Nested pattern in flea assemblages across the host's geographic range

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Understanding non-random patterns in the taxonomic composition of communities occurring in insular or fragmented habitats remains a major goal of ecology. Nested subset patterns are one possible departure from random community assembly that has been reported for communities of both free-living and parasitic animals. Here, we investigate the effects of extrinsic factors on the occurrence of nestedness among the assemblages of fleas found in different populations of the same host species, using data on 25 mammalian host species. The patterns of flea species composition among host populations spanned the entire spectrum from significantly nested to significantly anti-nested. After controlling for host phylogeny, we found that across host species, the tendency for flea assemblages to approach nestedness increased with increasing host geographic range size and with decreasing latitude of the host's geographic range. This tendency also decreased with an increase in a composite variable combining data on mean January and July temperature. The number of closely-related mammalian species living in sympatry with a given host species had no influence on whether or not the structure of flea assemblages among its populations departed from randomness. We propose explanations for these results that include: the possible gradual loss of flea species as a host expands its range from its initial area of origin, the lack of specific flea faunas in narrowly-distributed host species, interspecific differences in the dispersal abilities of flea species becoming amplified in hosts with broad geographical ranges, and the effect of latitude, climate and environment on the probabilities of host-switching and extinction in fleas. Overall, our results suggest that the structure of flea assemblages in mammalian hosts may be driven by features of host biology.

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The role of ecological and evolutionary rules that govern the structure of communities of plants and animals has been widely debated over the past decades (Anon. 1944, Strong et al. 1984, McIntosh 1987, Wiens 1992, Brown et al. 2002). However, as Patterson (1990) noted, "the existence of structure must be established before detailed explanatory models are necessary or useful". Consequently, one of the most important ecological questions is whether plants and animals live in structured, non-random communities or whether a set of co-occurring species represents an unstructured, random assemblage. Several approaches for the search of structure in species assemblages have been used (Diamond 1975, Connor and Simberloff 1979, Gotelli 2000). For example, the structure of metazoan ectoparasite communities of marine fish was assessed by studying the effects of interspecifc aggregation on the level of intraspecifc aggregation to test "the aggregation model of

coexistence" (Morand et al. 1999) and by using null model analysis to test for nonrandomness in species co-occurrences (Gotelli and Rohde 2002).

One method to test whether assemblages of organisms are structured is to search for a nested pattern, i.e. a pattern in which species comprising depauperate assemblages constitute non-random subsets of the species occurring in successively richer assemblages (Patterson and Atmar 1986, Brown 1995, Hecnar and M'Closkey 1997, Wright et al. 1998). Nested patterns have been found in communities of different taxa of both plants and animals (Patterson and Brown 1991, Hecnar and M'Closkey 1997, Honnay et al. 1999, Kelt et al. 1999, Matthews 2004, Baber et al. 2004).

In recent years, the search for nested patterns has been applied to parasite communities (Guégan and Hugueny 1994, Poulin 1996, Worthen 1996, Hugueny and Guégan 1996, Worthen and Rohde 1996, Rohde et al. 1998, Poulin and Guégan 2000, Matejusova et al. 2000, Poulin and Valtonen 2001, 2002, Timi and Poulin 2003, Vidal-Martinez and Poulin 2003). The rationale for the possible existence of nestedness in parasite communities is that nested species subsets are a common pattern in many types of communities found in insular or fragmented habitats (Patterson and Atmar 1986, Bolger et al. 1991). In this context, hosts can be viewed as biological islands for parasites (Kuris et al. 1980).

To date, however, the application of nestedness analyses to parasite communities has yielded few new insights for at least two reasons. First, most previous studies of nestedness in parasite communities have dealt with metazoan parasites of teleost fish (but see Poulin 1996, Guernier et al. 2004, Portoles et al. 2004, Zelmer et al. 2004). Therefore, it is reasonable to expect some consistency in the results of these studies. However, studies of nestedness in fish parasite communities have provided contradictory results, and there is currently no consensus on whether parasite communities are structured. In part, these contradictions stem from the type of statistical technique used (Guégan and Hugueny 1994 versus Worthen and Rohde 1996), although Rohde et al. (1998) demonstrated that different statistical approaches were not responsible for different results, at least in the assemblages of metazoan ectoparasites of 79 species, and gastrointestinal helminths of eight species, of marine fishes. Another reason for the conflicting results might be the complicated relationships between extrinsic and intrinsic factors that affect species composition of parasite communities. For example, Poulin and Valtonen (2001) reported that host size and dietary specialization can affect the occurrence and manifestation of nested patterns.

Second, previous nestedness analyses may have focused on the wrong spatial scale. Kuris et al. (1980) considered hosts as biological islands at three different levels: host individual, host population and host species.

It is the first level that has been considered in earlier studies of nestedness in parasite communities (infra-communities, namely an assemblage of parasite species in an individual host). Component communities (assemblages of parasite species exploiting a host population at one point in time) have received less attention (but see Guégan and Kennedy 1996, Calvete et al. 2004), although this higher hierarchical level is more relevant to nestedness analyses. Infracommunities are ephemeral assemblages greatly influenced by epidemiological processes, whereas component communities are structured by the kind of biogeographical processes relevant to the original idea of the nested subsets pattern developed by Patterson and Atmar (1986).

In the present study, we search for the occurrence of nested patterns in flea assemblages among host populations of the same species across the species' geographic range, using data on 25 Holarctic small mammal species. Fleas (Siphonaptera) are characteristic mammalian ectoparasites and are most diverse on small and medium-sized host species. They usually alternate between periods when they occur on the host body and periods when they occur in its burrow or nest. In most cases, the pre-imaginal development is entirely off-host. The larvae usually are not parasitic and feed on organic debris in the burrow and/or nest of the host. Species richness of flea assemblages as well as both the intensity and prevalence of flea infestation have been shown to be independent of host body size both at the level of individual host and host species (Krasnov et al. 1997, 2004a). This allowed us to assume the absence of the confounding effect of host size on the occurrence of non-randomness in flea communities.

Following Poulin and Guégan (2000) and Poulin and Valtonen (2001), we considered a flea community to be structured if it departed from random assembly in either direction, i.e. towards either nestedness or anti-nestedness. Nestedness occurs if flea assemblages can be arranged in such a way that depauperate assemblages consist of proper subsets of progressively richer ones. Alternatively, if flea species are always absent from assemblages richer than the most depauperate one in which they occur, then the assemblages are considered as anti-nested (Poulin and Guégan 2000). Anti-nested patterns, although rarely reported in the literature, indicate non-random assembly of species, via the action of unknown structuring factors (Poulin and Guégan 2000).

We hypothesized that the occurrence and manifestation of nested patterns in flea assemblages are affected by host-related factors (Poulin and Valtonen 2001). Our aims were a) to assess the frequency of non-random (nested and anti-nested) flea assemblages across these hosts and b) to explore the effects of extrinsic factors (the descriptors of the host geographic range,

environment and the taxonomic composition of the host's community) on the occurrence of these patterns.

Materials and methods

Data

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Insectivora and Rodentia) in 24 different regions (zoogeographically homogenous areas) (Table 1). Only mammal species which occurred in at least 3 regions and for which at least 10 individuals have been examined per region were included, because estimates of flea species richness could be inaccurate for small samples (Krasnov et al. 2004a). This yielded data for a total of 25 small mammal species (23 rodents and 2 insectivores).

The parameters used to describe the geographic range of each host species included the area of the geographic range and the latitude of the geometric center of the range. These variables were generated from distribution maps for each host species. Distribution range maps were composed as polygon maps using the ArcView 3.2 software based on maps from Hall (1981), Panteleev et al. (1990) and Zhang et al. (1997), with corrections of Mezhzherin (1997). Environmental factors were mean surface air temperature of January and mean surface air temperature of July, annual precipitation and Monthly Generalized Global Vegetation Index (MGGVI). These variables where calculated for each host species across its geographic range using 30' grid data (Kineman et al. 2000). Because some of these environmental variables were strongly correlated with each another (r = −0.84–0.74, p < 0.05 for all), we

Table 1. Data on small mammals from the 24 regions used in the analyses. Data include mammal species which occurred in at least 3 regions and for which at least 10 individuals have been examined per region.

Species	Regions
Allactaga elater	East Balkhash desert (Kazakhstan)[1], Moyynkum desert (Kazakhstan)[2], North Kyrgyzstan[3], Turkmenistan[4]
Apodemus agrarius	Altai mountains[5], Dzhungarskyi Alatau (Kazakhstan)[6], Kabarda (northern Caucasus)[7], North Kyrgyzstan, Novosibirsk region (southern Siberia)[8], Slovakia[9], Tarbagatai (eastern Kazakhstan)[10], Volga-Kama region[11]
A. sylvaticus	Adzharia (southern Caucasus)[12], Kabarda, Slovakia
A. uralensis	Dzhungarskyi Alatau, Kustanai region (northwestern Kazakhstan)[13], North Kyrgyzstan, Slovakia, Tarbagatai, Volga-Kama
Arvicola terrestris	Akmolinsk region (northern Kazakhstan)[14], Altai, Dzhungarskyi Alatau, Kabarda, Kustanai, Novosibirsk, Tarbagatai, Volga-Kama
Clethrionomys glareolus	Akmolinsk, Altai, Novosibirsk, Slovakia, Volga-Kama
C. rufocanus	Khabarovsk region (southern Russian Far East)[15], North Asian Far East[16], Novosibirsk
C. rutilus	Asian Far East, Altai, central Yakutia[17], Khabarovsk, Novosibirsk, Selenga region (central Siberia)[18], Volga-Kama
Cricetulus migratorius	Adzharia, Dzhungarskyi Alatau, East Balkhash, Kabarda, Moyynkum, North Kyrgyzstan, Kabarda, Turkmenistan
Cricetus cricetus	Akmolinsk, Altai, Dzhungarskyi Alatau, Novosibirsk
Dryomys nitedula	Adzharia, Dzhungarskyi Alatau, Tarbagatai, Volga-Kama
Lagurus lagurus	Akmolinsk, Kustanai, Novosibirsk
Meriones meridianus	East Balkhash, Moyynkum, Turkmenistan, Tuva[19]
M. tamariscinus	East Balkhash, Moyynkum, North Kyrgyzstan
Microtus agrestis	Altai, Novosibirsk, Volga-Kama
M. arvalis	Adzharia, Akmolinsk, Altai, Dzhungarskyi Alatau, Kabarda, Kustanai, Novosibirsk, Slovakia, Volga-Kama
M. gregalis	Akmolinsk, Altai, central Yakutia, Kustanai, North Kyrgyzstan, Novosibirsk
M. oeconomus	Asian Far East, Akmolinsk, Altai, Kustanai, Novosibirsk, Selenga, Volga-Kama
Mus musculus	Adzharia, Akmolinsk, Dzhungarskyi Alatau, East Balkhash, Kabarda, Khabarovsk, Moyynkum, North Kyrgyzstan, Novosibirsk, Pavlodar region (eastern Kazakhstan)[20], Selenga, Turkmenistan, Tuva, Volga-Kama
Neomys fodiens	Altai, Dzhungarskyi Alatau, Novosibirsk, Slovakia, Volga-Kama
Peromyscus maniculatus	California[21], Idaho[22], north New Mexico[23]
Pygeretmus pumilio	East Balkhash, Moyynkum, Turkmenistan
Rhombomys opimus	East Balkhash, Moyynkum, Turkmenistan
Sorex araneus	Altai, Dzhungarskyi Alatau, Slovakia, Volga-Kama
Spermophilus undulatus	Central Yakutia, Dzhungarskyi Alatau, Mongolia[24], Tuva

[1]Mikulin 1959a; [2]Popova 1967; [3]Shwartz et al. 1958; [4]Zagniborodova 1960 and unpubl.; [5]Sapegina et al. 1981; [6]Burdelova 1996; [7]Syrvacheva 1964; [8]Violovich 1969; [9]Stanko et al. 2002; [10]Mikulin 1958; [11]Nazarova 1981; [12]Alania et al. 1964; [13]Reshetnikova 1959; [14]Mikulin 1959b; [15]Koshkin 1966; [16]Yudin et al. 1976; [17]Elshanskaya and Popov 1972; [18]Pauller et al. 1966; [19]Letov et al. 1966; [20]Sineltschikov 1956; [21]Davis et al. 2002; [22]Allred 1968; [23]Morlan 1955; [24]Vasiliev 1966.

substituted them with the scores calculated from principal component analyses of these four variables. The resulting two "environmental factors" explained 91.5% of the variance; their eigenvalues were 2.69 and 1.23, respectively. Environmental factor 1 reflected mainly variation in precipitation and vegetation (factor loadings were 0.99 and 0.88, respectively), whereas environmental factor 2 reflected mainly variation in mean January and July temperature (factor loadings were 0.97 and 0.79, respectively).

The taxonomic composition of the community of each host species was characterized by the number of sympatric host species belonging to the same subfamily, averaged across host populations of the same species. These numbers were taken from the original survey reports. Because this variable was positively correlated with the size of the geographic range ($r = 0.78$, $p < 0.05$), we removed the effect of the geographic range size by substituting the original values of the number of co-occurring close relatives with the residuals of the regression of these values against the size of the geographic range in log-log space.

Evaluation of nestedness

There are various metrics of nestedness (see review in Wright et al. 1998); most are strongly dependent on the size of the input matrix (species by sites) which makes comparison of nestedness between different data sets difficult. Variation in the degree of nestedness can have methodological rather than biological causes (Wright et al. 1998, Timi and Poulin 2003). The detection of nestedness depends not only on matrix size (the number of cells in the matrix), but also on matrix fill (proportion of cells in the matrix that indicate presence as opposed to absence of a flea species). The only metric that appears independent of matrix size is matrix "temperature" (T) proposed by Atmar and Patterson (1993). This metric provides a standardized measure of matrix disorder by quantifying the deviation of an observed matrix from one of the same size and fill that is perfectly nested and ranges from 0 (perfectly nested matrix) to 100 (completely disordered matrix). Thus, nestedness is an estimate of the degree of non-random pattern in species distribution.

We computed the temperature (T) of each matrix (flea species versus host populations) for each of the 25 host species using the Nestedness Temperature Calculator Program (NTCP, Atmar and Patterson 1995). We applied parametric correlation analysis (Pearson's correlations) to evaluate the influence of both matrix size (calculated as number of host populations X number of flea species found across all conspecific host populations) and matrix fill on the resulting T values; see below. No effect was found ($r = 0.06$ and $r = -0.15$ for cross-

host species analysis and $r = 0.20$ and $r = -0.09$ across independent contrasts, respectively; $p > 0.3$ for all). For each host species, the observed matrix temperature was compared with the T values of 1000 randomly generated presence-absence matrices produced with Monte-Carlo simulations. The statistical probability of the observed pattern was given by the proportion of simulated T values that were lower than or equal to the observed T value and was used as a measure of the departure from the structure expected under random assembly (Guégan and Hugueny 1994, Hugueny and Guégan 1996, Vidal-Martinez and Poulin 2003). A p value ≤ 0.05 indicated communities that were significantly nested, whereas p values ≥ 0.95 characterized significantly anti-nested patterns. In other words, the structure of the flea assemblages becomes less nested and increasingly anti-nested with an increase in the p value.

Although the use of the Bonferroni correction has been recommended for the evaluation of nestedness across several communities (Worthen and Rohde 1996), we chose to use a less conservative procedure for two reasons. First, the Bonferroni adjustment of alpha-level has been increasingly criticized by statisticians and ecologists in recent years, because it often leads to the incorrect acceptance of the false null hypothesis when multiple comparisons are in fact independent of one another (Rothman 1990, Perneger 1998, 1999, Moran 2003, Garcia 2004, Nakagawa 2004) as is the case in our study. Second, the generated p values most likely form a continuum (Poulin and Valtonen 2001) and rather than using individual p values as rigid indicators of "significantly nested" species, we employed p values as metrics to place species on a nestedness continuum in order to evaluate the influence of host biology parameters on the probability of nestedness (see below). Nevertheless, we used Bonferroni corrections when determining the frequency of nestedness or anti-nestedness. Consequently, the results of nestedness evaluation are presented both with and without sequential Bonferroni correction. In addition, following Poulin and Valtonen (2001) and because of the small number of communities in our analyses, we classified assemblages as exhibiting strong trends towards nestedness or anti-nestedness if their p values were ≤ 0.15 or ≥ 0.85, respectively.

Statistical analyses

We compared assemblages exhibiting strong trends towards nestedness and anti-nestedness with respect to parameters of the host geographic range, environment and the taxonomic composition of host communities described above using two-tailed t-tests on log-transformed data. In addition, we conducted correlation analyses in which we treated p values obtained from

the nestedness calculation as a continuous variable and correlated them (after log-transformation) against log-transformed variables of host geographic range, and taxonomic composition of the host community, and the non-transformed composite environmental variables.

Initially, each host species was treated as an independent observation. Nevertheless, treating values obtained for different host species as independent observations can introduce bias into analyses. To control for the effects of host phylogeny, we re-analysed the data using the method of independent contrasts (Felsenstein 1985). The phylogenetic tree of hosts was derived from various sources (see details in Krasnov et al. 2004b). We computed independent contrasts from the log-transformed data, using the PDAP:PDTREE program (Garland et al. 1993, Midford et al. 2003) implemented in the Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2004). Here again, p values were treated as a continuous variable. Contrasts were standardized as suggested by Garland et al. (1992). Then, correlations between contrasts in p values and contrasts in other variables were computed as forced through the origin (Pagel 1992, Garland et al. 1992).

Table 2. Summary of the results of nestedness analyses of flea assemblages in 25 small mammalian host species from 24 regions. P value indicates whether an assemblage is nested (≤ 0.05), anti-nested (≥ 0.95) or random ($0.05 \leq p \leq 0.95$).

Host species	Matrix fill	Matrix T	p
A. elater	40.1	25.68	0.04
A. agrarius	24.1	39.83	0.35
A. sylvaticus	40.7	28.17	0.29
A. uralensis	27.9	38.56	0.28
A. terrestris	27.4	32.93	0.03
C. glareolus	39.2	36.25	0.28
C. rufocanus	45.8	17.76	0.13
C. rutilus	27.2	47.92	0.61
C. migratorius	18	47.43	0.96
C. cricetus	43.7	37.54	0.69
D. nitedula	30.5	12.67	0.14
L. lagurus	53.5	30.95	0.54
M. meridianus	35.6	21.43	0.01
M. tamariscinus	32.7	68.38	0.99
M. agrestis	43.7	32.89	0.65
M. arvalis	23.3	32.73	0.02
M. gregalis	30.2	52.29	0.89
M. oeconomus	28	47.35	0.76
M. musculus	12.06	22.99	0.05
N. fodiens	35.7	42.83	0.69
P. maniculatus	41.6	30.59	0.35
P. pumilio	55.5	30.22	0.58
R. opimus	45.4	39.75	0.86
S. araneus	38.6	22.99	0.04
S. undulatus	39.5	39.11	0.54

Results

Flea assemblages among 25 host species were significantly nested in 6 hosts, significantly anti-nested in 2 hosts and non-significantly structured in the remaining 17 hosts (Table 2). After a Bonferroni correction, the number of both nested and anti-nested assemblages dropped to one. Using the looser criterion of tending toward nestedness or anti-nestedness, there were 7 assemblages that tended toward nestedness and 4 assemblages that tended toward anti-nestedness.

Flea assemblages exhibiting a strong trend towards nestedness or anti-nestedness belonged to host species with significantly different geographic range sizes, with the former being characteristic of hosts with greater range size (t = 2.47, p < 0.04) (Fig. 1). In contrast, hosts with flea assemblages that tended toward either nestedness or anti-nestedness did not differ with respect to the latitude of the center of their geographic range (t = −0.53, p > 0.6). The same was true in relation to factors describing environmental variation (t = 1.42 for environmental factor 1 and t = 0.08 for environmental factor 2; p > 0.2 for both) and the number of co-occurring closely related (belonging to the same subfamily) species (t = 1.31, p > 0.20). Nevertheless, when treated as a continuous variable, the departure from random assembly (i.e. p value) was not correlated with any host variable in the cross-host species correlation analyses (r = −0.32–0.25, p > 0.1 for all).

Results of comparative analyses using independent contrasts differed somewhat from those of the conventional cross-host species analysis. Contrasts in p values were significantly negatively correlated with contrasts in the size of the host geographic ranges (r = −0.45, p < 0.02; Fig. 2) and contrasts in the environmental factor 2 (mean January and July temperature; r = −0.40, p < 0.05; Fig. 3) and significantly positively correlated with contrasts in the latitude of the center of the host geographic ranges (r = 0.39, p < 0.05; Fig. 4). However, we found no correlation between contrasts in p values
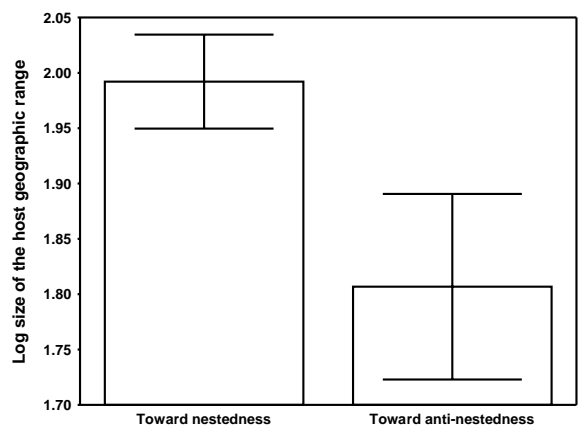

Fig. 1. Mean ($\pm$SE) size of the host geographic range (log-transformed) for seven flea assemblages that tended toward nestedness and four flea assemblages that tended toward anti-nestedness.

and either contrasts in the environmental factor 1 (precipitation and vegetation; $r = -0.35$, $p < 0.1$) or contrasts in the number of co-occurring closely related host species (corrected for the geographic range size) ($r = -0.11$, $p > 0.60$).

Discussion

Results of this study suggest two points. First, the organization of flea assemblages across host populations within host species forms a continuum among host species from true nestedness to true anti-nestedness. Second, features of the host geographic range and environment affect community organization of their flea parasites. Thus, it seems clear that nestedness and anti-nestedness can be driven by host biology (Calvete et al. 2004).

A continuum of community organization from nestedness to anti-nestedness was reported in several studies of infracommunities of ecto- and endoparasites of fish (Poulin and Guégan 2000, Poulin and Valtonen 2001), birds (Simkova et al. 2003, Calvete et al. 2004) and mammals (Fellis et al. 2003, Gouy de Bellocq et al. 2003). Furthermore, the proportion of nested and anti-nested flea assemblages found in our study is similar to that found for fish parasites. This suggests that nested patterns in parasite assemblages across host populations may be as uncommon as they are in parasite assemblages across host individuals, and confirms the findings of Poulin and Guégan (2000) and Poulin and Valtonen (2001) that both nestedness and anti-nestedness are infrequent in parasite communities. These results hint at the possibility that community organization of parasites at both hierarchical levels, namely host individuals and host populations, is governed by similar rules. These results also confirm findings of studies that searched for

Fig. 3. Relationships between the inverse probability of the flea assemblage being nested and the variable describing the increase in mean January and July temperature (environmental factor 2, see text for explanations). Data are phylogenetically independent contrasts.

structure in parasite assemblages using approaches other than nestedness (Poulin 1996, Morand et al. 1999, Gotelli and Rohde 2002). In all these earlier studies, departures from random patterns were not strongly pronounced.

In free-living organisms (mainly in mammals and birds), nested patterns observed across insular or fragmented habitats are considered to be a result of differential colonization or extinction probabilities among the available species (Patterson and Atmar 1986, Patterson 1990, Bolger et al. 1991). Nested patterns in parasite communities have also been explained by colonization-extinction dynamics (Guégan and Hugueny 1994). Moreover, Poulin and Guégan (2000) argued that interspecific differences in colonization rate may also be responsible for the anti-nested
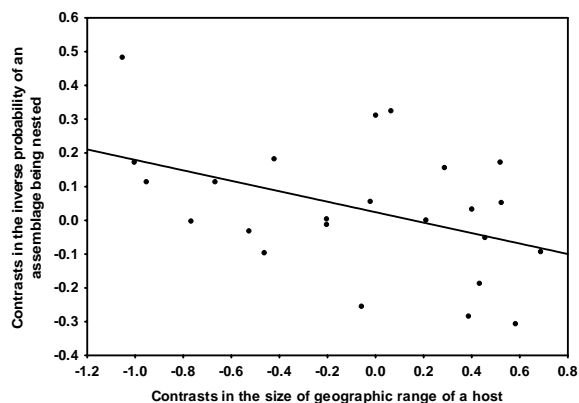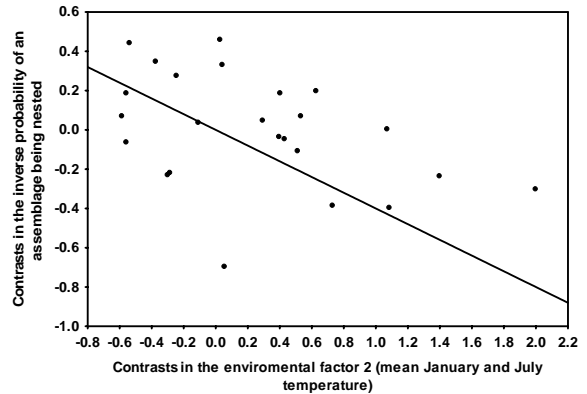

Fig. 2. Relationships between the inverse probability of the flea assemblage being nested and the size of the host geographic range. Data are phylogenetically independent contrasts.
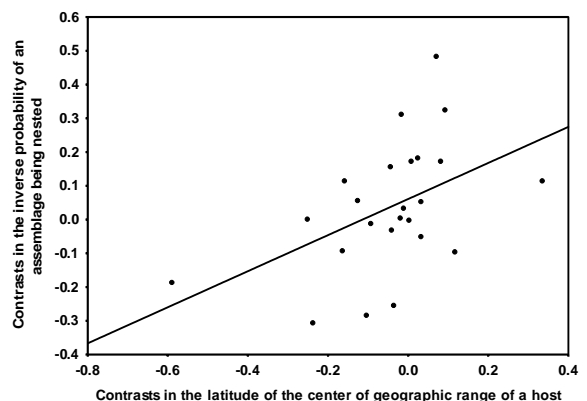

Fig. 4. Relationships between the inverse probability of the flea assemblage being nested and the latitude of the center of the host geographic range. Data are phylogenetically independent contrasts.

pattern, if rare and highly host specific species are characterized by poor colonization ability compared with locally abundant host-opportunistic species. Indeed, Poulin and Guégan (2000) demonstrated that there is a positive relationship between parasite prevalence and parasite local mean intensity and that as the prevalence or mean intensity of parasites increases in a fish population, the likelihood that the parasite infracommunities are nested also increases. These findings confirm a link between the positive prevalence-intensity relationship and the nestedness-anti-nestedness continuum.

The prevalence-intensity relationship is a parasitological equivalent of the more general spatial distribution-local abundance relationship that has been repeatedly reported for free-living organisms (Gaston 2003 for review). However, studies of this relationship in parasites have provided contradictory results with both positive (Barger and Esch 2002) and negative (Poulin 1998) relationships being reported. Consequently, Poulin and Guégan (2000) recommended that community studies should test for both the existence of a nested/anti-nested continuum and positive relationships between spatial distribution and local abundance in a similar stratum, as they did in their study. Our recent study on fleas parasitic on small mammals (Krasnov et al. 2004c) using the data from the same sources as in this study (although on a larger set of host species) showed that, in general, fleas exploiting many host species, or those exploiting taxonomically unrelated hosts, achieved higher abundance than specialist fleas. The present study, therefore, confirms that a linkage between the positive prevalence-intensity relationship and the nestedness-anti-nestedness continuum occurs not only at the level of parasite infracommunities but also at the higher hierarchical level.

In addition, the nestedness-anti-nestedness continuum of parasite infracommunities has been considered to reflect a kind of spatial organization of parasite species from coexistence to competitive exclusion and, thus, might be explained in the framework of species coexistence models (Poulin and Guégan 2000). Parasite species that belong to nested assemblages supposedly have reduced levels of interspecific aggregation relative to intraspecific aggregation and thus species coexistence is facilitated, whereas parasite species occurring in anti-nested assemblages tend to show a strong interspecific aggregation resulting in species exclusion (Morand et al. 1999). These considerations for parasite assemblages in host individuals can also be applied to parasite assemblages in host populations, especially given that fleas from different host individuals can co-occur in the same burrow both as adults and as pre-imagos (Krasnov and Khokhlova 2001). Nevertheless, Poulin and Valtonen (2001) found nestedness-anti-nestedness continua for both adult and larval parasites and concluded that the

consistent patterns observed in these communities are unlikely to be due to the effects of interspecific parasite interactions, because the latter are extremely unlikely in communities of larval endoparasites. However, in fleas, interspecific interactions can be expected in both adult (Day and Benton 1980) and larval communities (Marshall 1981). For example, competitive interspecific exclusion was found in experiments with flea larvae (Krasnov et al. 2005). Consequently, the nestedness-anti-nestedness continuum observed in the present study may be a consequence both of the ways in which the host acquires and loses parasite species as well as of ecological processes acting among parasite species. These two processes are not mutually exclusive.

As noted above, Poulin and Valtonen (2001) argued that the main reason for the nestedness-anti-nestedness continuum observed in endoparasites is via selective accumulation of parasite species rather than interactions among those parasite species. However, most helminth endoparasites are actively obtained by oral ingestion, whereas fleas generally are picked up passively from the local pool. This may be a major difference between the communities of helminth endoparasites, on the one hand, and those of arthropod ectoparasites and free-living organisms, on the other hand.

Our results demonstrate that host biology affects the organization of flea assemblages, in agreement with studies of other host-parasite systems (Guégan and Hugueny 1994, Poulin and Valtonen 2001, Timi and Poulin 2003, Calvete et al. 2004). In particular, host species that occupy larger geographic ranges are more likely to have a nested distribution of flea species among their populations (Guernier et al. 2004). This pattern can arise if a host has a particular assemblage of flea species in its area of origin, even though these flea species may not be necessarily host specific. When the host expands its geographic distribution, flea species can be gradually lost for a variety of reasons. For example, the burrow substrate and/or microclimate in a new region may not be suitable for the successful development of larvae of some flea species (Krasnov et al. 2001, 2002). As a result, a tendency toward nestedness would appear. The decrease in species richness of flea assemblages with decreasing host geographic range size reported for small mammals (Krasnov et al. 2004a) supports this possibility. In contrast, a tendency toward anti-nestedness could appear if a narrowly distributed host species had no specific flea fauna, and, in each locality, it is colonized by local flea species that normally parasitize other hosts. This is the case, for example, for the jird *Meriones tamariscinus* that lacks specific flea species and in each location is parasitized by fleas characteristic of other jirds, jerboas, or ground squirrels (Shwartz et al. 1958, Mikulin 1959b, Popova 1967). An alternative explanation could emphasize the average distance between host populations; as this increases, small differences in the

dispersal abilities of different flea species become more important, with consequent influences on the spatial structuring of the flea communities.

Other results suggesting the influences of host biology on the organization of flea assemblages are 1) the positive relationship between latitude of the host geographic range and the departure from random assembly and 2) the negative relationship between temperature across the host geographic range (as reflected by environmental factor 2) and the departure from randomness revealed in the comparative analysis using independent contrasts. Thus, nested flea assemblages are more prevalent in southern and warmer (i.e., in our data set, those inhabiting desert regions) compared to northern and cooler (i.e., in our data set, those inhabiting steppe and forest regions) host species. Perhaps this is due to the frequency of interspecific visits of each other's burrows in small mammals, which presumably is higher in steppe and forest regions (Kucheruk 1983) because of relatively higher small mammal density compared to those in the desert regions. This could increase host-switching and, therefore, lead to more scattered presences of flea species across the populations of a host species and, thus, to a lower likelihood of nestedness. However, Calvete et al. (2004) reported a positive relationship between nestedness probability and host density for the helminth communities of the red-legged partridge *Alectoris rufa*. As noted above, the apparent contradiction between our study and Calvete et al. (2004) might arise from differences in the way of a host to acquire the parasites with helminth endoparasites being actively obtained by oral ingestion and fleas being passively picked up. Consequently, flea habitat heterogeneity does not seem to play an important role in promoting nestedness as is the case for helminths (variation in dietary specialization and/or feeding rate of individual hosts; see Calvete et al. 2004 for details). On the other hand, the greater likelihood of the desert flea assemblages to be nested may stem from the fact that among flea assemblages in different populations of a desert host, flea extinction processes might prevail over flea colonization processes. The reasons for this could be the lack of sources for colonizing flea species (because of relatively low host density) and/or the extremely dry climate (because low relative humidity in burrows has a strong negative effect on the survival of pre-imaginal fleas, Krasnov et al. 2001). In conclusion, our results suggest that the structuring of flea assemblages within host species across host populations strongly depends on host biology, although this does not mean that ecological processes acting among flea species are not important.

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