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Co-occurrence and phylogenetic distance in communities of mammalian ectoparasites: limiting similarity versus environmental filtering

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Similarity between species plays a key role in the processes governing community assembly. The co-occurrence of highly similar species may be unlikely if their similar needs lead to intense competition (limiting similarity). On the other hand, persistence in a particular habitat may require certain traits, such that communities end up consisting of species sharing the same traits (environmental filtering). Relatively little information exists on the relative importance of these processes in structuring parasite communities. Assuming that phylogenetic relatedness reflects ecological similarity, we tested whether the co-occurrence of pairs of flea species (Siphonaptera) on the same host individuals was explained by the phylogenetic distance between them, among 40 different samples of mammalian hosts (rodents and shrews) from different species, areas or seasons. Our results indicate that frequency of co-occurrence between flea species increased with decreasing phylogenetic distance between them in 37 out of 40 community samples, with 14 of these correlations being statistically significant. A meta-analysis across all samples confirmed the overall trend for closely related species to co-occur more frequently on the same individual hosts than expected by chance, independently of the identity of the host species or of environmental conditions. These findings suggest that competition between closely related, and therefore presumably ecologically similar, species is not important in shaping flea communities. Instead, if only fleas with certain behavioural, ecological and physiological properties can encounter and exploit a given host, and if phylogenetic relationships determine trait similarity among flea species, then a process akin to environmental filtering, or host filtering, could favour the co-occurrence of related species on the same host.

The idea that intensity of competition depends on the similarity between competing species was proposed more than 150 years ago by Darwin (1859), and has since served as the basis for numerous empirical and theoretical studies leading to the development of such concepts as 'character displacement' (Brown and Wilson 1956), 'limiting similarity' (MacArthur and Levins 1967, Schoener 1974) and 'trait overdispersion' (Schluter 2000, Dayan and Simberloff 2005) (reviewed by Abrams 1983, Webb et al. 2002, Cavender-Bares et al. 2009, Pausas and Verdu 2010, Weiher et al. 2011). If competition is the main driver of community species composition, then species can coexist only if their overlap in resource use is reduced via ecological and/or morphological differences (Hutchinson 1959, Stubbs and Wilson 2004). Communities may also be assembled via environmental filtering. If persistence in a particular environment requires possession of certain adaptive traits, then any community in this environment will be comprised of species sharing these traits (Horner-Devine and Bohannan 2006, Kembel and Hubbell 2006, Ackerly and Cornwell 2007, Elias et al. 2009, Ingram and Shurin 2009). Obviously, the two processes have contrasting effects on the similarity of coexisting species. Indeed, there is evidence that some communities are assembled according to the limiting similarity principle (Kingston et al. 2000), whereas the composition of other communities suggests environmental filtering (Baraloto et al. 2012). Moreover, both limiting similarity and environmental filtering may operate in the same community but act on traits that relate to different scales [e.g. local-scale resource use (α-niche) versus environmental gradients (β-niche); Ingram and Shurin 2009, Weiher et al. 2011; see Pickett and Bazzaz 1978 for details on α- and β-niches].

Darwin's (1859) notion about the relationships between the intensity of competition and similarity of competitors applied specifically to congeneric species. This means that (a) closely-related species likely share many traits via common ancestry and (b) evolutionary relationships are expected to be associated with patterns of community composition (Brooks and McLennan 1993, Lovette and Hochachka 2006). Therefore, community assembly processes can be inferred from the phylogenetic relationships of co-occurring species with phylogenetic relatedness considered as a proxy for multiple species traits given conservatism of phenotypes due to common ancestry (Pausas and Verdu 2010; but see Losos 2008, Weiher et al. 2011).

The application of phylogenetic tools to data on community composition has proven to be a useful approach to better understand the reciprocal effects between community interactions and evolutionary and ecosystem processes (Cavender-Bares et al. 2009). Mounting phylogenetic information and the development of computational methods have resulted in a burst of studies that combined phylogenetic and ecological information for communities of a great variety of plant and animal taxa in various biotas (reviewed by Cavender-Bares et al. 2009, Pausas and Verdu 2010, Weiher et al. 2011). However, this approach has only rarely been applied to parasites (Mouillot et al. 2006) despite the fact they represent a large part of global biodiversity (Poulin and Morand 2004). Although phylogenetic relatedness does not always equate to ecological similarity (Losos 2008), the substitution of similarity by phylogenetic relatedness may be useful for those taxa in which functional traits cannot be measured reliably (Violle et al. 2011). This is the case for many parasite groups. In addition, parasite communities are useful models for studying community organization because most hosts are usually parasitized by several parasite species sharing a trophic level, and because of the discrete nature of the boundaries of parasite communities. The spatial distribution of parasites consists of a set of inhabited 'islands' or patches represented by their hosts, while the environment between these patches is definitely inhospitable. A community of parasites within an area is thus fragmented amongst host-individuals and host-species. The hierarchical terminology commonly accepted in parasitology distinguishes an infracommunity, i.e. an assemblage of parasites infesting an individual host, from a component community, i.e. an assemblage of parasites infesting a population of conspecific hosts (Holmes and Price 1986, Combes 2001, Poulin 2007).

Parasite communities of aquatic hosts range in structure from being non-randomly to randomly assembled, and from being characterized by predominantly positive to predominantly negative species interactions (Rohde et al. 1995, Dezfuli et al. 2001, Gotelli and Rohde 2002, González and Poulin 2005, Rohde 2005). Species co-occurrences in some ectoparasite communities on fish appear more likely to be structured by environmental filtering than by limiting similarity (Mouillot et al. 2005). In contrast, ectoparasite communities of terrestrial hosts are consistently found aggregative and characterized by positive species co-occurrences (Krasnov et al. 2006a, 2010, 2011a). This is true for ectoparasites belonging to different taxa and exploiting different hosts in different habitats located on different continents. However, the mechanisms behind ectoparasite co-occurrence remain unclear. For example, if positive co-occurrences are characteristic for distantly-related species, then their coexistence may be facilitated by limiting similarity. The only attempt to test whether co-occurring ectoparasites are represented mainly by congeneric or heterogeneric species was that of Krasnov et al. (2011a). They found that significantly associated pairs of parasite species were represented mainly by heterogenerics. However, the study of Krasnov et al. (2011a) was done on component communities of ectoparasites, while actual species interactions can only take place at the scale of infracommunities.

Here, we focus on infracommunities of fleas (Siphonaptera) parasitic on small mammals (rodents and soricomorphs) in temperate zones of Europe (Slovakia) and Asia (Siberia). Fleas are holometabolous insect parasites with obligatory haematophagous imagos and non-parasitic omnivorous larvae. We studied phylogenetic relatedness of co-occurring flea species and searched for the main shaping force of flea infracommunity assembly. We assumed that phylogenetic relatedness reflects trait similarity (Brooks and McLennan 1993). The co-occurrence of distantly-related species on the same host would indicate a key role for limiting similarity, whereas the co-occurrence of closely-related species would instead suggest a process similar to environmental filtering. In our dataset, flea infracommunities on an individual small mammal comprised two to four species. The small sizes of these communities do not allow reliable estimation of the degree of either phylogenetic clustering or phylogenetic overdispersion. Consequently, to achieve our objective, we used the species pairwise approach (Sfenthourakis et al. 2006, Gotelli and Ulrich 2010, Pitta et al. 2012, Sridhar et al. 2012) and examined the relationship between a metric of species association and phylogenetic distance for each pair of flea species across individual hosts.

Material and methods

Data

In west Siberia, mammals were captured in deciduous forests in the vicinity of Novosibirsk during the warm season (May–September) using pitfall traps with drift fences. Details of trapping design and procedures for the examination of captured mammals for ectoparasites are described elsewhere (Krasnov et al. 2010). In Slovakia, small mammals were collected using snap-traps across 18 locations in two main habitat types (lowland and mountain) during both the warm (May–September) and cold (October–April) seasons. Details of sampling procedures are given elsewhere (Stanko 1994, Stanko et al. 2002, Krasnov et al. 2006b). In total, our database included data on 24 278 individual hosts belonging to 43 species from which 38 511 individual fleas belonging to 37 species were collected (see Stanko et al. 2002, Krasnov et al. 2006b, 2011b and Korallo-Vinarskaya et al. 2013 for species lists).

Data organization

In west Siberia, small mammals were sampled in the same season and in the same habitat, whereas in Slovakia sampling was done in two habitat types that differed in their flea composition (Krasnov et al. 2006b) and during two seasons when seasonal flea species may or may not occur (Stanko 1994). Consequently, we constructed presence/absence matrices (see below) for each included sample, i.e. for (a) each host species in west Siberia and (b) each host species in each habitat type and each season in Slovakia. In addition, we included in our analyses only those host/habitat/season samples for which at least 15 host individuals infested with fleas were collected. Among flea species, we included only those for which at least five individuals per sample were collected. This resulted in 21 samples (each for a particular host species in a particular habitat in a particular season) for Slovakia and 19 samples (each for a particular host species) for west Siberia. Each sample included data on fleas collected from 15 to 299 host individuals. The data for each sample were organized as presence/absence incidence matrices in which a row represented a flea species, and a column represented an individual host.

Analyses of species co-occurrences using presence/absence matrices, rather than abundance data, are commonly accepted in community ecology (Gotelli and Rohde 2002). Recently, Hausdorf and Hennig (2007) proposed a method that can use abundance data. However, we believe that analysis of presence/absence data in relation to parasite assemblages is more biologically justified. This is because (a) measurements of occurrences are more certain than measurements of abundances (Gotelli and Rohde 2002) and (b) parasite assemblages are composed of different taxa that are characterized by substantially different species-specific levels of abundance (Krasnov et al. 2006c).

Phylogenetic information

The phylogenetic tree of fleas was based on the only available molecular phylogeny of fleas recently constructed by Whiting et al. (2008). This tree includes 128 flea species (ca 6% of the global fauna) belonging to 83 genera (ca 34% of all flea genera). Most of the flea genera, but not flea species, in our dataset are included in Whiting et al.'s (2008) tree. Consequently, the positions of the flea species which were not represented in the original tree of Whiting et al. (2008) were determined using their morphologically-derived taxonomy (details in Krasnov et al. 2011b). All branch lengths were set equal to 1.0. The tree was ultrametrized using the option 'chronopl' in the package 'ape' (2.8) (Paradis et al. 2004) implemented in R ver. 2.15. The results of the analyses did not differ whether an ultrametric or non-ultrametric tree was used. Pairwise phylogenetic distances were calculated as patristic distances using the package 'adephylo' (1.1–3) (Jombart and Dray 2010) implemented in R ver. 2.15.

Data analysis

Co-occurrence analyses were carried out using the software program PAIRS (Ulrich 2008). We used the *C*-score (Stone and Roberts 1990) as a metric of co-occurrence for each pair of flea species. Detailed descriptions of statistical properties and performance of this metric can be found in Gotelli (2000). In brief, the *C*-score is the average number of checkerboard units that are found for a pair of species (Stone and Roberts 1990, Gotelli 2000). In other words, it takes into account cases where one member of a pair of species is not present at a site, while the other member of the pair is, and vice versa, and cases when both species are present. A *C*-score calculated for each species pair (an observed *C*-score) was compared with the *C*-scores calculated for 5000 randomly assembled null matrices. Simulated incidence matrices were assembled by Monte Carlo procedures using a fixed-equiprobable (FE) algorithm. This algorithm does not constrain the number of flea species on a host and assumes that host individuals are equivalent in their probability of supporting a particular number of flea species. Biological justification for the use of the FE algorithm for the analysis of communities of ectoparasites on small mammals can be found elsewhere (Krasnov et al. 2006a, 2010). The *C*-score is an inverse indicator of the frequency of co-occurrence, so that a *C*-score larger than expected by chance indicates negative species co-occurrences, while a *C*-score smaller than expected by chance indicates positive co-occurrences (Haukisalmi and Henttonen 1993, Gotelli 2000, Gotelli and Arnett 2000, Gotelli and McCabe 2002, Gotelli and Rohde 2002). Following the approach of Sridhar et al. (2012), we used the standardized effect size (SES) of each pairwise *C*-score [(observed value-average of 5000 expected values)/standard deviation of expected values] as an inverse index of pairwise co-occurrence. The SES measures the number of standard deviations that the observed *C*-score is above or below the mean *C*-score of simulated matrices (details in Gotelli and McCabe 2002). Obviously, negative SES values indicate positive co-occurrence and positive SES values indicate negative co-occurrence between each two species, irrespectively of the significance of co-occurrence.

For each sample, we constructed an adjacency matrix of pairwise inverse index of co-occurrence and correlated this matrix with the adjacency matrix of pairwise phylogenetic distances using Mantel's test (Mantel 1967). We also tested for Mantel's correlation between the matrices of inverse co-occurrence index and phylogenetic distance combining the results of the calculation of the SES of the *C*-score from all samples. If the same pair of flea species was found in multiple samples, we averaged the SES of the pairwise *C*-score across these samples. Mantel's tests were performed using the package 'ecodist' (1.2.2) (Goslee and Urban 2007) implemented in R ver. 2.15.

Finally, we used the values of Mantel's r and its 95% confidence limits to test for the general trend of the relationship between co-occurrence and phylogenetic distance using meta-analysis. The meta-analyses that used both fixed effects and random effects models produced the same results. Here, we report the results of the analysis that used the fixed effects model only. Meta-analyses were carried out using the computer program Comprehensive Meta-Analysis ver. 2.2.

Results

The results of Mantel's tests of the correlation between the matrices of co-occurrence and matrices of phylogenetic distance are presented in Table 1. The correlations between the pairwise inverse indicator of co-occurrence (the SES of

Table 1. Number of flea species (n), Mantel's correlation (*r*) and 95% confidence limits (CI) between matrices of standardized effect size of the *C*-score and matrices of phylogenetic distances between pairs of flea species co-occurring on the same host individual in west Siberia and Slovakia. For Slovakian hosts, L and M are lowland and mountain habitats, respectively; W and C are warm and cold seasons, respectively. All p-values are two-tailed.

Region	Species (habitat, season)	n	*r*	Lower CI	Upper CI	p
Siberia	*Apodemus agrarius*	10	0.31	0.09	0.53	0.03
	Apodemus peninsulae	7	0.46	0.18	0.68	0.007
	Arvicola amphibius	9	0.25	0.01	0.40	0.07
	Cricetus cricetus	5	0.72	0.44	0.96	0.04
	Micromys minutus	6	0.27	0.05	0.55	0.14
	Microtus agrestis	13	0.26	0.12	0.37	0.02
	Microtus arvalis	8	0.24	0.06	0.46	0.09
	Microtus gregalis	14	0.22	0.12	0.35	0.02
	Microtus oeconomus	9	0.27	0.07	0.47	0.04
	Myodes glareolus	9	0.37	0.2	0.51	0.04
	Myodes rufocanus	7	0.28	0.03	0.38	0.04
	Myodes rutilus	8	0.05	−0.09	0.20	0.40
	Neomys fodiens	7	0.32	0.10	0.57	0.07
	Sicista betulina	8	0.23	0.08	0.4	0.06
	Sorex araneus	11	0.21	0.05	0.42	0.14
	Sorex isodon	6	0.67	0.60	0.77	0.004
	Sorex minutus	6	0.38	0.01	0.82	0.07
	Sorex tundrensis	5	0.44	0.27	0.72	0.08
	Talpa altaica	7	0.13	−0.21	0.39	0.33
Slovakia	*Apodemus agrarius*, L, W	7	0.22	−0.06	0.45	0.16
	Apodemus agrarius, L, C	8	0.22	0.02	0.40	0.12
	Apodemus agrarius, M, W	8	0.54	0.39	0.69	0.01
	Apodemus agrarius, M, C	18	0.16	0.06	0.24	0.03
	Apodemus flavicollis, L, W	7	0.26	−0.05	0.45	0.11
	Apodemus flavicollis, L, C	7	0.24	−0.07	0.40	0.15
	Apodemus flavicollis, M, W	13	0.12	−0.01	0.23	0.14
	Apodemus flavicollis, M, C	10	0.18	−0.04	0.39	0.10
	Microtus arvalis, L, W	5	0.19	0.06	0.92	0.24
	Microtus arvalis, L, C	5	−0.09	−0.61	0.22	0.70
	Microtus arvalis, M, W	4	0.07	−0.99	0.83	0.50
	Microtus arvalis, M, C	8	0.20	−0.11	0.41	0.15
	Microtus subterraneus, M, W	9	0.11	−0.08	0.36	0.24
	Microtus subterraneus, M, C	8	−0.02	−0.19	0.10	0.49
	Myodes glareolus, L, W	8	0.28	0.04	0.46	0.13
	Myodes glareolus, L, C	8	0.19	0.05	0.43	0.16
	Myodes glareolus, M, W	15	0.31	0.17	0.47	0.002
	Myodes glareolus, M, C	20	0.22	0.12	0.32	0.001
	Neomys fodiens, M, W	7	0.31	−0.01	0.68	0.02
	Neomys fodiens, M, C	9	−0.04	−0.23	0.22	0.55
	Sorex araneus, M, C	8	0.07	−0.12	0.36	0.32

the *C*-score) and phylogenetic distance were significant in only 14 of 40 samples. Nevertheless, the sign of Mantel's correlation coefficient was positive in 23 of the remaining 26 samples. In other words, frequency of co-occurrence tended to decrease with increasing phylogenetic distance between species (see illustrative examples with fleas on *Sorex isodon* from Siberia and *Apodemus agrarius* from Slovakia in Fig. 1).

Across all samples, the inverse indicator of pairwise co-occurrence was positively, albeit weekly, correlated with pairwise phylogenetic distance ($r = 0.19$, lower 95% confidence interval = 0.16, upper 95% confidence interval = 0.24, two-tailed $p = 0.0001$; Fig. 2). The meta-analytic estimate of Mantel's correlation coefficient was also significantly positive (point estimate ± standard error = 0.27 ± 0.01, lower 95% confidence interval = 0.24, upper 95% confidence interval = 0.30, Z-value = 19.41, $p < 0.001$).

Discussion

We did not find any evidence supporting limiting similarity as a mechanism of flea coexistence on the same host individual. On the contrary, our results demonstrated that flea infracommunities tended to consist mostly of closely related species. Assuming that phylogenetic relatedness mirrors physiological, morphological and behavioural similarity (Brooks and McLennan 1991, Harvey and Pagel 1991, Silvertown et al. 1997), the results of this study indicate that flea infracommunities are composed mostly of similar species. This pattern seems to be a general phenomenon, since it occurred in different host species or different environmental conditions, although it somewhat varied within host species between seasons, habitats or geographic regions.

Co-occurrence of closely related flea species on the same host individual provides additional evidence that the widely accepted assumption of increasingly intense interspecific

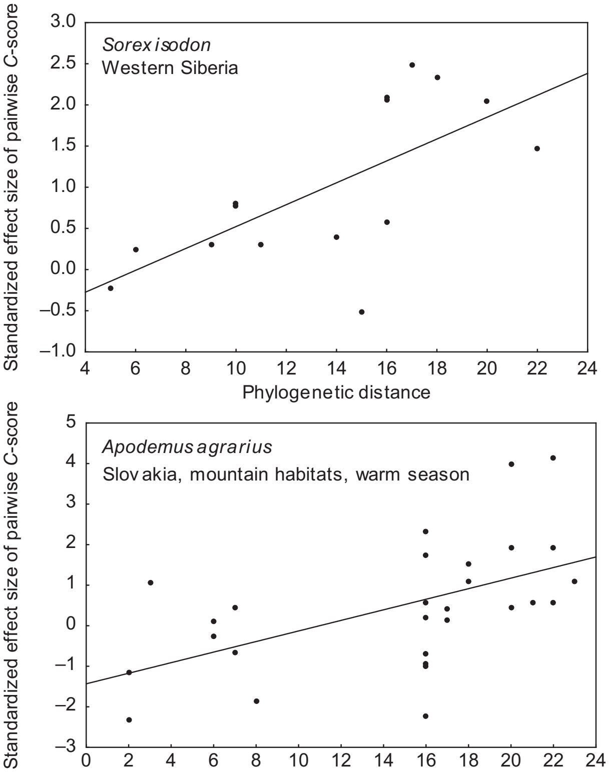

Figure 1. Relationships between the inverse indicator of co-occurrence (the standardized effect size of the pairwise *C*-score) and phylogenetic distance of fleas on *Sorex isodon* and *Apodemus agrarius*.

competition with an increase in phylogenetic relatedness among species is not as general as earlier thought. Little support for the generality of this assumption has been found in other studies. Communities of different taxa are characterized predominantly by coexistence of either closely-related or distantly-related species (reviewed by Vamosi et al. 2009). For example, Cahill et al. (2008) reported that intensity of competition increased with phylogenetic distance in monocotyledon plants, although the opposite was true for eudicotyledons. Hummingbird communities at high elevations in Ecuador are characterized by the coexistence of close relatives, while low-elevation communities mainly comprised phylogenetically distant species (Graham et al. 2009). At small spatial scales, co-occurring tree species in an Ecuadorian Amazonian forest tended to be more phylogenetically related than expected (Kraft and Ackerly 2010). Baraloto et al. (2012) found that similar species were clustered in local communities of tropical trees in French Guiana, although this pattern was weaker for phylogenetic than for functional trait similarity. In contrast, experiments with bacterivorous protists by Violle et al. (2011) supported more intense competition among closer relatives. These and other examples suggest that mechanisms of community assembly may be not only scale-dependent (Weiher et al. 2011) but may also differ among taxa.

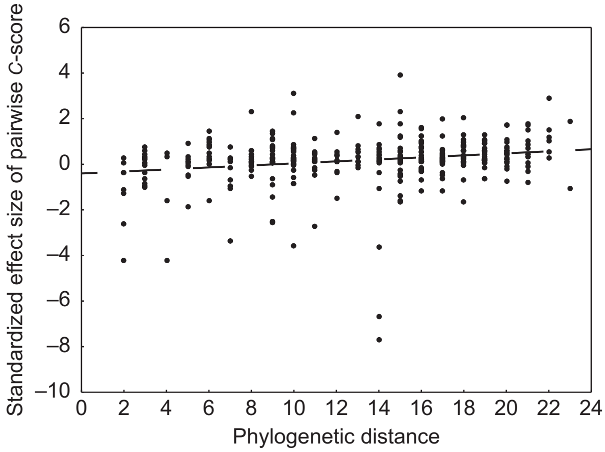

Figure 2. Relationships between the inverse indicator of co-occurrence (the standardized effect size of the pairwise *C*-score) and phylogenetic distance of fleas on small mammalian hosts across 40 samples.

The co-occurrence of closely-related fleas on the same host suggests that a process resembling environmental (or, in case of parasites, host) filtering is one of the forces structuring flea infracommunities. This echoes the findings of an earlier study on fish ectoparasite communities (Mouillot et al. 2005), and supports the concept of the encounter and compatibility filters of Combes (2001) that explain the formation of the host spectrum of a parasite (see also Euzet and Combes 1980, Holmes 1987). The encounter filter excludes all hosts that a parasite cannot encounter for ecological and behavioural reasons (e.g. a host and a parasite occur in different habitats), whereas the compatibility filter excludes all hosts that either cannot provide a parasite with adequate resources or are able to successfully eliminate parasites via their defence system. Parasite infracommunities are thus composed of species that (a) occupy the same habitat as a host, (b) are able to extract resources from that host and (c) can withstand host defences. In the case of fleas, hosts undoubtedly differ in the quality of the resources (physical and chemical characteristics of their blood as well as blood nutritional value) and the way these resources can be acquired by parasites (hair density, skin structure, defensibility). In addition, the species-specific abiotic conditions of a host's burrow (temperature, humidity, substrate structure) are important for both imaginal and larval fleas, with different flea species having different environmental preferences (Krasnov et al. 2001, 2002). As a result, each flea species is adapted to a particular set of host traits that guarantee the greatest fitness reward. Indeed, even highly host-opportunistic fleas achieve their highest fitness in one host species (Khokhlova et al. 2012). Consequently, both biotic and abiotic conditions related to the host may act as filters to restrict co-occurring species to a certain phylogenetic subset (Tofts and Silvertown 2000, Statzner et al. 2004; see also Krasnov et al. 2005a for fleas).

From an evolutionary perspective, the co-occurrence of closely related fleas in the same infracommunities suggests that flea species belonging to a particular lineage are adapted to the same host. This could happen, for example, in cases of intra-host speciation (Paterson and Gray 1997) resulting in the presence of two or more closely related parasite species on the same host species. Intra-host speciation has never been proven for fleas (Krasnov and Shenbrot 2002, Lu and Wu 2005), although the patterns of distribution of some fleas hint at the possibility of this scenario (Riddoch et al. 1984). However, evidence for intra-host speciation was found for other parasite taxa such as chondracanthid copepods (Paterson and Poulin 1999) and dactylogyrid monogeneans (Simkova et al. 2004).

From a physiological perspective, co-occurrence of parasite species on the same host individual might be achieved via parasite-induced immunosuppression in a host subjected to multiple challenges from different parasites (Bush and Holmes 1986, Jokela et al. 2000). The likelihood of immunosuppression may be higher if the immunogens of the parasites involved are similar which, in turn, is more likely if the parasites are phylogenetically close. The latter statement is indirectly supported by studies on component communities of fleas in which the abundance of a focal flea species was found to be higher when the co-occurring flea species were closely related with it (Krasnov et al. 2005a), although experimental studies suggest that this may not always be true (Khokhlova et al. 2004).

The body of a host individual represents a situation in which competition between closely-related (i.e. similar) parasite species may occur (Holland 1984, Patrick 1991, Lindsay and Galloway 1997). The positive co-occurrence of closely-related fleas in infracommunities found in our study suggests that these species may somehow avoid competition or, at least, substantially reduce the cost of competition (Sridhar et al. 2012). Blood of the host is not a limiting resource for arthropod ectoparasites (Khokhlova et al. 2002). They may compete for enemy-free space (Jeffries and Lawton 1984), that is for those body areas that are the least accessible to host grooming (Linsdale and Davis 1956). As a result, different ectoparasite species could be segregated among host body parts (Bush and Malenke 2008). However, a recent analysis of the distribution of arthropod ectoparasites across body parts of small mammalian hosts has demonstrated that this was not the case and that different ectoparasite species show a tendency to co-occur on the same body parts of the host (Pilosof et al. 2012). Another way in which the cost of interspecific competition in flea infracommunities may be reduced is by competition being shifted from taking place among imagos on the host's body to taking place among larvae in the host's burrow. Indeed, interspecific interactions between larval fleas belonging to the same genus have been found to be competitive (Krasnov et al. 2005b).

Host filtering is unlikely the only process shaping species composition of flea assemblages because co-occurrence of closely-related species does not preclude the presence of species from other phylogenetic lineages. This may happen because of a variety of reasons. For example, some species may occur on a host due to ecological fitting (Janzen 1985, Brooks et al. 2006), i.e. situations where the parasites track the resource (e.g. blood or adequate burrow environment) rather than host species per se, so they may invade new areas where the resource, but not the 'original' host species, is present. The occurrence of a species from a distant lineage in a more or less phylogenetically homogenous flea assemblage may also be associated with historical events such as biogeographic dispersal (see example with allactagine jerboas and pulicid fleas in Krasnov and Shenbrot 2002). Finally, the presence of a flea species on a host may merely result from occasional interspecific contacts or through visits of burrows belonging to other host species.

We recognize that phylogenetic assembly is a complementary approach that should be used with caution as a proxy for traits (Weiher et al. 2011). The assumption that phylogenetic relatedness reflects similarity has been criticised (Losos 2008, Vamosi et al. 2009). However, this assumption is almost unavoidable when working on the community ecology of taxa in which functional traits cannot be measured (Emerson et al. 2011). Moreover, the use of this assumption in our study allowed us to reveal a substantial phylogenetic component in the assembly of flea infracommunities on small mammals, while approaches employed in earlier studies of this host-parasite system (Mouillot et al. 2006, Krasnov et al. 2011a, 2012) did not allow this insight.

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