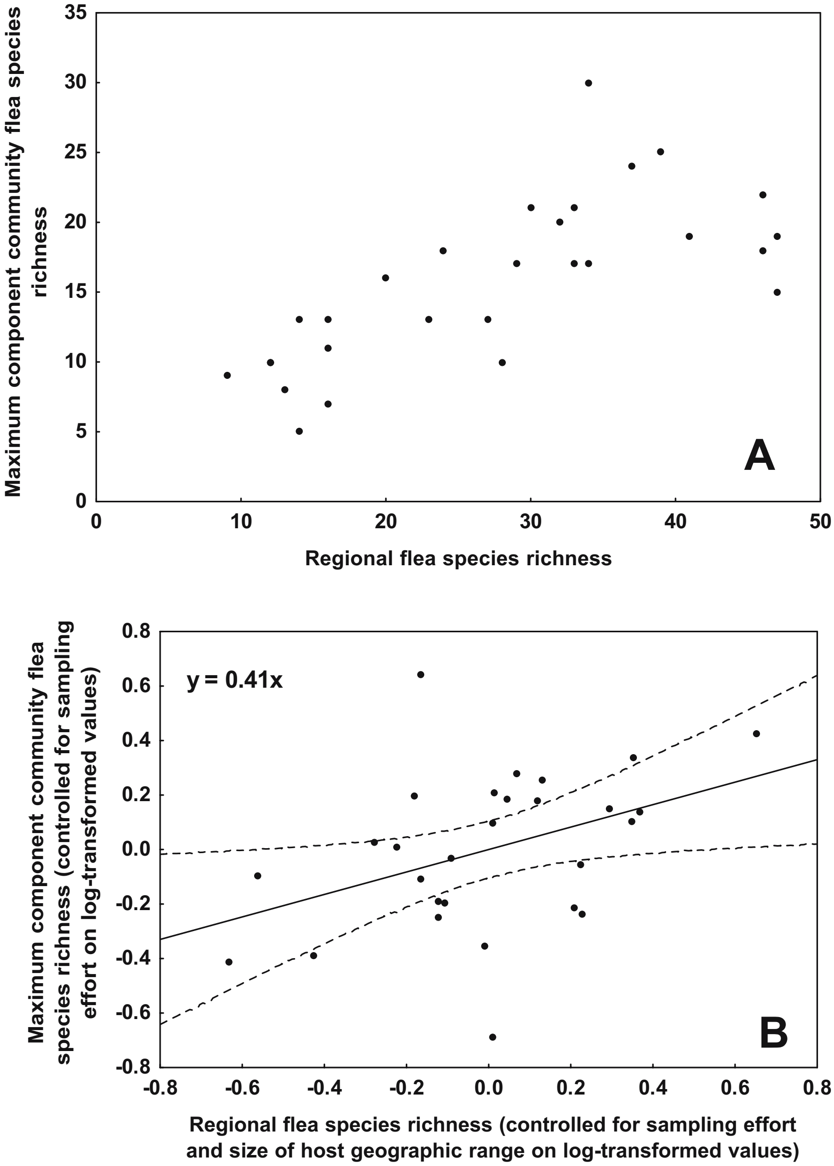
r^2 is not directly comparable between conventional and phylogenetically independent contrasts equations

different from zero (Table 1, Fig. 1). The same was true when we used independent contrasts (Table 1). This pattern was found to be geographically stable and was true for each of the three separate geographic regions both before and after controlling for the potential confounding effect of phylogeny (Table 1).

The tests of the relationship between maximum infracommunity flea richness and component community flea richness within host species are presented in Table 2. This relationship was significant with zero intercept in all 10 host species. The slope of the infracommunity versus component community flea richness relationship was significantly lower than 1 in eight host species (see Fig. 2a for an illustrative example with *Microtus arvalis*), whereas it did not differ significantly from 1 in *Microtus subterraneus* (Slovakia; Fig. 2b) and *Gerbillus dasyurus* (Negev).

The results of both conventional regression and regression using independent contrasts demonstrated that mean abundance was positively correlated with maximum infracom-

Fig. 3 Relationship between maximum component community flea species richness and regional flea species richness for 28 small mammal host species. **a** Raw data, **b** log-transformed values controlled for sampling effort and size of host geographic range, where appropriate. *Dotted lines* represent 95% confidence intervals



munity richness for the entire data set and the subset of Slovakian hosts, but no relationship between these parameters was found for the subset of hosts from the Negev desert (Table 3). The analyses of this relationship for the subset of hosts from central California generated discordant results. No significant relationship was found between mean flea abundance and infracommunity species richness using conventional regression, but this relationship appeared to be significantly positive after removal of the confounding effect of phylogeny (Table 3). In intraspecific analyses, a correlation between mean flea abundance and maximum infracommunity richness was found for all eight hosts from Slovakia and one of the two hosts from the Negev desert (*G. dasyurus*) (Table 4).

Component community species richness versus regional species richness

Maximum component community flea richness in 28 host species ranged from 5 to 30 with a median value of 16, whereas regional flea richness for these hosts ranged from 9 to 47 with a median value of 28. Maximum component community richness of fleas correlated positively with regional flea richness ($r^2=0.46$, $F=22.4$, $P<0.0001$; Fig. 3). The intercept of this relationship did not differ significantly from zero (-0.001 ± 0.02; $P>0.99$), whereas the slope was significantly lower than 1 (0.50 ± 0.10; $P<0.0001$). The same was true when the method of independent contrasts was used ($r=0.39$, $F=5.6$; intercept$=0.005\pm0.04$, $P=0.89$; slope$=0.47\pm0.19$, $P=0.03$). Finally, the mean abundance of fleas was not correlated with the maximum component community flea richness ($r^2=0.03$, $F=0.7$ for conventional regression and $r=0.23$, $F=1.4$ using independent contrasts; $P>0.2$ for both).

Discussion

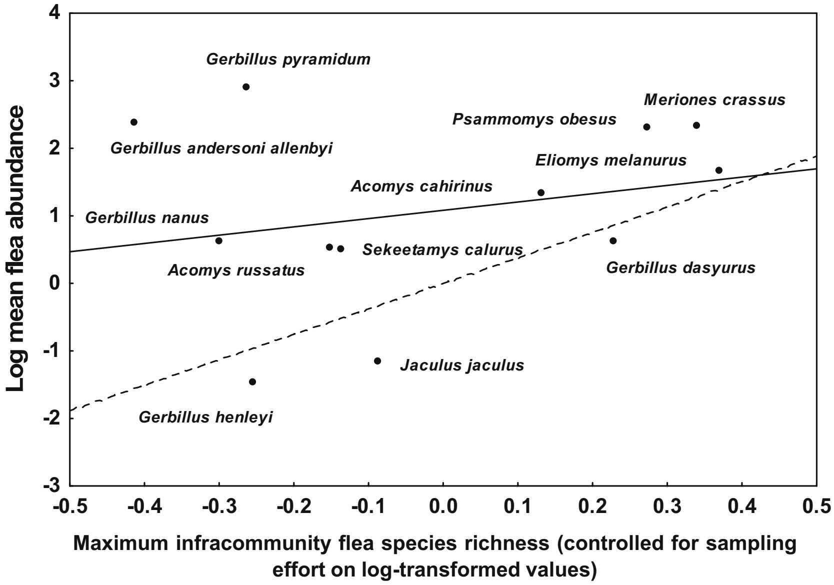
The results of this study demonstrated that (1) there is a curvilinear relationship between local and regional parasite species richness on two different scales (infracommunities versus component communities, and component community versus regional species pool) in fleas parasitic on small mammals; (2) the curvilinear relationship between infracommunity and component community species richness is not restricted to particular host taxa or geographic zones but instead occurs in various regions and landscapes and in hosts of various taxonomic affinities; and (3) density compensation occurs at the level of flea component communities but generally not at the infracommunity level.

The curvilinear relationship between infracommunity and component community flea richness suggests that the number of species in species-rich flea infracommunities is independent of the species richness of the component community of which they are part. This appeared to be true for both comparisons across host species and for comparisons across populations of the same host species. Thus at first glance, the flea infracommunities are "saturated" (at about 5–6 flea species per infracommunity; see Fig. 1a) and vacant niches seem to be generally unavailable in these communities. The observed pattern may arise because some species can be eliminated or not allowed to invade local communities due to some ecological constraints (Srivastava 1999). One of these constraints can be the negative interactions among species in an infracommunity. In general, demonstrating negative interspecific interactions among parasites is more difficult than among free-living animals. Nevertheless, Calvete et al. (2004) showed that the curvilinear relationship between local and regional species richness of gastrointestinal helminths parasitic in red-legged partridge (*Alectoris rufa*) was linked with the occurrence of negative pair-wise associations between helminth species. Moreover, the curvilinear local-versus-regional species richness relationship held even after controlling for the confounding factors of sampling effort and geographic distances of the sampled localities.

For the parasite–host system considered here, negative interactions between flea species within an infracommunity can be mainly responsible for the relative independence of infracommunity species richness from that of its component community. In fleas, negative interspecific interactions can be expected in both adults (e.g., Day and Benton 1980) and larvae (e.g., Marshall 1981). If negative competitive interactions among flea species in an infracommunity are indeed important, one would expect density compensation in species-poor infracommunities (Cornell 1993). However, we did not find evidence for density compensation (because of the significant linear relationship between mean flea abundance and infracommunity species richness) for the entire data set, for two of three geographic subsets (Slovakia and California, although it was true for California only after controlling for the confounding effect of host phylogeny) and for eight of 10 individual host species. Moreover, closer inspection of the relationship between mean flea abundance and infracommunity species richness for the subset of hosts from the Negev desert demonstrated that the lack of linear relationship between these two parameters was mainly due to two outliers, *Gerbillus andersoni allenbyi* and *Gerbillus pyramidum* (Fig. 4). After removing these two outliers, the regression became significant ($r^2=0.56$, $F=10.3$, $P<0.01$). One of these species (and, likely, the other as they are very closely related) is characterized by relatively strong "pre-invasive" immune readiness against fleas but relatively low "post-invasive" immune response (Khokhlova et al. 2004a), thus differing drastically from other studied rodents (Khokhlova et al. 2004b). Therefore, the high flea abundance at low flea species richness in these hosts can be explained by this exceptional pattern of immune response rather than by interactions between fleas.

These findings suggest that the curvilinear relationship between infracommunity and component community species richness may occur for reasons other than "saturation" stemming from competitive interspecific interactions. Indeed, Rohde (1998) demonstrated that curvilinearity in the local versus regional species richness relationship may be caused by processes other than species interactions

Fig. 4 Relationship between mean flea abundance (log-transformed) and maximum infracommunity flea species richness (log-transformed values controlled for sampling effort) across hosts from the Negev desert. *Solid line*, fitted linear function, *dashed line*, fitted linear function after removal of two outlier species (*G. a. allenbyi* and *G. pyramidum*)



within a local community. In particular, this curvilinearity may be a consequence of the differential likelihood of parasite species of occurring in an infracommunity. These differences can be related to differential transmission rate and life span (Rohde 1998). In the case of fleas, they can also be related to differential abiotic preferences of either imago or larval fleas of different species that can also contribute to the elimination of some flea species from some infracommunities. For example, in the central Negev desert, the flea *Xenopsylla ramesis* is absent from those individuals of *Meriones crassus* that occur in extremely dry habitats (Krasnov et al. 1997). One of the reasons for this appeared to be the high sensitivity of eggs, larvae, and newly emerged imago of this flea to relatively low humidity (Krasnov et al. 2001, 2002). The consistency of curvilinearity in the relationship between infracommunity and component community species richness and the consistent lack of evidence for density compensation across different host species and different geographic regions indicate that flea infracommunities are governed by processes acting at a higher than "local" level, and that further species could possibly be added over evolutionary time (Rohde 1998). However, the importance of processes acting at the "local" (infracommunity) level cannot be discarded. For example, apparent interspecific competition mediated via host defense systems (behavioral or immunological) could also be responsible for the upper limit on the number of species that are able to coexist in an infracommunity. Indeed, multiple immunogens from multiple flea species or attacks of multiple flea species on multiple body parts (Hsu et al. 2002) can increase the power of the host immune response or autogrooming effort, respectively. This may eliminate some flea species from some individual hosts. Different relative roles of processes, which are operating either at "local" (infracommunity) or "regional" (component community) levels in different host species resulting from differences in some presently unknown characteristics of their defense system, can be responsible for saturation of flea infracommunities in some hosts (*M. subterraneus* and *G. dasyurus*, see Results) but not in others.

On the other hand, the effect of host defense system on the number of coexisting flea species can be considered as a kind of physical limitation that can be a reason for community saturation *sensu* Loreau (2000). Moreover, Hillebrand (2005) argued that saturation of local communities can be expected only if there are uniform upper limits to local diversity that constrain all habitats (=hosts) in a region. This can exactly be the case when the relationship between species richness of infracommunities and that of component communities is considered because host individuals belong to the same species, and thus, their ability to cope with multiple parasite species is likely uniform.

The relationship between local and regional flea richness appeared to be the same at the larger scale than at the smaller scale; in other words, the relationship between richness of component communities and that of the regional flea pool seems to be similar to that found for infracommunities versus component communities. However, the absence of a relationship between mean flea abundance and component community species richness suggests the existence of density compensation. Therefore, component communities appeared to be saturated (with a plateau reached at about 25 flea species per component community; see Fig. 3a). The causes of this saturation are likely some intrinsic limiting factors that may play an important role in shaping flea component communities. One of the common factors responsible for community saturation is a negative interspecific interaction such as competition (Cornell 1993). Although direct interspecific competition between imago fleas within a host population has never been studied, such competition can occur among larval fleas. The latter (at least those of species exploiting small mammals) are not parasitic, develop off-host and feed on organic debris in the burrow and/or nest of the host.

Moreover, competitive interspecific exclusion was found in experiments with flea larvae (Krasnov et al. 2005). Preimago fleas from different host individuals (especially in social or colonial hosts) can co-occur in the same burrow and compete for the food sources (Krasnov et al. 2005). The mechanism of competition between larval ectoparasitic insects can be either exploitative (e.g., Braks et al. 2004) or direct via interspecific cannibalism (Lawrence and Foil 2002). In addition, the outcome of this competition can be environment-dependent. For example, in the central Negev, the flea *Xenopsyla conformis* is absent from populations of *M. crassus* in relatively mesic habitats where it is outcompeted by *X. ramesis* (Krasnov et al. 2005). As a result, some flea species can be excluded from some populations of the host. In other words, component communities of fleas seem to be governed by ecological rather than evolutionary limitations (see Srivastava 1999).

In conclusion, the results of this study demonstrated that similar patterns of relationship between "local" and "regional" species richness in the same host–parasite system but at different spatial scales may arise because of different mechanisms. This suggests that one needs to be cautious when interpreting local–regional species richness plots. Indeed, Bell (2003) has used neutral model simulations to demonstrate that changes in immigration rate can alter the form of the local–regional species richness relationship on their own, whereas Loreau (2000) has also shown that ecological interactions can generate linear local–regional species richness relationships. Furthermore, differential mechanisms leading to similar patterns of the local–regional species richness relationship in the same host–parasite system at different scales could be one explanation for the contrasting relationships reported between local and regional species richness in earlier studies of different host–parasite systems.

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