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RESEARCH PAPER

Diversification of ectoparasite assemblages and climate: an example with fleas parasitic on small mammals

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ABSTRACT

Aim We studied the relationships between the numbers of species and numbers of higher taxa (genera, tribes, subfamilies and families) in flea assemblages of small mammalian hosts with the aims of: (a) comparing these relationships across different regions, and (b) testing the hypothesis that flea assemblages in warmer regions diversify mainly via intrahost speciation, whereas those in colder regions diversify mainly via host switching.

Location The study used previously published data on flea assemblages on small mammalian hosts from 25 different regions of the Holarctic.

Methods The number of flea genera, tribes, subfamilies or families in an assemblage (host species) was plotted against the number of flea species in this assemblage for each region separately, and a power function was fitted to the resulting relationships. Then, the values of the exponent of the power function for a region were regressed against the mean annual temperature in this region, across all regions.

Results The relationships between the number of flea species and the numbers of flea genera, tribes, subfamilies or families on a host species in each region were found to be well described by simple power functions. The exponent of the power function of the relationship between the number of flea species and the number of flea genera per host tended to decrease with increasing local mean annual temperature. When two apparent outliers from the trend (corresponding to regions where sampling was not performed as in other regions) were omitted from the analysis, the negative relationship between temperature and the exponent of the power function between the number of flea species and number of flea genera per host became highly significant. No relationship was found between the values of the exponents of the power functions between the number of flea species and the number of flea tribes, subfamilies or families per host, and the mean local annual temperature.

Main conclusions The results suggest that the diversification of flea assemblages is associated with climatic variables. In warm regions, the greater number of congeneric species per flea assemblage, reflected by the lower exponent of the power function, may well be the outcome of intrahost speciation. This indicates that, as regional temperature increases, intrahost speciation becomes a relatively more important mode of diversification than acquisition of fleas via host switching.

Keywords

Climate, diversification, fleas, host switching, intrahost speciation, small mammals.

INTRODUCTION

Explaining geographical patterns in the diversity of species and higher taxa represents one of the central themes in ecology. It is not surprising, thus, that these patterns have been and are extensively studied in numerous areas and for numerous taxa of organisms (e.g. Brown, 1995; Gaston, 2003). Patterns of diversity of parasite assemblages have attracted much attention not only

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because parasites form a large proportion of the diversity of life (Windsor, 1998; Poulin & Morand 2004), but also because of the important role of parasites in the regulation of populations and communities of their hosts (e.g. Poulin, 1998; Poulin & Morand, 2000, 2004). Numerous attempts to explain patterns of parasite diversity across biogeographical areas, as well as both within and among host species, have been published, yet very few general rules have emerged from these studies (see Rohde, 1999; Poulin & Morand, 2000, 2004 and references therein).

Geographic patterns of parasite diversity such as latitudinal gradients have been tentatively explained by numerous biotic and abiotic factors (see Rohde, 1999 for review). In particular, the available data on latitudinal gradients in parasite species diversity can be explained by the assumption that higher energy input (e.g. measured as local solar radiation or temperature) determines evolutionary rates, and that evolutionary rates and the time during which parasite communities have existed under relatively constant conditions generate the observed gradients (Rohde, 1992, 1999). Presumably, a greater input of solar energy leads to faster evolution via increased mutation rates, accelerated physiological processes and shortened generation time (Rohde, 1992). These explanations are based on studies of ectoparasites of marine fish; in contrast, the patterns of diversity of parasite assemblages of terrestrial hosts are much less known.

Diversification of parasite assemblages (increase in species diversity within a host lineage) over evolutionary time can result from a range of different evolutionary events (Poulin, 1998; Page, 2003). At one extreme of the continuum of possibilities, the parasite taxon can speciate on a host without an accompanying host speciation event and can, thus, produce multiple closely related parasite lineages on the host's descendants (duplication events; e.g. Clayton *et al.*, 1992; Simkova *et al.*, 2004). At the other extreme, a new parasite can be acquired via colonization from a different host lineage (host-switching event; e.g. Hoberg *et al.*, 1997). Mouillot & Poulin (2004) proposed that the relative importance of these two processes in shaping the diversification of parasite assemblages can be indicated by the value of the exponent of the power relationship between the number of higher taxa (e.g. genera) and species richness. In woody plant communities, Enquist *et al.* (2002) found that these exponents were statistically invariant across and within biogeographical regions, types of plant physiognomy, and geological time. The same is not true for assemblages of intestinal helminth parasites, where the value of the exponents varies according to the identity of the vertebrate host taxa (Mouillot & Poulin, 2004).

Mouillot & Poulin (2004) suggested that if the exponent of this function has a value close to one across several comparable parasite assemblages, this would indicate that host switching has been the main cause of diversification. Indeed, if each species in an assemblage is taxonomically independent of the other species, it must therefore have had a separate origin. In contrast, an exponent clearly inferior to one indicates that several species belong to the same genus or genera, suggesting that they have a common ancestor and that they may have radiated from this common ancestor within a host lineage. In other words, if the number of host switches in the past is approximately equal to the current number of species (the exponent close to one), diversification of parasite assemblages stems mainly from host switching. If, however, there are currently much more species than there were host switches (the exponent much less than one), the diversification of parasite assemblages is likely the result of intrahost parasite speciation. Combining this idea with the ideas of Rohde (1992, 1999), we might expect that in the relatively colder regions, the main way for an assemblage to diversify is via host switching; this process does not require speciation, and should lead to roughly only one species per genus on any given host species. In contrast, the number of species per genus can be expected to increase in the relatively warmer regions, where warmer temperatures can increase evolutionary rates and favour speciation (Rohde, 1992).

Here, we studied the relationships between numbers of species and numbers of higher taxa (genera, tribes, subfamilies and families) in flea assemblages of small mammalian hosts in 25 Holarctic regions. Fleas (Siphonaptera) are characteristic mammalian ectoparasites and are most diverse on small and medium-sized species (only about 6% of about 2000 species are parasites of birds). 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, preimaginal development is entirely off-host. The larvae are usually not parasitic and feed on organic debris in the burrow and/or nest of the host.

The aims of this study were: (a) to test for the power relationship between numbers of flea species and numbers of higher taxa; (b) to compare these relationships across different regions; and (c) to test the hypothesis that flea assemblages in warmer regions diversify mainly via intrahost speciation, whereas those in colder regions diversify mainly via host switching. As a result, we expect a negative relationship between local mean annual temperature and the value of the exponent of the power function between number of species and number of higher taxa per host species. Although mean annual temperature is a crude environmental parameter that can mask a large number of biologically important factors, climate data on a finer scale are unavailable for most regions. Also, for many ecological and evolutionary processes, large-scale climate indices are often better predictors of local phenomena than fine-scale weather measures (Hallett *et al.*, 2004).

MATERIALS AND METHODS

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Insectivora, Lagomorpha and Rodentia) in 25 different regions of the Holarctic (Table 1). These sources provided data on the number of individuals of a particular flea species found on a number of individuals of a particular host species. We cross checked the flea species lists with the catalogue of Lewis & Lewis (1990) to resolve cases of synonymy. Single findings of a flea species on a host species or in a region were considered accidental and were not included in the analyses. Only host species for which at least 10 individuals have been examined per region were included, because estimates of flea diversity could be inaccurate for smaller samples. In total, we

Table 1 Data on small mammals and fleas from the 25 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)

Region	Number of host species	Number of flea species	Source
Adzharia, southern Caucasus	12 (8391)	20 (1756)	Alania *et al.*, 1964
Akmolinsk region, northern Kazakhstan	8 (264)	19 (1789)	Mikulin, 1959a
Altai mountains	19 (1473)	9 (1949)	Sapegina *et al.*, 1981
California	8 (1543)	17 (2254)	Davis *et al.*, 2002
Central Yakutia	6 (535)	17 (770)	Elshanskaya & Popov, 1972
Dzhungarskyi Alatau, Kazakhstan	15 (5230)	22 (5224)	Burdelova, 1996
East Balkhash desert, Kazakhstan	11 (473)	35 (7272)	Mikulin, 1959b
Idaho	12 (3898)	28 (10,709)	Allred, 1968
Kabarda, northern Caucasus	9 (1642)	21 (1755)	Syrvacheva, 1964
Khabarovsk region, southern Russian Far East	8 (6607)	21 (5226)	Koshkin, 1966
Kustanai region, north-western Kazakhstan	8 (159)	14 (375)	Reshetnikova, 1959
Moyynkum desert, Kazakhstan	12 (45,433)	31 (260,720)	Popova, 1967
Mongolia	5 (1741)	20 (18,593)	Vasiliev, 1966
Negev Desert	13 (1230)	11 (4882)	Krasnov *et al.*, 1997 and unpublished data
North Asian Far East	14 (1667)	16 (1405)	Yudin *et al.*, 1976
North Kyrgyzstan	13 (4996)	34 (8840)	Shwartz *et al.*, 1958
North New Mexico	20 (8706)	31 (23,693)	Morlan, 1955
Novosibirsk region, southern Siberia	20 (1912)	28 (4311)	Violovich, 1969
Pavlodar region, eastern Kazakhstan	7 (78)	11 (317)	Sineltschikov, 1956
Selenga region, central Siberia	7 (978)	11 (990)	Pauller *et al.*, 1966
Slovakia	13 (9932)	22 (10,861)	Stanko *et al.*, 2002
Tarbagatai region, eastern Kazakhstan	12 (316)	30 (1525)	Mikulin, 1958
Turkmenistan	14 (235,968)	37 (908,815)	Zagniborodova, 1960
Tuva	13 (3145)	28 (28,758)	Letov *et al.*, 1966
Volga–Kama region	20 (33,380)	31 (33,770)	Nazarova, 1981

used data on 298 mammal samples, representing 367,967 individuals of 137 species, from which 1,297,525 individual fleas of 254 species were recovered.

We counted the number of flea species, genera, tribes, subfamilies and families for each host species in each region. The taxonomical structure of Siphonaptera was based on Hopkins and Rothschild (1953, 1956, 1962, 1966, 1971), Traub *et al.* (1983) and Medvedev (1995, 1998). We plotted the number of flea genera, tribes, subfamilies or families in an assemblage (host species) against the number of flea species in this assemblage for all host species for the whole data set and for each region separately, and fitted a power function ($y = b_0 * x^{b_1}$) to the resulting relationships. We did not treat each host–region combination as an independent data point, because some host species occurred in more than one region. Consequently, for the analysis of the whole data set, the data for these hosts were averaged across regions. A preliminary analysis in which each host–region combination was treated as an independent data point instead provided similar results.

The values of the exponents of the power functions for the whole data set and for each region were considered as parameters that describe the relative importance of the two processes that lead to the diversification of flea assemblages. First, within-host speciation would result in congeneric species of fleas occurring on the same host species, and thus a relatively low exponent value. Second, rampant host switching by fleas would create assemblages of taxonomically independent species, and thus a relatively high exponent value. To test the hypothesis that the rate of parasite diversification via within-host speciation is higher in warmer regions, we regressed the values of the exponent of the power function for a region against mean annual temperature in this region, across all 25 regions. Mean annual temperature was calculated using 30′ grid data, and then averaged across all grids within a region (Kineman *et al.*, 2000).

RESULTS

Across the entire data set, the relationships between the number of flea species and the numbers of flea genera, tribes, subfamilies or families on a host species were found to be described by simple power functions ($b_1 = 0.84$, $r^2 = 0.96$, $F_{1,135} = 1666.5$ for species–genera relationship; $b_1 = 0.72$, $r^2 = 0.89$, $F_{1,135} = 1054.8$ for species–tribes relationships; $b_1 = 0.69$, $r^2 = 0.88$, $F_{1,135} = 956.6$ for species–subfamilies relationship; $b_1 = 0.46$, $r^2 = 0.72$, $F_{1,135} = 354.4$ for species–families relationships; $P < 0.001$ for all; Fig. 1). The same was true also for each separate region (Table 2). An illustrative example for the Volga–Kama region is shown in Fig. 2.

The relationship between the number of flea species and the number of flea genera per host was stronger (i.e. the exponent

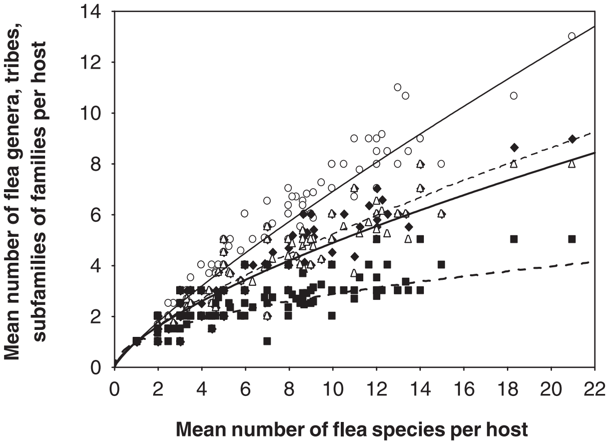

Figure 1 Relationship between the number of flea species and flea genera (circles, normal line), flea tribes (diamonds, dashed line), flea subfamilies (triangles, bold line) and flea families (squares, bold dashed line) per host across 137 small mammalian host species in 25 Holarctic regions.

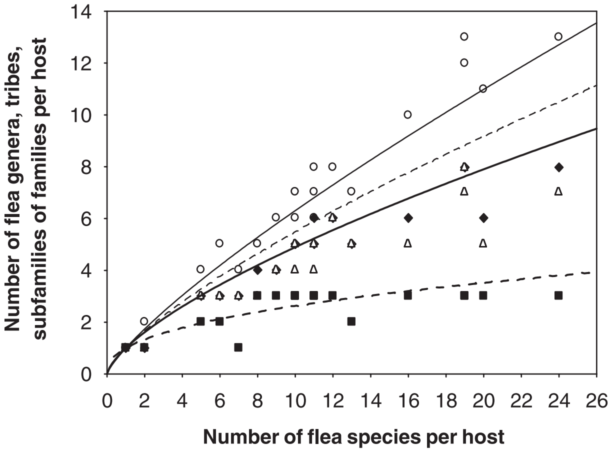

Figure 2 Relationship between the number of flea species and flea genera (circles, normal line), flea tribes (diamonds, dashed line), flea subfamilies (triangles, bold line) and flea families (squares, bold dashed line) per host across 20 small mammalian host species in the Volga–Kama region.

Table 2 Summary of the regressions fitting a power function ($y = b_0 * x^{b_1}$) to the relationship between the number of flea species and the number of flea genera, tribes, subfamilies and families on a mammalian host species in 25 Holarctic regions. All b_0 are not significant ($P > 0.2$). All regressions and b_1 coefficients are significant ($P < 0.05$). *Flea assemblages of each host species in the Akmolinsk region represented all flea families inhabiting this region

		Genera			Tribes			Subfamilies			Families		
Region	d.f.	b_1	r^2	F	b_1	r^2	F	b_1	r^2	F	b_1	r^2	F
Adzharia	1,10	0.78	0.91	107.0	0.68	0.86	60.99	0.63	0.81	53.25	0.47	0.7	23.7
Akmolinsk*	1,6	0.88	0.95	118.8	0.66	0.88	42.7	0.55	0.71	14.9	—	—	—
Altai	1,17	0.93	0.98	743.5	0.77	0.92	185.9	0.77	0.82	185.9	0.66	0.69	37.9
California	1,6	0.94	0.99	338.7	0.70	0.97	432.3	0.68	0.98	344.1	0.44	0.89	44.5
Yakutia	1,4	0.77	0.97	136.9	0.59	0.90	37.6	0.59	0.90	37.6	0.56	0.72	10.6
Dzhung. Alatau	1,13	0.87	0.97	409.6	0.72	0.91	134.3	0.72	0.91	134.3	0.45	0.71	32.2
East Balkhash	1,9	0.74	0.79	33.9	0.94	0.78	32.1	0.94	0.84	45.2	0.65	0.61	14.1
Idaho	1,10	0.82	0.88	75.9	0.62	0.85	59.7	0.62	0.85	59.7	0.39	0.81	43.8
Kabarda	1,7	0.79	0.79	26.0	0.64	0.83	35.3	0.5	0.76	21.7	0.25	0.72	18.2
Khabarovsk	1,6	0.88	0.99	660.5	0.83	0.92	69.0	0.77	0.93	75.6	0.31	0.61	9.4
Kustanai	1,6	0.85	0.94	101.5	0.97	0.91	61.0	0.93	0.85	36.9	0.43	0.73	16.5
Moyynkum	1,3	0.87	0.96	77.3	0.66	0.99	273.3	0.66	0.99	273.3	0.42	0.89	16.3
Mongolia	1,10	0.78	0.96	251.3	0.68	0.94	164.5	0.65	0.93	141.3	0.54	0.76	32.1
Negev	1,11	0.8	0.94	175.7	0.77	0.94	164.6	0.77	0.94	164.6	0.72	0.92	144.5
Asian Far East	1,18	0.81	0.86	114.1	0.68	0.83	86.1	0.68	0.83	86.1	0.43	0.61	28.6
Kyrgyzstan	1,12	0.86	0.96	279.7	0.78	0.9	106.4	0.75	0.9	113	0.54	0.9	105.6
New Mexico	1,11	0.83	0.98	590.5	0.81	0.88	81.7	0.76	0.88	84.5	0.39	0.57	14.7
Novosibirsk	1,17	0.91	0.91	171.0	0.86	0.75	52.1	0.77	0.72	44.6	0.30	0.39	10.9
Pavlodar	1,5	0.95	0.98	243.1	0.75	0.85	29.0	0.75	0.85	29.0	0.66	0.94	85.5
Selenga	1,5	0.91	0.98	54.7	0.76	0.88	39.5	0.81	0.82	23.2	0.63	0.83	25.6
Slovakia	1,11	0.78	0.83	55.9	0.63	0.82	50.2	0.58	0.81	47.8	0.39	0.57	14.7
Tarbagatai	1,10	0.86	0.96	259.8	0.79	0.96	232.6	0.74	0.94	157	0.43	0.81	43.6
Turkmenistan	1,12	0.93	0.98	767.7	0.76	0.98	388.1	0.67	0.93	160.5	0.48	0.89	98.9
Tuva	1,11	0.89	0.97	397.9	0.74	0.81	48.5	0.7	0.8	43.5	0.36	0.56	13.8
Volga–Kama	1,18	0.8	0.97	615.2	0.74	0.94	299.7	0.69	0.91	195.2	0.42	0.64	31.6

was higher) than that between the number of flea species and the number of flea tribes, subfamilies or families for both the whole data set and each region separately [0.74–0.95 (0.85 ± 0.01 on average) vs. 0.59–0.97 (0.74 ± 0.18 on average), $t = 6.41$; 0.50–0.94 (0.70 ± 0.02 on average), $t = 5.92$; 0.25–0.72 (0.47 ± 0.02 on average), $t = 13.41$, respectively, paired *t*-test, $P < 0.001$ for all]. In turn, for both the whole data set and each region separately, the relationship between the number of flea species and the number of flea tribes per host was stronger than that between the number of flea species and the numbers of flea subfamilies ($t = 4.01, P < 0.001$) or families ($t = 9.18, P < 0.001$), whereas the relationship between the number of flea species and the number of flea subfamilies per host was stronger than that between the number of flea species and the number of flea families ($t = 9.51$, $P < 0.001$).

The exponents of species–genera relationships for flea assemblages were, in general, lower that those found by Enquist *et al.* (2002) for plant communities (0.94) and those found by Mouillot & Poulin (2004) for the communities of helminth parasites in fish and bird hosts (0.97 and 0.92, respectively). Indeed, the exponents found here attained values greater than 0.92 in only 4 of the 25 regions, and were lower than 0.88 in as many as 16 of the 25 regions. In addition, in 15 of 25 regions these exponents were somewhat higher than those reported by Mouillot & Poulin (2004) for helminth parasites of mammals (0.83), although the value of the exponent of the number of species vs. number of genera relationship for the whole data set was close to that found by Mouillot & Poulin (2004). Moreover, the exponents of the number of species–number of families relationship in most regions as well as that for the whole data set were apparently lower than those found by Enquist *et al.* (2002) for plant communities [0.56–0.84, 0.683 on average; Supplementary material for Enquist *et al.* (2002)]. However, in seven of 25 regions these exponents were only slightly lower, equal to, or slightly higher than those reported for plants from different regions (Table 2).

The exponent of the power function of the relationship between the number of flea species and the number of flea genera per host in a region tended to decrease with an increase in the mean annual temperature of the region (Fig. 3). This trend was on the verge of significance ($r^2 = 0.15$, $F_{1,23} = 4.05$, $P = 0.056$). The two apparent outliers from the negative trend represent the central Yakutia region (lower than expected value of the exponent; point in lower left corner of the plot) and Turkmenistan (higher than expected value of the exponent; point in upper right corner of the plot). The data for these two regions differ from the data for other regions as follows. The data set for the central Yakutia was compiled from a census of mammals and their fleas conducted in an extremely limited territory (about 2.5 km of the valley of the Kenkeme river; Elshanskaya & Popov, 1972). In contrast, the data for Turkmenistan were collected over 10 years across a vast territory and a wide variety of habitat types (Zagniborodova, 1960 and unpublished data). It is therefore likely that parasite diversity of mammals from Yakutia was underestimated, whereas that of mammals of Turkmenistan was overestimated (i.e. by pooling flea assemblages, from different habitats, that do not normally co-occur). In contrast, in all other regions, a large homogeneous habitat was sampled. When these two outliers were omitted from the analysis, the negative relationship between temperature and the value of the exponent of the power function between the number of flea species and the number of flea genera per host in a region became highly significant ($r^2 = 0.41$, $F_{1,21} = 14.5$, $P < 0.001$). In contrast, no relationship was found between the values of the exponents of the power functions between the number of flea species and the number of flea tribes, subfamilies or families per host in a region, and the mean annual temperature in this region ($r^2 = 0.01$, $F_{1,23} = 0.19$; $r^2 = 0.0004$, $F_{1,23} = 0.01$; and $r^2 = 0.01$, $F_{1,23} = 0.25$, respectively, $P > 0.62$ for all; Fig. 4).

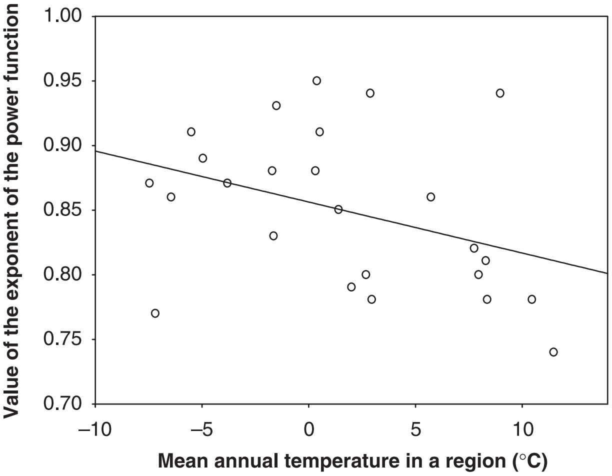

Figure 3 Relationship between mean annual temperature in the region and the value of the exponent of the power function between the number of flea species and the number of flea genera per host species, across 25 Holarctic regions.

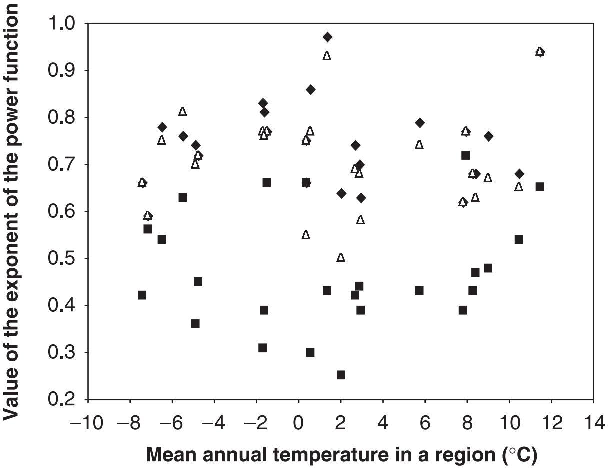

Figure 4 Relationship between mean annual temperature in the region and the value of the exponent of the power function between the number of flea species and the number of either tribes (diamonds), subfamilies (triangles) or families (squares) per host species, across 25 Holarctic regions.

DISCUSSION

The results of this study demonstrate that multiple congeneric species of fleas parasitic on the same host species are characteristic of some mammal faunas but not of others. The within-host presence of multiple congeneric fleas occurred mainly in warmer regions as suggested by the negative relationship between the mean annual temperature and the value of the exponent of the power function between the number of flea species and the number of flea genera per host. Although our findings are based on correlations and may not reflect a causal relationship, they support the hypothesis of Rohde (1992, 1999) that a higher energy input in warmer regions promotes higher rate of evolution, and thus of local speciation. The increase of evolutionary rate under higher energy input may be the outcome of an increase in the mutation rate, the acceleration of physiological processes and shortened generation time. Indeed, the shortening of the generation time at higher temperature has been reported for a number of flea species (e.g. Krasnov *et al.*, 2001), whereas metabolic rate (measured as an emission of CO_2) in fleas increases with increasing temperature (Fielden *et al.*, 2004).

Mutations, speed of physiological processes and generation time do not determine the rate of speciation on their own but together with other mechanisms that result in genetic isolation. However, it is likely that species that have higher mutation rates, faster physiological processes and shorter generation times encounter conditions where genetic isolation can occur more frequently than species with lower mutation rate, slower physiological processes and shorter generation time, all else being equal (Rohde, 1999). An increase in the speciation rate of parasites at higher temperatures is likely not accompanied by a simultaneous increase in the speciation rate of their mammalian hosts. The main reason for this is that host speciation cannot keep up with parasite speciation because of the difference in their generation times, which are much shorter for parasites. Also, in the case of mammalian hosts, homeothermy negates many of the effects of external temperature on internal processes, including mutation rates.

This hypothesis can explain, at least partly, why the flea assemblages in warmer rather than in colder regions diversified more via intrahost speciation as indicated by the value of the exponent of the power function. It cannot explain, however, why flea assemblages in the colder regions diversified mainly by host switching, especially given that the dispersal abilities of parasite species are restricted at lower temperatures (Rohde, 1985, 1992, 1999). Nevertheless, flea transfers from host to host (both intra- and interspecific) occur mainly when hosts visit each other's burrows (e.g. Hartwell *et al.*, 1958; Ryckman, 1971) or via body contact between host individuals (e.g. Rödl, 1979; Krasnov & Khokhlova, 2001). Rodent burrows in temperate and colder regions are deeper, more complicated and more frequently visited by individuals of other species than those in warmer regions (Kucheruk, 1983). These processes can facilitate host switching by fleas, independently of temperature effects on the mobility of fleas themselves. This provides an alternative hypothesis to our suggestion of temperature-mediated speciation rates. In addition, in our analysis, colder regions are those from the northern hemisphere. Rodent faunas of these regions are relatively poor not only in terms of species richness but also in taxonomic diversity, and are dominated by the *Clethrionomys*, *Microtus* and *Sorex* genera. Each of these genera is represented in local faunas by several closely related species. This can facilitate parasite switching among closely related host species. Finally, it is also possible that some characteristics of the behaviour, physiology or ecology of mammals in colder climates limit the opportunities for intrahost speciation by fleas, independently of the direct effect of temperature on flea evolutionary rates. There are, however, no obvious host traits that might play such a role.

The lack of any relationship between the values of the exponents of the power functions between the number of flea species and the number of flea tribes, subfamilies or families per host in a region suggests that, although intrahost speciation produces multiple congeneric species, the deeper intrahost splits (at the level of tribes, subfamilies or families) are unlikely. Within a given host species, we can only expect intraspecific divergence eventually leading to two congeneric parasite species; the origin of new high-level taxa like tribes, subfamilies or families most probably involves switching to new higher host taxa or new geographical regions. For example, the origin of the family Ischnopsyllidae is related to the switch from rodents to chiropterans (Medvedev, 1996, 1998). Numerous examples of the effect of the dispersal into new geographical regions on the evolution of fleas at the family, subfamily and tribal level are presented by Traub (1980).

Generally, the value of the exponents of species–genera relationships for the whole data set on flea assemblages found in this study was similar to that reported for mammalian endoparasites but lower than those reported for fish and bird endoparasites (Mouillot & Poulin, 2004). This hints at similar mechanisms influencing the rate of intrahost speciation of ecto- and endoparasites in mammals, and these mechanisms can be related to some, still unknown, host features. On the one hand, these findings suggest that there are some general rules governing the diversification and taxonomic partitioning of parasite communities within the same higher taxon of hosts exactly as there are some general rules that govern the diversification and taxonomic partitioning of communities of free-living organisms (Enquist *et al.*, 2002). On the other hand, the lack of invariance of the exponent value of the power function across regions found in this study, in contrast to that found for plant communities (Enquist *et al.*, 2002), suggests that local conditions might strongly affect fundamental processes and mechanisms of diversification. These can be, for example, climate (as suggested by the negative relationship between the annual temperature and the exponent of the power function linking species and genera) and environmental heterogeneity (as suggested by the highly environmentally diverse Turkmenistan region not conforming with the general trend).

Finally, the sharp difference between the values of the exponent of the power function of the relationship between species number and familial number found in this study and those found for plant communities (Enquist *et al.*, 2002) points to fundamental differences in the pattern and mode of diversification between parasite communities and communities of free-living organisms. This difference could be due to the extremely complicated nature of the environment of parasites that includes the host *per se*, the environment of the host, and the intricate relationships between the host and its environment.

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