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RESEARCH PAPER

Geographical variation in the 'bottom-up' control of diversity: fleas and their small mammalian hosts

Boris R. Krasnov[1]*, Georgy I. Shenbrot[1], Irina S. Khokhlova[2] and Robert Poulin[3]

[1]*Ramon Science Center and Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 84990 Midreshet Ben-Gurion, Israel,* [2]*Desert Animal Adaptations and Husbandry, Wyler Department of Dryland Agriculture, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 84990 Midreshet Ben-Gurion, Israel and* [3]*Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand, E-mail: krasnov@bgu.ac.il; khokh@bgu.ac.il; robert.poulin@stonebow.otago.ac.nz*

ABSTRACT

Aim We searched for signs of the 'bottom-up' diversity effect in the association between fleas (Siphonaptera) and their small mammalian hosts (Rodentia, Insectivora and Lagomorpha). We asked (1) whether a strong dependence of flea species richness on host species richness is characteristic for both Palaeoarctic and Nearctic realms; (2) if yes, whether the ratio of host species per flea species along the host diversity gradient is similar between the Palaeoarctic and Nearctic; and (3) whether factors other than host species richness (i.e. geographical position, climate and landscape) might better explain variation in flea species richness than host species richness.

Location The study used previously published data on species richness of fleas and their small mammalian hosts from 26 Palaeoarctic and 19 Nearctic regions.

Methods We regressed the number of flea species on the number of small mammal species across regions, separately for Palaeoarctic and Nearctic realms, using both non-transformed data as well as data corrected for the confounding effects of host sampling effort and sampling area. To test whether flea species richness is determined by external factors unrelated to the host, we used stepwise multiple regressions of flea species richness against host species richness and parameters describing the geographical position, climate and relief of a region.

Results When non-transformed data were analysed, flea species richness was positively correlated with host species richness in both the Palaeoarctic and Nearctic, although the slopes of the two regressions differed significantly. After removal of the confounding effects of host sampling effort and sampling area, Palaeoarctic flea species richness remained strongly positively correlated with host species richness, whereas in the Nearctic, flea species richness appeared to be completely independent of host species richness. Results of the multiple regressions using corrected data demonstrated that in the Palaeoarctic, flea species richness was correlated with both the number of host species and the mean altitude of the region, whereas in the Nearctic, flea species richness only tended to be weakly correlated with latitude (however, this correlation turned out to be non-significant after Bonferroni correction).

Main conclusions We found evidence of bottom-up control of flea diversity in the Palaeoarctic regions only, and not in the Nearctic. We explore several potential explanations for the different patterns observed in the two biogeographical realms, including differences in (1) levels of host specialization, (2) history of host–parasite associations and (3) landscape effects on flea diversification. We conclude that these factors combine to create different macroecological patterns in different biogeographical realms, and that diversity is not governed by the same forces everywhere.

Keywords

Bottom-up control, ectoparasites, fleas, host diversity, small mammals, species richness.

*Correspondence: Boris R. Krasnov, Ramon Science Center and Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 84990 Midreshet Ben-Gurion, Israel.
E-mail: krasnov@bgumail.bgu.ac.il

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INTRODUCTION

The community structure of organisms is affected by a variety of biotic and abiotic factors. One of the most important forces that affects the structure of a community is the relationship between this community and communities of higher and/or lower trophic levels. In other words, a strong link between the diversity of consumers and the diversity of resources is characteristic of any natural food web (Polis & Strong, 1996). Indeed, 'top-down' effects, occurring when the diversity of communities at a higher trophic level affects the diversity of communities at a lower trophic level, have been demonstrated (e.g. Jakobsen *et al.*, 2004). On the other hand, 'bottom-up' effects, which occur when the diversity at lower trophic levels controls the diversity at higher trophic levels, also exist (e.g. Siemann, 1998; Brändle *et al.*, 2001). Furthermore, top-down and bottom-up forces can act on communities simultaneously (Hunter & Price, 1992).

Manifestation of top-down and bottom-up effects varies among communities. In many cases, no or only a weak indication of either top-down or bottom-up effects is found (e.g. Branson, 2005; Royo & Carson, 2005). The reasons for this variability in the relative strength of top-down and bottom-up effects include a variety of factors, such as heterogeneity within a trophic level (Hunter & Price, 1992; Jiang & Morin, 2005) and length of the food chain (Duffy *et al.*, 2005). In addition, the manifestation of top-down or bottom-up effects can vary among similar communities from different locations (Fleming, 2005; Pennings & Silliman, 2005). For example, the diversity of tropical nectarivorous birds and bats has been shown to be determined by the diversity of their food plants in the New World but not in the Old World (Fleming, 2005).

Patterns in diversity within a food web have been studied mainly among free-living organisms. However, in the last decade, the number of studies that include parasitic organisms as an integral part of food webs has increased (e.g. Siemann, 1998; Rodriguez & Hawkins, 2000; Thompson *et al.*, 2005; Vazquez *et al.*, 2005). Indeed, parasites have numerous advantages as models for investigating patterns and processes in animal communities. These advantages include the relative ease of obtaining replicated samples and the fact that parasites of the same taxon share a trophic level. In addition, parasites are at the top of a food web and, thus, can principally be used for investigation of both top-down (i.e. effects of parasites on their hosts) and bottom-up (i.e. effects of hosts on their parasites) diversity effects. However, parasites rarely drive their host to extinction, and they rarely serve as prey. Therefore, patterns of parasite diversity are most often considered from the point of view of bottom-up forces (e.g. Watters, 1992).

The traditional dichotomy between top-down and bottom-up control may not apply to parasites because of a lack of predators potentially controlling parasite diversity. However, the absence of top-down control does not mean that bottom-up forces automatically apply. Still, studies on parasites have suggested the occurrence of strong bottom-up effects. For example, a strong positive correlation between parasite and host species richness has been shown for unionid mussels and fish (Watters, 1992), trematodes and shorebirds (Hechinger & Lafferty, 2005), and for fleas and their small mammalian hosts (Krasnov *et al.*, 2004a). An ecological reason for this pattern could be the enhancement of consumer diversity by resource diversity (a higher diversity of resources may allow a larger number of consumer species to coexist; Pimm, 1979). Alternatively, an evolutionary reason for the pattern could be the diversification of parasites as a response to diversification of hosts, similar to a process of specialization of free-living species to a range of habitat properties (Rosenzweig, 1992). However, studies that related parasite and host diversity either considered data from a single region or pooled several different regions together. In the latter case, the pooling could mask the true region-specific relationship between parasite and host diversity, which can vary due to differences in the history of the relationships between the various communities (Fleming *et al.*, 1987) or differences in abiotic conditions (Pennings & Silliman, 2005). The history of the relationships may, in turn, be affected by region-specific evolution driven by local climate and/or landscape.

In this study, we searched for signs of the bottom-up diversity effect in the association between fleas (Siphonaptera) and their small mammalian hosts (Rodentia, Insectivora and Lagomorpha). Fleas are obligatory haematophagous parasites of higher vertebrates. They are most diverse on small burrowing mammal species. Fleas usually alternate between periods when they occur on the body of their host and periods when they occur in its burrow or nest. In nearly all cases, pre-imaginal flea development is entirely off-host. As a result, fleas must be strongly influenced by the characteristics of their off-host environment (Krasnov *et al.*, 1997). Consequently, the species diversity of fleas should covary with some parameters related to the host environment, such as climate (Krasnov *et al.*, 2005). We tested the dependence of flea species richness on small mammal species richness across different regions of the Palaeoarctic and Nearctic. The data were separated into Nearctic and Palaeoarctic subsets (1) because we asked whether the relationship between flea and host species richness varies geographically and (2) as a way of achieving independent tests of the hypothesis by using two distinct land masses with distinct faunas. Additionally, we also took into account external physical factors as potential determinants of flea diversity. Specifically, we asked (1) whether a strong dependence of flea species richness on host species richness is characteristic for both regions; (2) if yes, whether the ratio of host species per flea species along the host diversity gradient is similar between the Palaeoarctic and Nearctic; and (3) whether factors other than host species richness (i.e. geographical location, climate and landscape) might better explain variation in flea species richness than host species richness.

It should be noted, however, that the existence, strength and importance of bottom-up effects can be explicitly established only in experimental rather than in observational studies. However, it is extremely difficult to manipulate parasite diversity within a community context. Consequently, a study based on field data and involving parasites as a specific trophic level can suggest the occurrence of bottom-up control of diversity by observing a dependence of parasite diversity on host diversity, although it cannot prove this unambiguously.

MATERIALS AND METHODS

Data were obtained from 45 published studies (26 from the Palaeoarctic and 19 from the Nearctic) that reported the number of flea species found on the number of small mammal species in a particular region (see Appendix S1 in Supplementary Material). The compilation of the data set was based on a thorough search of the primary literature, whether published in English or not, going back to the middle of the 20th century and thus beyond the range covered by most bibliographic data bases. We used only sources where (1) sampling effort (the number of hosts examined) was reported and (2) the sampling area could be calculated.

Initially, to test for the effect of host species richness on parasite species richness and to determine the average number of host species necessary for the maintenance of a flea species, we regressed the nontransformed number of flea species on the non-transformed number of small mammal species across regions, separately for Palaeoarctic and Nearctic realms. However, comparison of species richness among regions of different sizes and among studies with unequal sampling effort requires the removal of these confounding effects (Rosenzweig, 1995; Morand & Poulin, 1998). To remove the effect of the area of a region and that of sampling effort, we regressed the number of host species found and the number of flea species recorded against both the area sampled and the number of hosts examined, in logarithmic space. Both small mammal and flea species richness were affected by area and sampling effort ($r^2 = 0.37$, $F = 12.2$ and $r^2 = 0.30$, $F = 9.2$, respectively, $P < 0.001$ for both). Original values of host and flea species richness were then substituted by their residual deviations from the multiple regressions. The effect of host species richness on parasite species richness was tested using both simple linear and robust (via M-estimation) regressions of the corrected values of flea species richness against corrected values of small mammal species richness, separately for Palaeoarctic and Nearctic realms. An ANCOVA was used to compare the intercepts and slopes between Palaeoarctic and Nearctic regressions for both non-transformed and corrected data. Prior to each regression analysis, the assumption of homoscedasticity of error variance in flea species richness (both transformed and untransformed) was assessed by visual examination of a plot of the standardized residuals against the standardized predicted values from the regression. In all cases the residuals were randomly scattered around 0 and showed a relatively even distribution.

To test whether flea species richness is determined by external factors unrelated to the host, we calculated for each region parameters that describe (1) its geographical position (latitude of the centre of a region), (2) its climate (mean annual precipitation, mean surface air temperature for January and mean surface air temperature for July across a region) and (3) its relief (mean and standard deviation of the elevation across a region). These variables were calculated across the sampling area in each region using 30′ grid data from the Global Ecosystems Database (Kineman *et al*., 2000). This data base provides high-quality world-wide metadata on a variety of parameters including those of climate and relief. Coordinates of the sampling area in each region were obtained either directly or from the information in the original sources. Then, we used stepwise mixed model multiple regressions to test whether these factors explain variation in flea species richness better than host species richness. The critical value of P to be used to control entry and removal of variables from the model was established at 0.05. The ranges of environmental parameters were very similar for Palaeoarctic and Nearctic regions (Table 1).

Table 1 Ranges of geographical position, climate and relief parameters of Palaeoarctic and Nearctic data sets

Parameter	Palaeoarctic data sets	Nearctic data sets
Latitude (°)	32.7–69.4	28.6–65.6
Mean annual temperature (°)	−9.3–18.0	−4.2–21.7
Mean January temperature (°)	−28.5–10.3	−23.6–15.3
Mean July temperature (°)	10.8–26.5	14.8–28.9
Mean annual precipitation (mm)	285.8–1639.5	221.0–1478.5
Mean elevation (m a.s.l.)	53.5–2453.2	3.0–2083.0

In addition, treating species richness values of different regions as independent observations can introduce a bias in the analysis because these regions have different biogeographical histories, and the degree of faunal similarity can also differ between different regions in the data base. To control for the effects of historical biogeographical relationships, we repeated the analyses using the method of independent contrasts (Felsenstein, 1985) after constructing a region cladogram based on the information on presence/absence of host species and host phylogeny (see details in Krasnov *et al*., 2004a). A region cladogram was constructed using Brooks parsimony analysis (BPA; Brooks, 1985, 1990; Wiley, 1988a,b). It consists of a Wagner parsimony analysis using presence/absence of species and their hypothetical ancestors, which are coded and analysed as characters (Morrone & Crisci, 1995). This analysis uses an area-by-taxon matrix, produced by binary coding of the terminal taxa and their hypothetical ancestors. We used a working phylogeny of mammals derived from various sources (see Krasnov *et al*., 2004a for details). The region cladogram was constructed based on hosts rather than on fleas because the parasites are undoubtedly dependent on hosts rather than vice versa.

To compute independent contrasts, we used the PDAP:PDTREE program (Garland *et al*., 1993; Midford *et al*., 2005) implemented in the Mesquite Modular System for Evolutionary Analysis (Maddison & Maddison, 2005). The procedures followed Garland *et al*. (1992). These analyses provided the same results as the analyses described above, and therefore their results are not reported here.

Commonly, ecological covariates alone may be sufficient to explain spatial autocorrelation in species distributions. Thus, autocorrelation in the raw response data is not a concern, but autocorrelation in the residual variation of a model that includes environmental variables is (Betts *et al*., 2006). We used Moran's index to test for autocorrelation in residuals of two multiple regression model sets. The calculations of Moran's index were conducted using spatial statistics tools of ArcView 9.1. The value of this index for the Palaeoarctic data set was 0.069 (z-score = 0.405) and for the Nearctic data set it was 0.090 (z-score = 0.80), thus demonstrating the absence of spatial autocorrelation in the data.

We avoided an inflated Type I error possibly associated with multiple tests by performing Bonferroni adjustments of alpha levels.

RESULTS

The mean number of hosts per region did not differ significantly between realms (16.0 ± 1.0 in the Palaeoarctic and 13.9 ± 1.5 in the Nearctic; $t = 0.51$, $P = 0.6$ for transformed data corrected for sampling effort and sampling area). In contrast, the number of flea species per region was higher in the Palaeoarctic than in the Nearctic (22.3 ± 1.8 vs. 14.3 ± 2.1, respectively; $t = 2.9$, $P < 0.001$ for transformed data corrected for sampling effort and sampling area).

When non-transformed data were analysed, flea species richness was positively correlated with host species richness in both regions ($r^2 = 0.44$, $F_{1,24} = 19.1$ for Palaeoarctic and $r^2 = 0.38$, $F_{1,15} = 9.1$ for Nearctic, $P < 0.01$ for both; Fig. 1). Relationships between these two parameters were described by the following equations: FSR = 1.16HSR and FSR = 0.85HSR, where FSR is flea species richness and HSR is host species richness. Intercepts of both regressions did not differ significantly from zero (4.84 ± 4.44, $P = 0.39$ and 2.45 ± 4.32, $P = 0.57$), whereas the ANCOVA indicated that slopes of the two regressions differed significantly ($F_{1,40} = 7.0$, $P < 0.01$). In addition, when a data set from New Mexico (upper right point in Fig. 1b) was omitted from the analysis, the relationship between flea and host species richness for the Nearctic became nonsignificant ($r^2 = 0.16$, $F_{1,15} = 2.8$, $P = 0.11$).

After removal of the confounding effects of host sampling effort and sampling area, Palaeoarctic flea species richness remained strongly positively correlated with host species richness ($r^2 = 0.38$, $F_{1,24} = 14.9$ for regular linear regression and proportion of variation in response explained by the model for robust regression = 0.37; $P < 0.001$ for both; Fig. 2a). On the contrary, in the Nearctic, flea species richness appeared to be independent of host species richness ($r^2 = 0.07$, $F_{1,15} = 1.1$ for regular linear regression and proportion of variation in response explained by the model for robust regression = 0.02; $P > 0.3$ for both; Fig. 2b). Slopes of the flea–host species richness relationships differ significantly between biogeographical realms (ANCOVA, $F_{1,40} = 4.5$, $P < 0.03$).

Results of the multiple stepwise regressions using corrected data demonstrated that in the Palaeoarctic, flea species richness was positively correlated with both host species richness and mean elevation (E) as FSR = –0.02 + 0.93HSR + 0.0001E ($r^2 = 0.51$, $F_{2,23} = 11.6$, $P < 0.001$), although host species richness per se was not correlated with mean elevation ($r^2 = 0.02$, $F_{1,24} = 0.5$, $P > 0.8$). In the Nearctic, flea species richness was negatively correlated with latitude (L) only as FSR = 2.02 – 0.03L, although the significance of this relationship disappeared after Bonferroni correction ($r^2 = 0.52$, $F_{1,17} = 5.32$, $P = 0.04$). In both realms, flea species richness was not correlated with any of the climatic variables.

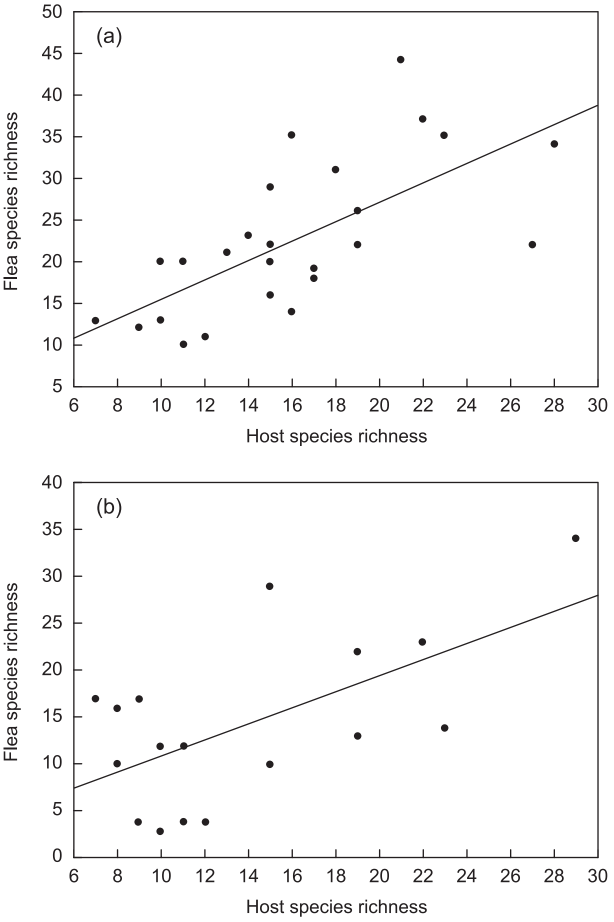

Figure 1 Relationship between non-transformed host species richness and flea species richness across different regions in the Palaeoarctic (a) and Nearctic (b).

DISCUSSION

The results of this study indicated geographical variation in the occurrence of 'bottom-up' effects in the relationship between flea and host species richness. The 'bottom-up' pattern was strongly expressed in the Palaeoarctic but not in the Nearctic. From an ecological perspective, this suggests that host diversity controls flea diversity in the Palaeoarctic, but no control of flea diversity by host diversity occurs in the Nearctic. In addition, regressions on non-transformed data indicated that it requires fewer host species to support one flea species in the Palaeoarctic compared with the Nearctic (slopes 1.16 vs. 0.85, respectively). This suggests that flea–host interactions in the Palaeoarctic are relatively specialized compared with those in the Nearctic. This is because each flea species interacts with relatively fewer host species in the Palaeoarctic than in the Nearctic.

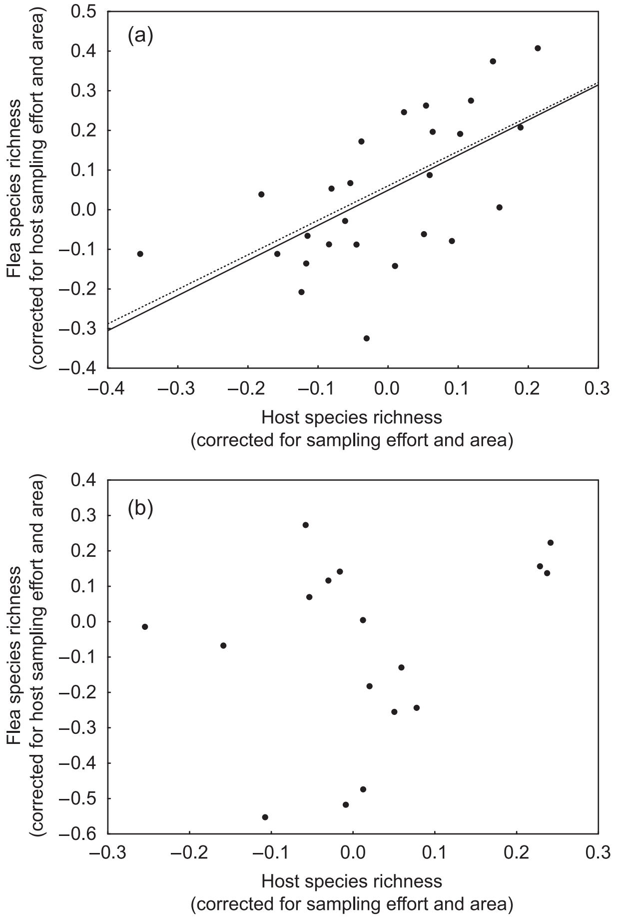

Figure 2 Relationship between host species richness and flea species richness (both variables controlled for area and host sampling effort) across different regions in the Palaeoarctic (a) and Nearctic (b): solid line, simple linear regression; dashed line, robust regression.

Fleming *et al*. (1987) and Fleming (2005) studied relationships between the diversity of food plants and the diversity of nectarivorous and frugivorous birds and bats and found the evidence for 'bottom-up' control in Neotropic but not in Palaeotropic communities. They argued that this hemispheric difference is related to differences in the spatio-temporal predictability of food resources between the Old World and the New World and that higher spatio-temporal predictability in the New World has driven the evolution of consumers towards specialization. In these studies, the conclusion about the difference in spatio-temporal predictability was based on differences in regional and community species richness, body sizes, dietary overlap of consumers and ranging patterns. In our case, there is no apparent difference in spatio-temporal predictability between the Palaeoarctic and Nearctic host assemblages because the number of hosts per region did not differ between realms. Another potential explanation for the difference between the patterns observed in the Palaeoarctic and Nearctic might be that the quality of host resources (e.g. immunocompetence) consistently differs between the two biogeographical realms because the mammalian taxa of Eurasia are not the same as those of North America [some families (e.g. Heteromyidae) are endemic to one land mass and absent from the other].

The geographical variation in the 'bottom-up' pattern could be explained by between-realm historical differences in flea–host associations. Positive correlation between parasite and host species richness suggests that diversification of parasites could be a response to diversification of hosts (Krasnov *et al*., 2004a). The latter can either stem from host speciation promoting parasite diversification by an increase of the probability of parasite co-diversification (Combes, 2001; Clayton *et al*., 2003), or be the result of host immigration and ensuing parasite diversification by the introduction of new parasite species. Although co-diversification of parasites and their hosts is rarely congruent (Poulin, 1998) and is often complicated by a number of evolutionary events (see Page, 2003 for review), the predictability of the relationship between the number of parasites and the number of their hosts would likely be higher if the main reason for parasite diversification was a response to host speciation rather than a response to host immigration. Indeed, the relationship between the number of Palaeoarctic fleas and their hosts appeared to be more predictable than that in the Nearctic, and Palaeoarctic fleas are, on average, more host-specific than Nearctic fleas. Although no strong evidence of co-diversification between some flea taxa and their mammalian hosts is available (Krasnov & Shenbrot, 2002; Lu & Wu, 2005), fleas, nevertheless, are thought to exploit the group of hosts with which they co-evolved or hosts that evolved later, but not more ancestral mammalian lineages (Traub, 1980). The hosts that support the majority of flea species are representatives of several families and subfamilies of rodents (such as Arvicolinae, Murinae, Gerbillinae, Cricetinae) and insectivores (such Soricidae) that originated in the Old World (see Traub, 1980 and references therein). Furthermore, the only flea family that is suggested to have a North American origin (Ceratophyllidae) is also the evolutionarily youngest family (Traub, 1980; Medvedev, 2005). These different lines of evidence suggest a longer history of flea–host associations in the Palaeoarctic than in the Nearctic and, thus, can explain the stronger link and higher predictability of flea–mammal relationships in the former. Another, albeit indirect line of evidence supporting earlier Palaeoarctic compared with Nearctic associations between fleas and their hosts, is that the number of Palaeoarctic flea species exceeds by almost three times the number of Nearctic fleas (890 species vs. 299 species, respectively; Medvedev, 2005). An additional, not necessarily alternative, explanation for the occurrence of the 'bottom-up' pattern in the Palaeoarctic but not in the Nearctic is that this pattern is a consequence of a relatively high level of consumer specialization. The higher level of specialization of Palaeoarctic fleas could be the evolutionary result of a higher number of flea species in the Palaeoarctic than in the Nearctic regions that exploit a similar number of host species. Competition among fleas could lead to their specialization on different host species.

The richness of the flea fauna in a region appeared to be affected also by environmental factors. The reason for fleas to be dependent not only on their hosts but also on the off-host environment is that the pre-imaginal development of fleas occurs almost always off-host. As a result, flea species composition in a location can be determined not only by host species composition but also by environmental parameters (Krasnov *et al*., 1997). In the Palaeoarctic, the number of flea species in a region increased with an increase in the region's mean elevation, although it was not affected by the variation in elevation. High mean elevation of a region reflects the presence of mountains, which presumably increases the environmental variation within the region, resulting in a high number of flea species. However, no relationship between either mean or the variation in elevation of a region and flea species richness was found for the Nearctic regions. This between-realm difference can be the result of the higher variety of mountain systems, where fleas and hosts were sampled, in the Palaeoarctic than in the Nearctic. Indeed, our mountain Palaeoarctic data sets included those from the Tatras, Scandinavian Mountains, Caucasus, Ural, Tian Shan, Khangay, Dzhungarian Alatau, Tarbagatay Mountains, Sayan range, Koryak Mountains and Atlas Mountains, whereas the mountain Nearctic data sets came from the Rocky Mountains, Sierra Nevada and Cascade Mountains only.

In the Nearctic, flea species richness was negatively correlated with latitude, thus conforming with the well-known pattern of a latitudinal gradient of species richness (e.g. Rohde, 1992; Rosenzweig, 1992). However, this correlation turned out to be non-significant after Bonferroni correction. Studies of this pattern in parasites have provided contradictory results. First, this pattern was documented for ectoparasites (e.g. Rohde & Heap, 1998) but not for endoparasites (e.g. Poulin, 1995). Second, the trend that was reported for flea assemblages on separate host species was the opposite of the main latitudinal gradient rule (Krasnov *et al*., 2004b). The absence of a latitudinal gradient pattern for endoparasites has been explained by the relative stability of their environment (inside the host's body) (Rohde & Heap, 1998), whereas ectoparasites, in contrast, are exposed to environmental conditions that change with latitude. On the other hand, the life history patterns of some parasite taxa (e.g. strong dependence on host burrows in fleas) can disrupt the relationship between latitude and their species richness, at least when the latter is considered at the level of host species (see Krasnov *et al*., 2004b). Nevertheless, the standard latitudinal trend in flea species richness was revealed when the analysis was performed at the level of host communities (this study). However, this trend was relatively weak and was manifested only when no other factor affected flea richness, as was the case with the Nearctic. In other words, in the Palaeoarctic, the latitudinal trend in the number of flea species may be merely obscured by other, stronger, determinants of flea richness.

Recently, we reported a positive correlation between host and flea species richness across 37 different regions from all the world's main biogeographical realms other than Australasia and Wallacea (Krasnov *et al*., 2004a). The results of the present study, although not contradicting our earlier results, demonstrate that macroecological trends can vary among biogeographical realms. A strong trend occurring in one realm may mask a weaker trend or even an absence of trend in another realm. Consequently, one should be cautious when pooling data from regions with different biogeographical histories into a single data set for a macroecological analysis.

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SUPPLEMENTARY MATERIAL

The following material is available online from
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Appendix S1 Data on mammalian and flea species richness

BIOSKETCHES

Boris Krasnov and **Georgy Shenbrot** are senior researchers at the Ramon Science Center and Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev. Boris Krasnov studies the evolutionary ecology of host–parasite relationships and population ecology and ecophysiology of haematophagous ectoparasites. The main interests of Georgy Shenbrot lie in the areas of community ecology and systematics of desert rodents.

Irina Khokhlova is a member of the Wyler Department of Dryland Agriculture, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev. She does research on the ecophysiology of animals, in particular the energy and water needs and expenditures of desert mammals as well as the effect of ectoparasites on hosts' physiological parameters.

Robert Poulin is a professor in the Department of Zoology, University of Otago. His research interests include all ecological and evolutionary aspects of host–parasite interactions. In particular, his recent work has focused on the patterns of parasite biodiversity and the underlying processes behind them, and the impact of parasitism on host ecology and on the functioning of ecosystems.

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