

## Abundance patterns and coexistence processes in communities of fleas parasitic on small mammals

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The abundance of a given species in a community is likely to depend on both the total abundance and diversity of other species making up that community. A large number of co-occurring individuals or co-occurring species may decrease the abundance of any given species via diffuse competition; however, indirect interactions among many co-occurring species can have positive effects on a focal species. The existence of diffuse competition and facilitation remain difficult to demonstrate in natural communities. Here, we use data on communities of fleas ectoparasitic on small mammals from 27 distinct geographical regions to test whether the abundance of any given flea species in a community is affected by either the total abundance of all other co-occurring flea species, or the species richness and/or taxonomic diversity of the flea community. At all scales of analysis, i.e. whether we compared the same flea species on different host species, or different flea species, two consistent results emerged. First, the abundance of a given flea species correlates positively with the total abundance of all other co-occurring flea species in the community. Second, the abundance of any given flea species correlates negatively with either the species richness or taxonomic diversity of the flea community. The results do not support the existence of diffuse competition in these assemblages, because the more individuals of other flea species are present on a host population, the more individuals of the focal species are there as well. Instead, we propose explanations involving either apparent facilitation among flea species via suppression of host immune defenses, or niche filtering processes acting to restrict the taxonomic composition and abundance of flea assemblages.

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Ecological interactions between species in a community may take the form of a variety of direct and indirect interactions that ultimately affect species coexistence and community organization (Martin and Martin 2001). An understanding of patterns in community organization and mechanisms that produce and support them requires information on how the abundance of an individual

species in a community is affected by the abundance and diversity of the other species that compose this community. Both positive and negative processes operate in a community. Their relative importance is affected by various biotic and abiotic factors present in the specific environment (e.g. Menge 2000). In general, negative or positive relationships between the abundances of species

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co-occurring in a community can indicate competitive or facilitating relationships between these species, respectively (Rosenzweig 1981, Schall 1990). Negative interactions can also signal asymmetric competition leading to exclusion (Levine and Rees 2002) or antagonistic relationships between species (Lombardero et al. 2003). Moreover, theoretical studies have shown that competition is not necessarily the only or dominant form of interaction. In some environments positive interactions prevail (e.g. Bertness and Callaway 1994).

Patterns in community organization have been studied mainly in free-living organisms. However, in the last two decades, the number of studies of community organization in parasitic organisms has increased drastically (see review in Combes 2001). In particular, this is because of the numerous advantages of using parasites to investigate patterns and processes in animal communities. These advantages include, for example, a relative ease of obtaining replicated samples (e.g. host individuals or host species) and the fact that parasites of the same taxon share a trophic level (Simberloff 1990). Another advantage of parasite communities is that most hosts are usually parasitized by several closely related parasites that use the same resource and, thus, the study of community organization of parasites allows one to investigate the potential role of diffuse competition in parasite communities. This type of competition occurs when a species competes with a constellation of other species in various combinations and densities (MacArthur 1972). For example, the decrease in the abundance of a parasite with an increase in the abundance of all other co-occurring parasites would suggest the occurrence of diffuse competition (Bock et al. 1992). The latter can also be revealed by negative relationships between the abundance of a given parasite species and the species richness or any other measure of diversity of the entire parasite assemblage, given that a higher number of species leads to more intense competition (MacArthur 1972).

The above is true if the species in a community interact directly. Indeed, the original model of MacArthur (1972) does not incorporate indirect interactions. Later models of diffuse competition that account for indirect interactions have concluded that a high number of species could reduce the intensity of interactions or even lead to facilitation (Davidson 1980, Vandermeer 1990, Stone and Roberts 1991). Parasites undoubtedly influence one another via their effects on hosts. Suppression of host defense systems resulting from the high abundance of one or more parasite species or/and high parasite diversity (that supposedly requires multiple defense responses) could lead to facilitation among parasite species. As a result, the abundance of a given species should be positively correlated with either the abundance of other co-occurring species or their diversity or both. Facilitation could also occur if only one of

the two parameters of the entire community (overall abundance and diversity) is positively correlated with the abundance of a given species, whereas the other is not.

In any case, studying the relationships between the abundance of a parasite species and the descriptors of the entire parasite community can give insights into processes that govern parasite communities. Much previous research on parasite communities has been conducted at the level of parasite infracommunities (assemblages of parasite species in an individual host) (e.g. Bush and Holmes 1986a, b, Haukisalmi and Henttonen 1993, Forbes et al. 1999). On the contrary, component communities (= xenocommunities) of parasites (assemblages of parasite species in a host population) and compound communities (assemblages of parasite species in a host community) have received much less attention. One reason for the scarcity of studies of the relationships among parasite species at higher scales may be the difficulty of assessing interactions between parasite species occurring in different host individuals and/or different host species. This is undoubtedly true for endoparasites such as intestinal helminths. However, ectoparasitic species, especially periodic ones such as fleas and mesostigmatid mites, spend a significant amount of time off-host (though they spend considerably more time on the hosts than is required merely to obtain a bloodmeal) and easily switch between individual hosts both within and between host species (Rödl 1979, Krasnov and Khokhlova 2001). Moreover, many larval ectoparasites from different host species co-occur in multi-species host and parasite assemblages in burrow colonies constructed by some rodents (e.g. *Rhombomys opimus*; Kucheruk 1983). Consequently, species interactivity in the communities of periodic ectoparasites cannot be refuted a priori.

Demonstrating species interactions in the field is logistically difficult. Although manipulative studies of competition, i.e. by field removal experiments, have produced a number of examples of pair-wise interspecific competitive interactions under natural conditions (see Gurevitch et al. 1992 for review), this approach is limited by the practical impossibility of performing experimental studies on all pairs of species in a community. Therefore, alternative methods have been devised to measure species interactions from census data (e.g. MacArthur and Levins 1967, Schoener 1974, Crowell and Pimm 1976, Fox and Luo 1996, Shenbrot and Krasnov 2002). Although some of these methods have been criticized (Rosenzweig et al. 1985, Abramsky et al. 1986), census data can nevertheless provide hints about the type of species interactions that might prevail in a community and, thus, can serve as a basis for further manipulative experiments and/or more sophisticated analysis. In addition, experimental removals are extremely difficult (if at all possible) in parasite communities.

Fleas (Siphonaptera) are characteristic mammalian ectoparasites most abundant and diverse on small and medium-sized species. In most fleas, all stages of the life cycle are spent off the host, except for the adults that feed intermittently on the host. Here, we used published data on the abundance of fleas on small mammalian hosts across 27 geographic locations and examined how the overall abundance and diversity of flea communities affect the abundance of individual flea species in these communities. In particular, we explored alternative hypotheses of either diffuse competition (negative relationships between the abundance of a given species and the abundance and/or diversity of the entire community) or facilitation (positive relationships between the abundance of a given species and the abundance and/or diversity of the entire community) among flea species parasitizing the same population of mammals. In addition, rather than taking the mere number of flea species in assemblages as a measure of flea diversity, we also applied a measure of diversity that takes into account the taxonomic or phylogenetic affinities of the various flea species (Clarke and Warwick 1998, 1999, Warwick and Clarke 2001). This measure was modified by Poulin and Mouillot (2003, 2004) and successfully applied in parasitological context (Krasnov et al. 2004b). This measure places the emphasis on the taxonomic distance between flea species rather than on their number, providing a different perspective on flea diversity, namely a measure of the composition, and not the size, of an assemblage.

## Materials and methods

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Didelphimorphia, Insectivora, Lagomorpha and Rodentia) in 27 different regions (Table 1). 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. Only mammal species for which at least 10 individuals per region have been examined and from which at least four flea species per region have been recovered were included in the analyses.

For each flea species on each host species in each region we calculated the mean abundance of this species, the mean pooled abundance of other co-occurring flea species, overall flea species richness and values of taxonomic distinctness and its variance (see below) of the co-occurring flea assemblage. We used the mean number of flea individuals per individual host of a given species as a measure of mean flea abundance. Other measurements of infection level, such as prevalence and intensity of flea infestation, were not available for the majority of the regions considered. Estimates of parasite abundance may be biased if some parasites or hosts are studied more intensively than others (Stanko et al. 2002).

Consequently, unequal study effort among host species may result in confounding variation in estimates of flea abundance. In addition, hosts of different body size can support different number of fleas. To ensure that variation in among-host sampling effort and body size did not bias estimates of flea abundance, we regressed log-transformed estimates of flea abundance per host against the log-transformed number of hosts examined and the log-transformed body surface area of hosts for each flea species in each region. Body surface area of a host species was estimated from host body mass following Walsberg and Wolf (1995). Data on mean body mass were obtained either from original sources or from Silva and Downing (1995). Estimates of flea abundance per host were affected by sampling effort ( $r^2=0.23$ ,  $F_{1,1796}=531.2$ ,  $p<0.0001$ ) but not affected by host body size ( $r^2=0.04$ ,  $F_{1,1796}=85.6$ ,  $p>0.36$ ). Consequently, in subsequent analyses we substituted the original values of flea abundance by residuals of the regression of log-transformed flea abundance against the log-transformed number of hosts examined.

The two measures of flea species diversity we used were a) the number of flea species found on a host species, or species richness, corrected for sampling effort (residuals of the log-log linear regression against number of hosts examined; see below) and b) average taxonomic distinctness ( $\Delta^+$ ) of the fleas present along with its variance ( $\Lambda^+$ ). When these flea species are placed within a taxonomic hierarchy, the average taxonomic distinctness is the mean number of steps up the hierarchy that must be taken to reach a taxon common to two flea species, computed across all possible pairs of flea species (Clarke and Warwick 1998, 1999, Warwick and Clarke 2001, Poulin and Mouillot 2003, 2004). The greater the taxonomic distinctness between flea species, the higher the number of steps needed, and the higher the value of the index  $\Delta^+$ . Using the taxonomic classification of Hopkins and Rothschild (1953, 1956, 1962, 1966, 1971), Traub et al. (1983) and Medvedev (1998), all flea species included here were fitted into a taxonomic structure with 8 hierarchical levels above species, i.e. subgenus (or species group), genus, tribe, subfamily, family, superfamily, infraorder, and order (Siphonaptera). We restricted our use of taxonomic levels to these basic ones because they are the only ones available for all flea taxa included here. The maximum value that the index  $\Delta^+$  can take is thus 8 (when all flea species belong to different infraorders), and its lowest value is 1 (when all flea species belong to the same subgenus or species group). The variance in  $\Delta^+$ ,  $\Lambda^+$ , provides information on any asymmetries in the taxonomic distribution of flea species in assemblages (Clarke and Warwick 1998, 1999, Warwick and Clarke 2001, Poulin and Mouillot 2003). To calculate  $\Delta^+$  and  $\Lambda^+$ , DM and RP developed a computer program using Borland C++ Builder 6.0

Table 1. Data on small mammals and fleas from the 27 regions used in the analyses. Numbers in parentheses represent the total numbers of sampled individuals (data include mammal species in which no fewer than 10 individuals were examined and from which at least four flea species per region have been recovered).

| Region  | Number of host species | Number of flea species | Source                         |
|---|------------------------|------------------------|--------------------------------|
| Adzharia, southern Caucasus                   | 8 (8120)               | 20 (1655)              | Alania et al. 1964             |
| Akmolinsk region, northern Kazakhstan         | 8 (264)                | 19 (1789)              | Mikulín 1959a                  |
| Altai mountains                               | 15 (1383)              | 8 (1821)               | Sapegina et al. 1981           |
| California                                    | 3 (1118)               | 14 (1228)              | Davis et al. 2002              |
| Central Yakutia                               | 4 (500)                | 17 (862)               | Elshanskaya and Popov 1972     |
| Dzhungarskiy Alatau, Kazakhstan               | 11 (5137)              | 21 (5193)              | Burdelova 1996                 |
| East Balkhash desert, Kazakhstan              | 9 (451)                | 34 (7071)              | Mikulín 1959b                  |
| Idaho   | 6 (3669)               | 25 (9881)              | Allred 1968                    |
| Kabarda, northern Caucasus                    | 8 (1628)               | 21 (1675)              | Syrvacheva 1964                |
| Kamchatka peninsula, eastern Russian Far East | 2 (1219)               | 7 (250)                | Paramonov et al. 1966          |
| Khabarovsk region, southern Russian Far East  | 4 (2849)               | 19 (3202)              | Koshkin 1966                   |
| Kustanai region, northwestern Kazakhstan      | 7 (143)                | 13 (355)               | Reshetnikov 1959               |
| Moyynkum desert, Kazakhstan                   | 9 (45399)              | 27 (260646)            | Popova 1967                    |
| Mongolia                                      | 3 (1718)               | 18 (18400)             | Vasiliev 1966                  |
| Negev Desert                                  | 2 (685)                | 7 (3064)               | Krasnov et al. 1997 and unpub. |
| North Asian Far East                          | 5 (1007)               | 13 (810)               | Yudin et al. 1976              |
| North Kyrgyzstan                              | 8 (4050)               | 33 (8510)              | Shwartz et al. 1958            |
| North New Mexico                              | 10 (6981)              | 24 (17026)             | Morlan 1955                    |
| Novosibirsk region, southern Siberia          | 16 (1870)              | 27 (4147)              | Violovich 1969                 |
| Pavlodar region, eastern Kazakhstan           | 2 (28)                 | 6 (41)                 | Sineltshikov 1956              |
| Selenga region, central Siberia               | 3 (853)                | 8 (959)                | Pauller et al. 1966            |
| Slovakia                                      | 8 (9805)               | 22 (10763)             | Stanko et al. 2002             |
| Southeastern Brazil                           | 3 (337)                | 7 (216)                | de Moraes et al. 2003          |
| Tarbagatai region, eastern Kazakhstan         | 7 (215)                | 26 (1306)              | Mikulín 1958                   |
| Turkmenistan                                  | 12 (235918)            | 37 (908540)            | Zagniborodova 1960             |
| Tuva  | 10 (2499)              | 23 (28324)             | Letov et al. 1966              |
| Volga-Kama region                             | 18 (33292)             | 30 (33570)             | Nazarova 1981                  |

(available at <<http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2>>).

Estimates of parasite species richness also may be biased if some hosts are studied more intensively than others (Morand and Poulin 1998). Indeed, log-transformed values of flea richness were strongly affected by sampling effort ( $r^2=0.44$ ,  $F_{1,1796}=1405.1$ ,  $p<0.001$ ). Each value of flea richness was thus substituted by its residual deviation from a linear regression on the log-transformed number of hosts examined. This provided a measure of flea richness that is independent of sampling effort. The number of flea species exploiting a host species in a region was not correlated with either  $\Delta^+$  or  $\Lambda^+$  ( $r^2=0.001-0.06$ ,  $F_{1,1796}=3.1-5.6$ ,  $p>0.1$  for both), indicating that these measures were not influenced by the number of species in a host's flea assemblage.

We analyzed relationships between the abundance of a flea species and a) the pooled abundance of co-occurring flea species in the assemblage and b) species richness, taxonomic distinctness and taxonomic asymmetry of the flea assemblage. This was done firstly within flea species among all host species on which they occurred, and then within host species among all the flea species they harboured. In addition, we analyzed these relationships across the whole pool of flea species and the whole pool of host species.

First, we selected flea species that were recorded in at least 10 different host species across all regions. Each host-flea combination was treated as an independent data point. Some host and flea species occurred in more

than one region; measurements of abundance and diversity for these combinations were averaged across regions. Nevertheless, treating values of abundance and diversity of fleas calculated for different host species as independent observations can introduce a bias in the analysis. To control for the effects of host phylogeny, we used the method of independent contrasts (Felsenstein 1985). The phylogenetic trees of hosts were derived from various sources (see Krasnov et al. 2004a for details). To compute independent contrasts, we used the PDAP:PD-TREE program (Garland et al. 1993, Midford et al. 2003) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2004). Independent contrasts were standardized as suggested by Garland et al. (1992). To test for the correlation between a flea's abundance (dependent variable) and the abundance of all other co-occurring fleas, or the species richness, taxonomic distinctness and taxonomic asymmetry of flea assemblages (independent variables), we regressed standardized contrasts of the dependent variable against standardized contrasts of the independent variables using major axis regression forced through the origin (Pagel 1992, Garland et al. 1992) for each flea species.

Then, we combined the data for each flea species on each host species and analyzed them across all flea species via the method of independent contrasts calculated using flea phylogeny. The phylogenetic tree of fleas was constructed using the taxonomic classification

described above, as there exists no comprehensive phylogenetic hypothesis for all flea taxa.

After that, we analyzed relationships between the abundance of a flea species and that of all other co-occurring flea species in an assemblage, the species richness, taxonomic distinctness or taxonomic asymmetry of a flea assemblage, within host species but among flea species. For this analysis, we selected host species that occurred in at least six regions and were parasitized by at least four flea species per region. Ten host species met these criteria. Then, we selected the most abundant flea species of all fleas parasitizing a given host species in a given region. We analyzed the relationships between the abundance of the locally most abundant flea species and either the abundance of all other co-occurring flea species, the species richness, taxonomic distinctness or taxonomic asymmetry of flea assemblages for each host species separately via the method of independent contrasts using the phylogenetic trees of fleas constructed as described above. In these analyses, associations of the same host species with the same flea species from different regions were treated as sister species.

Finally, we selected the most abundant flea species on each host species across all regions and analyzed the relationships between the abundance of these globally most abundant flea species and either the abundance of all other co-occurring flea species or one of the parameters of diversity of flea assemblages. This was done across all host species via the method of independent contrasts using the phylogenetic trees of hosts constructed as described above.

We did not use the Bonferroni correction of the alpha level because this approach has been increasingly criticized by statisticians and ecologists in recent years. The Bonferroni correction has been shown to often lead to the incorrect acceptance of the false null hypothesis (Rothman 1990, Perneger 1998, 1999, Moran 2003, Garcia 2004).

## Results

Across the 27 regions, there were a total of 1798 flea species-host species-region combinations. Overall, these associations involved 230 flea species and 92 host species. There were 41 flea species that occurred in at least 10 host species across all regions.

In 37 of these 41 flea species, mean abundance was significantly correlated either with mean abundance of all other co-occurring flea species or with one or more measures of the diversity of flea assemblages, or both. In particular, across host species, the mean abundance of a flea increased significantly with an increase in the mean abundance of co-occurring fleas of other species in 25 flea species ( $r = 0.41-0.97$ ,  $p < 0.05$  for all; Table 2); no negative relationships were observed. Moreover, the

mean abundance of a flea decreased significantly with an increase in the value of one or more measurements of flea assemblage diversity ( $r = -0.41-0.72$ ,  $p < 0.05$  for all; Table 2) in 23 species. Of these, species richness of flea assemblages correlated negatively with the mean abundance of a flea in seven species, whereas the same was true for taxonomic distinctness of flea assemblages ( $\Delta^+$ ) in seven species and for taxonomic asymmetry of flea assemblages ( $\Lambda^+$ ) in 13 species (Table 2). No positive relationship was found between the mean abundance of a flea species and any of the measure of the diversity of flea assemblages. In addition, in 12 flea species, the mean abundance of a flea species was significantly correlated with both the mean abundance of co-occurring flea species and one or more measure of diversity of flea assemblages (Table 2). An illustrative example using the flea *Frontopsylla hetera* is presented in Fig. 1. In addition, in four flea species, no relationship was found between mean abundance and either mean abundance of other co-occurring flea species or any parameter of diversity of flea assemblage of a host species ( $r = -0.27-0.22$ ,  $p > 0.1$  for all; Table 2).

In general, the relationships between the mean abundance of a flea on a host species and the abundance and diversity of the entire flea assemblage of this host remained significant, albeit weak, when the data for each flea species on each host species were combined and analyzed across flea species using the independent contrasts method. Indeed, the mean abundance of a flea on a host species correlated positively with the mean abundance of all other co-occurring fleas on this host ( $r = 0.33$ ,  $p < 0.00001$ ; Fig. 2a) and correlated negatively with species richness ( $r = -0.16$ ,  $p < 0.01$ ; Fig. 2b), taxonomic distinctness ( $\Delta^+$ ;  $r = -0.14$ ,  $p < 0.05$ ; Fig. 2c) and taxonomic asymmetry ( $\Lambda^+$ ;  $r = -0.18$ ,  $p < 0.001$ ; Fig. 2d) of the flea assemblage of this host.

The abundance of the most abundant flea species on a given host species across different regions was positively correlated with the abundance of all other co-occurring fleas in 9 of ten analyzed host species ( $r = 0.69-0.96$ ,  $p < 0.05$  for all; Table 3). In seven host species, the abundance of the locally most abundant flea species was negatively correlated either with species richness (one host species, *Microtus oeconomus*,  $r = -0.69$ ,  $p < 0.05$ ) or taxonomic distinctness (four host species,  $r = -0.78-0.83$ ,  $p < 0.05$  for all; Table 3) or taxonomic asymmetry (three host species,  $r = -0.62-0.75$ ,  $p < 0.05$  for all; Table 3) of the flea assemblage of that host in a given region. An illustrative example using the rodent *Arvicola terrestris* is presented in Fig. 3.

In the across host species analysis, the abundance of the globally most abundant flea species was positively correlated with the abundance of all other co-occurring fleas ( $r = 0.62$ ,  $p < 0.0001$ ; Fig. 4a) and was negatively correlated with the taxonomic asymmetry of the flea assemblage ( $r = -0.27$ ,  $p < 0.005$ ; Fig. 4b). However,

Table 2. Summary of significant correlations (Pearson product-moment correlation using independent contrasts) between the abundance of a flea species and either the abundance of all other co-occurring flea species (A), the species richness (SR), taxonomic distinctness ( $\Delta^+$ ) or taxonomic asymmetry ( $\Lambda^+$ ) of the flea assemblage, across different host species, for 41 flea species. \*  $-p < 0.05$ , \*\*  $-p < 0.01$ .

| Flea species                                    | A      | SR      | $\Delta^+$ | $\Lambda^+$ |
|---|--------|---------|------------|-------------|
| <i>Amalaraeus penicilliger</i>                  | 0.27   | -0.40** | -0.47**    | -0.12       |
| <i>Amphipsylla primaris</i>                     | 0.58** | 0.01    | 0.13       | -0.14       |
| <i>Amphipsylla rossica</i>                      | 0.24   | -0.31   | -0.32      | -0.38*      |
| <i>Citellophilus tesquorum</i>                  | 0.08   | -0.52** | -0.24      | -0.2        |
| <i>Citellophilus trispinus</i>                  | -0.03  | -0.09   | -0.27      | 0.22        |
| <i>Coptopsylla lamellifer</i>                   | 0.54** | -0.30   | 0.01       | -0.6**      |
| <i>Ctenophthalmus agyrtes</i>                   | 0.48*  | 0.05    | -0.04      | 0.03        |
| <i>Ctenophthalmus arvalis</i>                   | 0.08   | 0.02    | -0.55**    | 0.09        |
| <i>Ctenophthalmus assimilis</i>                 | -0.12  | -0.16   | 0.16       | 0.07        |
| <i>Ctenophthalmus breviatus</i>                 | 0.66** | -0.09   | -0.24      | -0.23       |
| <i>Ctenophthalmus dolichus</i>                  | 0.77** | 0.21    | -0.46      | 0.27        |
| <i>Ctenophthalmus orientalis</i>                | -0.20  | -0.37   | -0.28      | -0.53*      |
| <i>Ctenophthalmus uncinatus</i>                 | 0.26   | 0.19    | -0.35      | -0.28       |
| <i>Ctenophthalmus wagneri</i>                   | 0.48*  | -0.42   | 0.09       | -0.19       |
| <i>Corrodopsylla birulai</i>                    | 0.11   | -0.001  | -0.31      | -0.56**     |
| <i>Doratopsylla dasyncema</i>                   | 0.19   | -0.61** | -0.71**    | 0.08        |
| <i>Echidnophaga oschanini</i>                   | 0.73** | 0.16    | -0.63**    | -0.43       |
| <i>Frontopsylla elata</i>                       | 0.12   | -0.12   | 0.14       | -0.08       |
| <i>Frontopsylla elatoides</i>                   | 0.63** | 0.29    | -0.38      | 0.08        |
| <i>Frontopsylla hetera</i>                      | 0.97** | 0.24    | 0.22       | -0.72**     |
| <i>Frontopsylla protera</i>                     | -0.27  | 0.008   | 0.02       | -0.48*      |
| <i>Hystriochopsylla talpae</i>                  | 0.61** | -0.41*  | -0.21      | 0.20        |
| <i>Leptopsylla taschenbergi</i>                 | -0.10  | -0.002  | -0.18      | -0.62**     |
| <i>Megabothris rectangulatus</i>                | 0.45*  | -0.01   | -0.17      | -0.41*      |
| <i>Megabothris turbidus</i>                     | 0.43*  | 0.13    | -0.44*     | -0.28       |
| <i>Megabothris walkeri</i>                      | 0.65** | 0.03    | -0.01      | -0.42*      |
| <i>Neopsylla mana</i>                           | 0.42*  | 0.01    | 0.02       | 0.05        |
| <i>Neopsylla pleskei</i>                        | 0.65** | -0.49*  | 0.09       | -0.45*      |
| <i>Neopsylla setosa</i>                         | 0.53** | -0.06   | -0.64**    | -0.37       |
| <i>Nosopsyllus (Gerbillophilus) laeviceps</i>   | 0.63** | 0.02    | -0.12      | -0.2        |
| <i>Nosopsyllus (Gerbillophilus) turkmenicus</i> | 0.61*  | -0.13   | 0.25       | -0.61*      |
| <i>Nosopsyllus (N.) consimilis</i>              | 0.44*  | 0.05    | -0.25      | -0.54**     |
| <i>Palaeopsylla soricis</i>                     | 0.003  | -0.44*  | -0.05      | -0.28       |
| <i>Pectinocentrus pavlovskii</i>                | -0.08  | -0.06   | -0.42*     | -0.18       |
| <i>Peromyscopsylla bidentata</i>                | 0.19   | -0.49*  | -0.03      | 0.03        |
| <i>Peromyscopsylla silvatica</i>                | 0.71** | -0.35   | -0.003     | -0.39       |
| <i>Rhadinopsylla cedestis</i>                   | 0.79** | -0.2    | -0.37      | -0.56**     |
| <i>Rhadinopsylla integella</i>                  | 0.61*  | -0.28   | -0.1       | -0.002      |
| <i>Stenoponia vlasovi</i>                       | 0.64*  | 0.09    | 0.13       | -0.19       |
| <i>Xenopsylla conformis</i>                     | 0.49*  | 0.17    | 0.27       | -0.32       |
| <i>Xenopsylla gerbilli</i>                      | 0.75** | 0.06    | 0.17       | -0.33       |

neither species richness nor taxonomic distinctness of the flea assemblage of a host species affected the abundance of the globally most abundant flea species of this host species ( $r=0.10$  and  $r=-0.09$ ,  $p < 0.3$  for both).

## Discussion

The results of this study demonstrate that, in general, the abundance of an individual flea species correlates positively with the abundance of all other flea species in a component community or a compound community, and correlates negatively with their diversity. These patterns are remarkably consistent, whatever the scale used (within flea species, within host species, among flea species, among host species). This suggests that these patterns are robust and widespread.

Our results provide absolutely no support for diffuse competition in the traditional sense because the more individuals of other species are present on a host population, the more individuals of the focal species are there as well. This may suggest that some host species, but not others, represent better habitats for multiple flea species. Superiority of a given habitat (host species) compared to other habitats (other host species) from the “viewpoint” of a consumer (a flea) can be quantitative (the amount of resources) or qualitative (the pattern of resource acquisition) or both (Morris 1987). An example of a quantitative between-host difference might be the absolute amount of blood available for flea imagoes or the amount of organic matter in the host’s burrow or nest available for flea larvae. The former can depend on the body size of the host species, whereas the latter can depend on the type of nest material, the time that the host spends in the nest, and host behavior (e.g. defecation inside or outside the nest). However, the lack

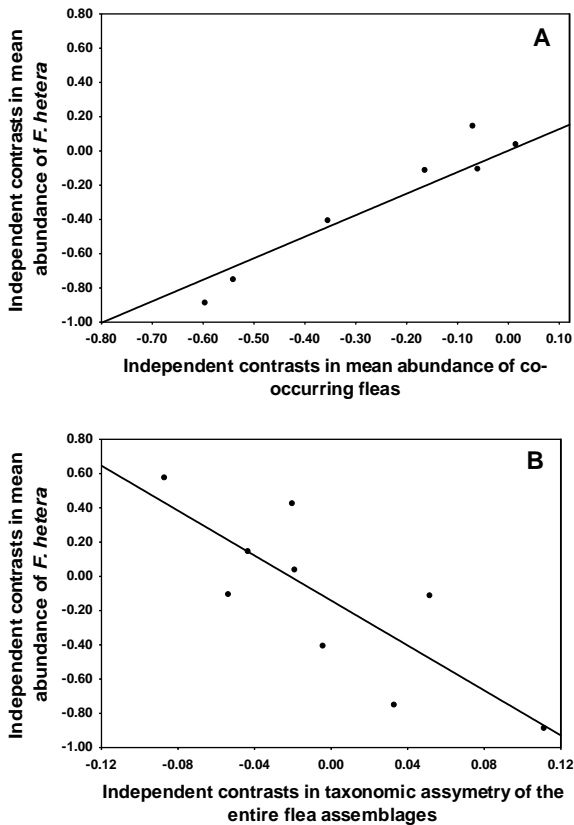


Fig. 1. Relationships between the mean abundance of *Frontopsylla hetera* and the abundance of all other co-occurring flea species (A) and taxonomic asymmetry (B) of flea assemblages across different host species, using independent contrasts.

of relationships between host body size and abundance of flea assemblages (see Methods) advocates the rejection of the former explanation. On the contrary, the

amount of larval food in the burrow should be important for all flea species as flea larvae are food generalists able to feed on various kinds of organic matter. Indeed, the complexity and depth of the burrow of a host species can be a good predictor of the abundance and diversity of flea assemblages on this species. For example, the great gerbil *Rhombomys opimus* constructs highly complicated and deep burrows and has one of the most abundant and richest flea assemblages among rodents (Zagniborodova 1960, 1968). Another example is offered by the sympatric gerbillines *Meriones crassus* and *Gerbillus dasyurus* that differ sharply in their pattern of burrow use. *Meriones crassus* is much more territorially conservative than *G. dasyurus* (Krasnov et al. 1996, Khokhlova et al. 2001) and also harbor more abundant flea assemblages (Krasnov et al. 1997).

Examples of qualitative among-host species differences include variation in the absolute amount of blood that an individual insect obtains during a bloodmeal (e.g. Webber and Edman 1972) and the efficiency of blood digestion by a flea (e.g. Vatschenok 1988). Hosts also vary in their skin structure (which determines the ease of blood sucking) and fur density (which determines the ease of flea movement). Differences among host species in resource acquisition by fleas can also be linked to the differential defense abilities (either behavioural or immunological) of host species. For example, hosts with different limb morphology differ in their manipulative abilities (e.g. Wishaw et al. 1998), and thus presumably in their effectiveness for anti-ectoparasite grooming. Consequently, a host species with relatively low grooming ability would represent a better habitat for many flea species than a host species with higher grooming ability. For example, the mean abundance of fleas on *Microtus*

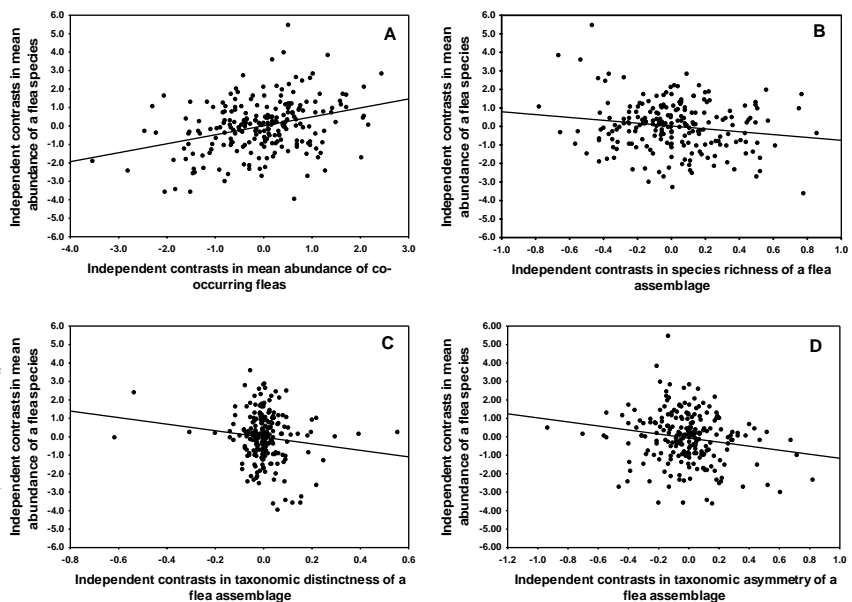


Fig. 2. Relationships between the mean abundance of a flea on a host species and the abundance of all other co-occurring flea species (A) and the species richness of the flea assemblage on that host (B), its taxonomic distinctness (C) and taxonomic asymmetry (D) across 230 flea species using independent contrasts.

Table 3. Summary of significant correlations (Pearson product-moment correlation using independent contrasts) between the abundance of the most abundant flea species and either the abundance of all other co-occurring flea species (A), the species richness (SR), taxonomic distinctness ( $\Delta^+$ ) or taxonomic asymmetry ( $\Lambda^+$ ) of the flea assemblage, for 10 mammalian hosts across different regions. \*  $-p < 0.05$ , \*\*  $-p < 0.01$ .

| Host species                  | A      | SR     | $\Delta^+$ | $\Lambda^+$ |
|-------------------------------|--------|--------|------------|-------------|
| <i>Apodemus agrarius</i>      | 0.82*  | -0.14  | -0.18      | -0.75*      |
| <i>Apodemus uralensis</i>     | 0.79*  | -0.05  | -0.83**    | -0.25       |
| <i>Arvicola terrestris</i>    | 0.95** | 0.10   | -0.73**    | 0.09        |
| <i>Clethrionomys rutilus</i>  | 0.83** | -0.19  | 0.19       | 0.20        |
| <i>Cricetulus migratorius</i> | 0.69*  | 0.13   | -0.81**    | -0.002      |
| <i>Microtus arvalis</i>       | 0.82** | -0.15  | 0.14       | -0.62**     |
| <i>Microtus gregalis</i>      | 0.74*  | -0.22  | 0.08       | -0.25       |
| <i>Microtus oeconomus</i>     | 0.37   | -0.69* | -0.11      | -0.68**     |
| <i>Mus musculus</i>           | 0.90** | 0.21   | -0.78*     | 0.22        |
| <i>Sorex araneus</i>          | 0.96** | 0.04   | 0.16       | 0.23        |

*oeconomus* (relatively low manipulative ability) is higher than that on *Mus musculus* (relatively high manipulative ability) (on average across different region, 1.33 versus 0.54 fleas per individual,  $t = 3.23$ ,  $p < 0.005$  after correction for sampling effort).

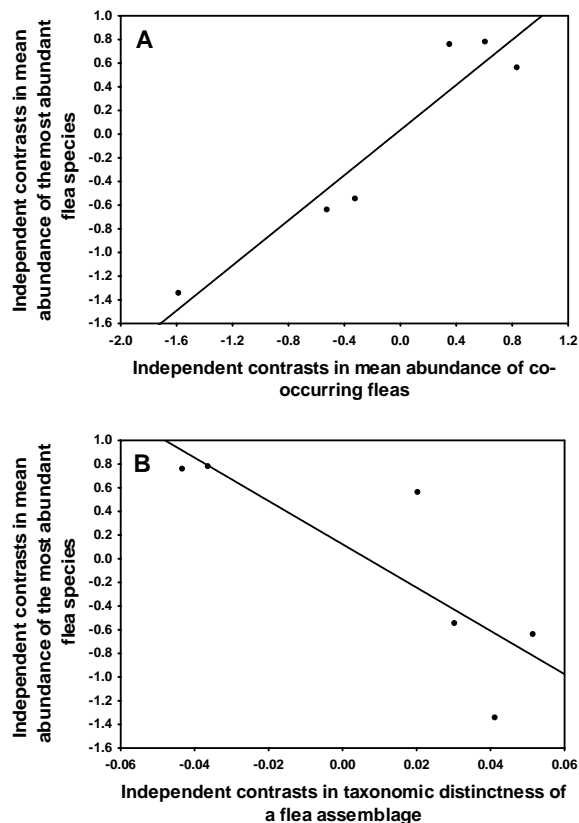


Fig. 3. Relationships between the abundance of the most abundant flea and the abundance of all other co-occurring flea species (A) and taxonomic distinctness (B) of flea assemblages in *Arvicola terrestris* across different regions, using independent contrasts.

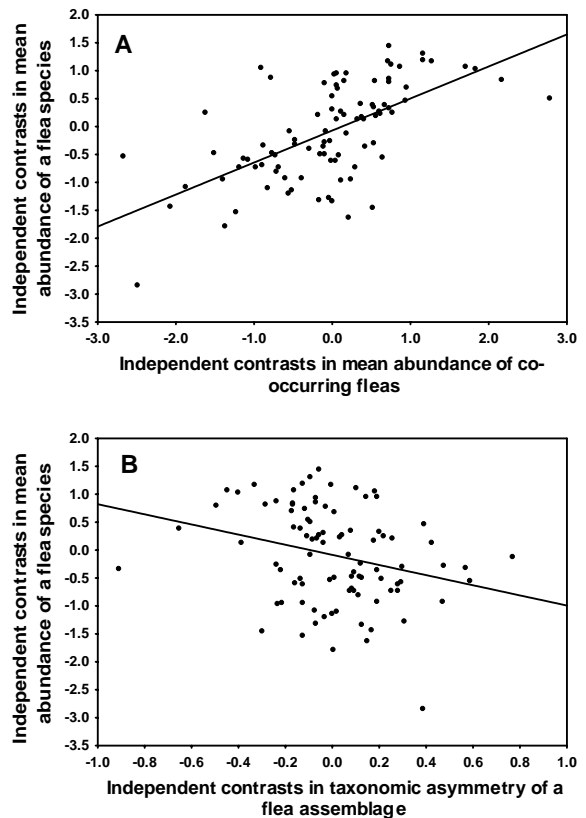


Fig. 4. Relationships between the abundance of the most abundant flea and the abundance of all other co-occurring flea species (A) and taxonomic asymmetry (B) of the flea assemblages across 93 host species, using independent contrasts.

Host species can differ also in their ability to defend themselves against fleas using their immune system. Species-specific differences in the ability to mount both humoral and cell-mediated immune responses have been reported even for closely related rodent species (Klein and Nelson 1998a, b). Consequently, a host species with lower immunocompetence can be exploited by a higher number of individuals of multiple flea species than a host species with higher immunocompetence. However, it is unknown whether different flea species respond similarly to the immune responses of the same host species. This question is in need of experimental tests and remains to be answered.

The above considerations are related to differences among host species. However, similar considerations can be applied to differences among host populations. For example, some populations of the same host species can represent better habitats for fleas than other populations because of among-host populations differences in defensive abilities against parasites using the immune system. Between-population variation in immune ability has been shown for various host species and has been



related to various extrinsic and intrinsic factors (e.g. Couch et al. 1993, Meagher 1999).

All the above suggests important indirect (host-mediated) facilitation among flea species within component and compound communities living on small mammals. Furthermore, the fitness of a host is determined by various factors (availability of spatial and energetic resources, predation, intra- and inter-specific competition). The fitness of a parasitized host is also limited by competition with the parasite, which may hijack part of the available resources. In this sense, for the host a parasite is only a competitor, while for the parasite the host is both a competitor and the resource (Combes 2001). Therefore, the main pattern of interactions among flea species in component communities can be referred to as apparent facilitation [positive interactions mediated by a shared competitor (Davidson 1980, Levine 1999)]. Apparent facilitation has been shown to be an important pattern in the communities of various free-living organisms, both animals and plants (e.g. Davidson 1980, Miller 1994, Levine 1999). Apparent facilitation in terms of parasite-induced immunodepression has been repeatedly reported for parasites, although mainly at the infracommunity scale (Bush and Holmes 1986a, Cox 2001).

Nevertheless, apparent facilitation is thought to be more likely to arise in assemblages where the different pairs of competitors compete for different resources, or use different mechanisms to acquire resources (Davidson 1985). Few would deny that flea species compete for the same resource (imago for blood and larvae for organic matter). However, the acquisition of the resource (e.g. pattern and location of a bloodmeal) can be strikingly different in different flea species (e.g. Hsu et al. 2002).

The relationships between the abundance of a given flea species and the diversity of flea assemblages were consistently negative. In general, the abundance of a given flea species is highest in assemblages consisting of few species of limited taxonomic diversity. On the one hand, this supports the existence of some form of negative interactions among species, such that the abundance of a given flea species is lower when many other species are also present. On the other hand, this supports the occurrence of facilitation mediated via the host, since the abundance of a given flea species is higher when co-occurring flea species are closely related (taxonomically) with it. The latter can be linked to the higher likelihood of immunosuppression if the immunogens of the parasites involved are similar which, in turn, is more likely if the parasites are phylogenetically close (a phenomenon opposite to cross-resistance).

We also observed that the flea species showing a significant negative association between their abundance and the taxonomic diversity ( $\Delta^+$ ) of the flea assemblage, do not show a similar trend with the variation in

taxonomic distinctness ( $\Delta^+$ ), and vice-versa (Table 2). This finding suggests that the various processes affecting abundance of flea species can operate separately. Thus, an alternative hypothesis could be related to the niche filtering process where environmental conditions (both biotic, related to the host, or abiotic) act as a filter to restrict co-occurring species to a certain functional, phylogenetic or taxonomic subset (Tofts and Silvertown 2000, Stutzner et al. 2004). Strong niche filtering, possibly mediated by host immune responses, would lead to only closely-related flea species occurring together on hosts where conditions are favorable for them to achieve high abundance. Weaker niche filtering would allow the co-occurrence of several unrelated flea species, some of which may achieve low abundance because local (host) conditions are not optimal for their requirements.

Strong direct competition among closely-related flea species could negate the positive effects of joint immunosuppression; however, the consistent negative relationships we found between the abundance of given flea species and the taxonomic diversity of the assemblages they belong to indicate that competitive effects are unimportant.

All the above supports the idea that both facilitation and competition operate among the same species either simultaneously or with the strength of each process varying in time or space (Callaway and King 1996, Callaway and Walker 1997, Levine 1999). Consequently, a community has to be considered from a more synthetic perspective, where species interactions should be viewed as complex combinations of negative and positive components (Callaway and Walker 1997, Levine 1999). Furthermore, it is possible that multiple pair-wise competitive interactions within a community can amount to net positive effects by incorporating interactions with a shared competitor (host) (Levine 1999). In other words, both direct and indirect effects should be taken into account when considering interactions in the context of entire communities (Stone and Roberts 1991).

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