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Scale-dependence of phylogenetic signal in ecological traits of ectoparasites

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The non-independence of traits among closely related species is a well-documented phenomenon underpinning modern methods for comparative analyses or prediction of trait values in new species. Surprisingly such studies have mainly focused on life-history or morphological traits of free-living organisms, ignoring ecological attributes of parasite species in spite of the fact that they are critical for conservation and human health. We tested for a phylogenetic signal acting on two ecological traits, abundance and host specificity, using data for 218 flea species parasitic on small mammals in 19 regions of the Palaearctic and Nearctic, and a phylogenetic tree for these species. We tested for the presence of a phylogenetic signal at both regional and continental scales using three measures (Abouheif/Moran's *I*, Pagel's λ, and Blomberg et al.'s *K*). Our results show 1) a consistent positive phylogenetic signal for flea abundance, but only a weaker and erratic signal for host specificity, and 2) a clear dependence on scale, with the signals being stronger at the continental scale and relatively weaker or inconsistent at the regional scale. Whenever values of Blomberg et al.'s *K* were found significant, they were <1 suggesting that the effects of phylogeny on the evolution of abundance and host specificity in fleas are weaker than expected from a Brownian motion model. The most striking finding is that, within a continental fauna, closely-related flea species are characterized by similar levels of abundance, though this pattern is weaker within local assemblages, possibly eroded by local biotic or abiotic conditions. We discuss the link between history (represented by phylogeny) and pattern of variation among species in morphological and ecological traits, and use comparisons between the Palaearctic and Nearctic to infer a role of historical events in the probability of detecting phylogenetic signals.

Evolution of species derived from common ancestors often results in these species sharing many features pertaining to a variety of traits (Hansen and Martins 1996, Blomberg and Garland 2002). Historically, this tendency for phylogenetically related species to resemble one another has been described with terms such as "phylogenetic inertia" (Wilson 1975), "phylogenetic conservatism" (Ashton 2001), "phylogenetic correlation" (Gittleman et al. 1996), and "phylogenetic effect" (Derrickson and Ricklefs 1988). Recently, Blomberg and Garland (2002) and Blomberg et al. (2003) have argued that the use of some of these terms suggests the action of certain evolutionary mechanisms, although such mechanisms cannot be inferred or estimated from comparative data. Instead, Blomberg and Garland (2002) and Blomberg et al. (2003) have recommended the use of the term "phylogenetic signal" for the pattern of resemblance among phylogenetically-related species without implying any evolutionary mechanism or process that could have caused this resemblance. Indeed, Revell et al. (2008) have demonstrated, using simulations, that different evolutionary rates and processes may produce similar phylogenetic signals.

The relationship between phylogenetic relatedness and phenotypic or ecological similarity has lead to the general recognition of phylogeny as a potential confounding factor in comparative analyses. Consequently, numerous methods have been developed to control for this confounding effect (Felsenstein 1985, Harvey and Pagel 1991, Pagel 1994, 1999, Garland et al. 1999, Rohlf 2001, Freckleton et al. 2002, Freckleton 2009), although acceptance of these methods is not universal (Price 1997, Losos 1999). In the majority of comparative studies, these methods have been applied to demonstrate the effects of numerous variables on the evolution and ecology of various taxa while accounting for the effect of phylogenetic non-independence of taxa. Fewer studies, however, have focused on phylogenetic signal, although the phylogenetic dependence of traits cannot be assumed a priori but must be demonstrated from observational and phylogenetic (i.e. tree) data (Freckleton et al. 2002, Blomberg et al. 2003).

The detection and estimation of phylogenetic signals remain important for the analyses of comparative data because they not only allow control for the confounding effect of phylogenetic dependence, but also for prediction of the value of a given trait for a species that has not yet been studied based on its phylogenetic position and the values of this trait in closely-related species (Garland and Ives 2000, Blomberg et al. 2003). The latter is especially important for parasites because the estimation of phenotypic and ecological traits in parasites is difficult due to their small size and often "cryptic" natural history. Nevertheless, phylogenetic signal in parasites has rarely been the focus of rigorous studies (but see Sasal et al. 1998, Mouillot et al. 2005, 2006).

The majority of evolutionary studies have searched for phylogenetic dependence in phenotypic traits such as body mass (Desdevises et al. 2003), shape (Piras et al. 2009) or the morphometrics of internal organs (Lavin et al. 2008). In contrast, ecological or interaction-dependent traits such as behaviour, abundance, geographic range size or niche breadth have attracted less attention, although several studies have been carried out (Brandle et al. 2002, Blomberg et al. 2003, Valladares et al. 2008, Warren et al. 2008). The authors of these studies have generally found weak phylogenetic signals for ecological traits. This could be because these traits are so strongly affected by a variety of abiotic (filters) and biotic (e.g. competition) factors that their evolutionary patterns become obscured (Anderson et al. 2004). However, considering ecological traits such as abundance in a phylogenetic context may represent a powerful tool for investigating the structure of communities and revealing the main underlying forces (Kelly et al. 2008). In addition, the results of any phylogenetic study of ecological traits may be spatially scale-dependent. For example, a phylogenetic signal in distribution of abundances may be shaped by the degree of competitive interactions that may decrease with increasing scale (see Vamosi et al. 2009 for a recent review). On small scales, the distribution of abundances among species may reveal a negative phylogenetic signal (i.e. closely-related species having different abundances) if the community is dominated by competitive interactions. However, on large scales, the phylogenetic signal in abundances may be positive if species-specific traits that determine the limits of abundance (e.g. interrelated body size, metabolic rate and fecundity) are themselves phylogenetically dependent.

We studied the relationship between phylogeny and two ecological traits (abundance and host specificity) in fleas parasitic on small mammals in 19 different regions of the Palaearctic and Nearctic. Host specificity is an important property of any parasitic species. In general, it measures the range of tolerable conditions for a parasite. Our earlier results with fleas suggest that abundance and host specificity of these insects may be phylogenetically constrained, but are still strongly influenced by local environmental conditions (Krasnov et al. 2004a, 2006, Mouillot et al. 2006). In this study, we specifically tested whether the phylogenetic relatedness of fleas affect the similarity in their abundance and/or host specificity by comparing the significance and magnitude of phylogenetic signals at two spatial scales (regional and continental). We predicted that a phylogenetic signal in flea abundance and host specificity would be detected mainly at a continental rather than regional scale because local abundance and host specificity can be strongly affected by local biotic and abiotic environments that blur the pattern. However, we may identify consistent differences between lineages in their capacity to reach high abundances or to infest many hosts at a continental scale because the full potential of species' niches is more likely to be realized at that larger scale.

Materials and methods

Data on abundance and host specificity

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Soricomorpha, Erinaceomorpha, Rodentia and Lagomorpha) in 10 different regions of the Palaearctic and nine different regions of the Nearctic (Supplementary material Table S1). 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 included in the analyses only those flea species for which more than two individuals have been collected in a region. In total, we used data on 218 flea species collected from 120 096 individual mammals.

For each flea species in each region, we calculated mean abundance as the mean number of individuals of a flea species collected per individual host. Fleas may reach different levels of abundance depending on which host species they infest (Krasnov et al. 2004b). Consequently, in each region we focused on the principal host species for each flea species. The parasite's principal host is the host that supports the largest part of its population. Thus, we identified this host as the host species on which the flea attains its highest abundance (Krasnov et al. 2004b). Only records of the flea on the regional principal host were used in the analyses of abundance within a region. When flea abundance was analysed across an entire continent, we averaged the highest regional abundances of each flea species across all regions. Estimates of parasite abundance may be biased if some parasites or hosts are studied more intensively than others (Krasnov et al. 2004b). Consequently, unequal study effort among host species may result in confounding variation in estimates of flea abundance. Indeed, estimates of flea abundance were affected by sampling effort (in log-log space; $r^2 = 0.10$, $F_{1,434} = 52.6$, $p < 0.0001$). In subsequent analyses we substituted the original values of flea abundance by residuals of the regression of log-transformed flea abundance against the log-transformed number of hosts examined.

We used the number of mammalian species on which the flea species was found as a measure of host specificity for each flea species in each region. This number was weakly, but significantly correlated with sampling effort (i.e. number of all host individuals examined in the region; in log-log space, $r^2 = 0.02$, $F_{1,434} = 11.9$, $p < 0.001$). In subsequent analyses we substituted the original values of number of hosts exploited by residuals of the regression of their log-transformed values against the log-transformed number of hosts examined per region. When host specificity measures were analysed within a continent, we averaged the regional values of number of hosts exploited across regions.

Phylogenetic information

Phylogenetic trees of fleas were based on the only available molecular phylogeny of fleas (Whiting et al. 2008), which included 128 flea species (ca 6% of global fauna) belonging to 83 genera (ca 34% of all flea genera). To analyse their dataset, Whiting et al. (2008) applied both maximum parsimony (MP) as implemented in the program POY (Giribet 2001) and maximum likelihood (ML) based on the multiple sequence alignment program Muscle (Edgar 2004). This resulted in a strict consensus tree of 96 equally parsimonious trees from MP analysis, and a single best tree from ML analysis. The phylogenies were similar, although there were small differences in the placement of some of the higher-level clades. These differences were mostly related to clades absent from our dataset (e.g. Pygiopsylloidea, Chimaeropsyllidae, Macropsyllidae). We used the MP version of Whiting et al.'s (2008) flea phylogeny; since each of our analyses included only a subset of the species in Whiting et al.'s phylogeny, the resulting "pruned" trees were roughly identical whether the ML or MP tree was used as a starting point.

Our data sets included most of the genera present in Whiting et al.'s (2008) dataset, even if this was not the case at the species level. Consequently, the positions of flea species that were not represented in the original tree of Whiting et al. (2008) were determined according their morphologically-derived taxonomy (see taxonomic references in Poulin et al. 2006). Because the only available information on the vast majority of fleas is limited to brief morphological descriptions and dichotomous identification keys, within-genus topology was established according to the subdivision of genera into subgenera and/or species groups, and/or was based on morphological characters used for identification (see Poulin et al. 2006 for taxonomic references and Krasnov and Shenbrot 2002 for an example of constructing a phylogenetic tree from morphological data for a set of flea species). All branch lengths were arbitrarily set to an equal length of 1, and polytomies were treated as soft.

Analytical approach and data analyses

Several methods for the detection of a phylogenetic signal and/or measurement of its magnitude have been developed (Cheverud et al. 1985, Gittleman and Kot 1990, Abouheif 1999, Pagel 1999, Rohlf 2001, Blomberg et al. 2003). Each of these methods has its merits and disadvantages (Pavoine et al. 2008), so it is difficult to choose among them (Hansen and Martins 1996). In this study we tested for a phylogenetic signal in either flea abundance or the number of hosts exploited within regions as well as after combining regions within a continent (Palaearctic and Nearctic) using three measures, namely Moran's *I* based on Abouheif (1999), Pagel's (1999) λ, and Blomberg et al.'s (2003) *K.*

Abouheif's (1999) method represents an adaptation of the test for serial independence (TFSI) for comparison of the states of traits among several species. Essentially, the TFSI compares the average squared differences between two successive observations in a sequence of continuous observations to the sum of all successive squared differences (Pavoine et al. 2008). Abouheif's (1999) adaptation of this test for phylogenetic data is based on the idea that the topology of a tree may be represented in a variety of ways by rotating the nodes within the tree. Each of these permutations results in a particular sequence of species and thus in a particular sequence of values of the trait of interest. From this sequence, an observed statistic C_{mean} is calculated. The *C*-statistic represents the critical values of TFSI tabulated by Young (1941) and thus allows evaluation of the significance of the serial independence (see details in Abouheif 1999). Then, the original data are randomly shuffled so that species are randomly placed on the tips of the original topology and the TFSI is applied to all possible permutations of the given topology. This allows calculating the randomized C_{mean} which is then compared with the observed C_{mean}, with the null hypothesis of no phylogenetic autocorrelation in the data being either accepted or rejected. Pavoine et al. (2008) revisited Abouheif's (1999) test and demonstrated that the C_{mean} statistic uses a Moran's *I* statistic such that this test is a form of Moran's test that uses a particular matrix of phylogenetic proximity (matrix **A**; Pavoine et al. 2008). The diagonal value of this matrix (i.e. proximity of a species to itself) equals the inversed product of the number of branches descending from each interior node in the path connecting this species to the root of the tree, whereas a non-diagonal value (i.e. proximity between two species) equals the inversed product of the number of branches descending from each interior node in the path connecting these two species (see details in Pavoine et al. 2008). Thus, matrix **A** focuses on the topology of the tree rather than on branch lengths of the phylogeny. Blomberg and Garland (2002) criticized Abouheif's (1999) test because it does not use branch length information and does not rely on a particular model of character change, so it is unclear how the results would be affected by different evolutionary models. On the contrary, Pavoine et al. (2008) argued that the tree topology is a key component of evolutionary history and considered the lack of underlying evolutionary model to be an advantage rather than a shortcoming of the method. Furthermore, Pavoine et al. (2008) introduced a new matrix of phylogenetic proximity, matrix **M**, which is related to both the aforementioned matrix **A** and May's (1990) measure of the taxonomic distinctiveness of a set of species. In this matrix, calculations of both diagonal and non-diagonal elements are similar to those for matrix **A**, but the number of branches is summed instead of multiplied. Pavoine et al. (2008) demonstrated the advantages of both matrices **A** and **M** for the detection of phylogenetic autocorrelation through simulations over other matrices of phylogenetic proximity. Calculations of Abouheif/Moran statistics were performed using package "ade4" (Chessel et al. 2004) implemented in the R software environment (R Development Core Team 2005). We used 999 random permutations to obtain p-values. We ran the analyses using both matrices **A** and **M**. Both runs produced similar results. Here, we report only the results obtained when matrix **M** was used.

Pagel's (1999) λ uses maximum likelihood optimization to investigate the degree to which a trait exhibits phylognetic signal. λ is a multiplier of the off-diagonal elements of the variance/covariance matrix describing tree topology and branch lengths. It ranges from zero to 1 and thus gradually eliminates phylogenetic structure. A zero value indicates that the evolution of the trait is independent of phylogeny, while $\lambda = 1$ indicates a Brownian motion model of evolution of the trait on a given phylogenetic tree. Under this model, evolutionary changes along branches are expected to have zero values. Their distribution is normal with a variance proportional to branch length (Felsenstein 1985). We calculated λ using the package "geiger" implemented in the R software environment (Harmon et al. 2008). We tested the significance of phylogenetic signal by comparison of log likelihood obtained from the observed tree topology and log likelihood obtained from a tree without phylogenetic signal (that is, when $\lambda = 0$) using log likelihood ratio tests.

Blomberg et al.'s (2003) K assumes a Brownian motion model of evolutionary process. K is calculated as the quotient of observed and expected mean square error (MSE) ratios. The observed ratio is the MSE of the tip data, measured from the phylogenetically correct mean, divided by the MSE of the data calculated using the variance-covariance matrix derived from the tree. The expected ratio is computed from the phylogenetic tree with Brownian motion as the evolutionary process. In other words, K compares the observed phylogenetic signal in a trait to that under Brownian motion trait evolution (Blomberg et al. 2003). The higher the K statistic, the stronger the phylogenetic signal in a trait. K has a value of 1 for any trait in which Brownian motion is the true evolutionary model, which implies some degree of phylogenetic signal or conservatism. K values that do not differ significantly from zero indicate no effect of phylogeny, whereas K values >1 indicate strong phylogenetic signal and conservatism of traits. We calculated K using the package "picante" implemented in the R software environment (Kembel et al. 2009). The statistical significance of phylogenetic signal was evaluated by comparing observed patterns of the variance of independent contrasts of the trait to a null model involving shuffling species across the tips of the phylogenetic tree using 999 permutations (Kembel et al. 2009).

Both Pagel's (1999) λ and Blomberg et al.'s (2003) K have been shown to detect phylogenetic signal well in situations when only partial phylogenetic information is available (Freckleton et al. 2002, Blomberg et al. 2003). This may be the case when explicit data on branch lengths are absent, so that lengths are established arbitrary (for example, are set to be equal to 1).

Results

Our results show 1) a consistent positive phylogenetic signal for flea abundance, but a weaker and erratic signal for host specificity, and 2) a clear dependence on scale, with the signals being stronger at the continental scale and weaker or inconsistent at the regional scale (see Table 1 for Abouheif/Moran I and Supplementary material Table S2 and S3 for Pagel's λ and Blomberg et al.'s K).

No significant phylogenetic signal was detected for either abundance or the degree of host specificity of fleas in the majority of regional assemblages (Table 1, Supplementary material Table S2 and S3). Nevertheless, a negative phylogenetic signal (i.e. negative correlation between closely-related taxa) was only detected for either abundance or host specificity in extremely few regions (and only marginally significant for the number of hosts exploited in Adzharia) and by a single metric (Abouheif/Moran's I), whereas significant positive phylogenetic signals for abundance were detected in four regions, and significant positive

Table 1. Results of Abouheif/Moran's (Pavoine et al. 2008) test (see text for details) of phylogenetic independence of abundance and host specificity (number of hosts exploited) in fleas parasitic on small mammals in 10 Palaearctic and nine Nearctic regions. SO is the standard deviate of the observed statistic from the mean null expectation (see text for details). Positive and negative values of SO indicate that the values of the observed statistic are greater or smaller, respectively, than the values expected when species are randomly placed on the tips of the original topology. P-values are related to the alternative hypothesis (trait values are phylogenetically dependent).

Scale	Region/continent	Abundance			Host specificity		
		Moran's I	SO	p	Moran's I	SO	p
Regional	California central	0.07	0.94	0.35	−0.05	−0.97	0.34
	California southwest	0.07	1.19	0.17	−0.10	−1.48	0.12
	Colorado	−0.03	−0.81	0.39	0.05	0.99	0.33
	Connecticut	−0.002	−0.19	0.86	0.03	0.32	0.79
	Idaho	0.06	1.33	0.18	0.07	1.47	0.14
	Montana	0.01	0.15	0.86	0.10	1.40	0.15
	New Mexico	0.06	1.44	0.14	0.07	1.68	0.09
	Wisconsin	0.09	1.06	0.25	0.14	1.25	0.23
	Wyoming	0.17	2.03	0.04	0.07	0.83	0.44
	Adzharia	−0.03	−0.91	0.34	−0.12	−2.25	0.04
	Akmolinsk	0.08	1.57	0.1	0.09	1.89	0.05
	Azerbaijan	0.14	2.67	0.01	0.01	−0.01	0.99
	Mongolia	0.01	0.3	0.75	0.002	−0.07	0.93
	Moscow	0.005	0.01	0.99	−0.01	−0.15	0.88
	Moyynkum	0.03	0.92	0.37	0.15	3.39	0.004
	Kyrgyzstan	0.04	1.15	0.24	0.06	1.38	0.14
	Novosibirsk	0.08	1.96	0.04	0.05	1.03	0.32
	Slovakia	0.01	0.12	0.9	−0.004	−0.12	0.91
	Volga-Kama	0.02	0.46	0.64	0.02	0.38	0.71
Continental	Nearctic	0.08	4.18	0.001	−0.01	−0.51	0.61
	Palaearctic	0.03	3.51	0.005	0.04	3.9	0.002

signals for the number of hosts exploited in three regions. In each of these regions, a phylogenetic signal was detected in one trait only.

At the scale of continental faunas, significant positive phylogenetic signals for abundance were found for both realms (Table 1), and one was also found for the number of hosts exploited in the Palaearctic. In other words, closely-related fleas are characterized by more similar levels of abundance or host specificity than expected by chance, although the latter is true for the Old World fleas only. An illustrative example using the abundance of the Palaearctic fleas belonging to three families (Ceratophyllidae, Leptopsyllidae, and Pulicidae) is presented in Fig. 1.

The three methods used to assess phylogenetic signal yielded consistent results. Among four regional and two continental assemblages for which significant phylogenetic signal for abundance was detected, it was supported by all three metrics for two regional (Azerbaijan and Wyoming) and both continental assemblages, and by two metrics for one regional assemblage (Novosibirsk) (Table 1,

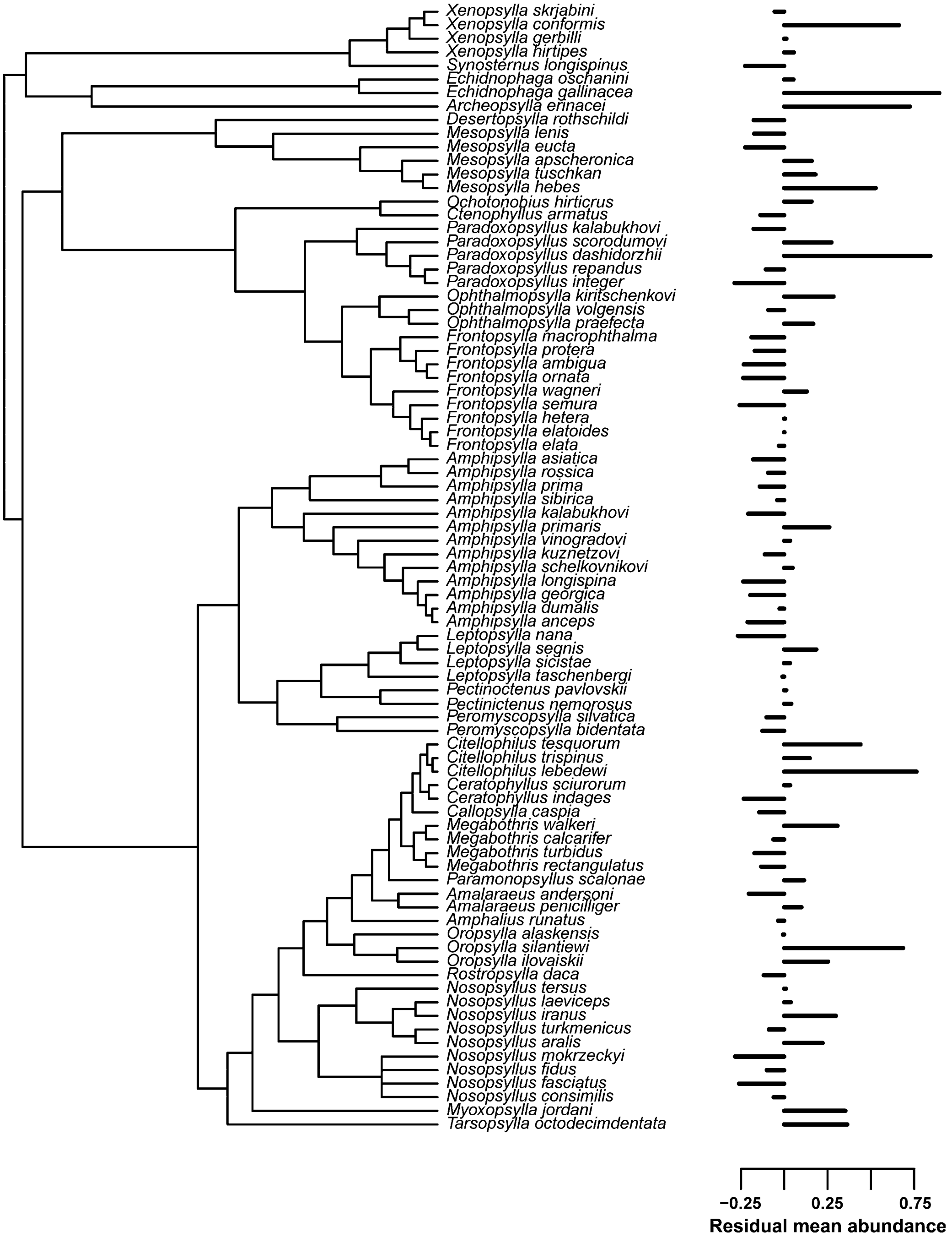

Figure 1. Abundances of the Palaearctic fleas belonging to three families (Ceratophyllidae, Leptopsyllidae, and Pulicidae) plotted against their phylogenetic positions [created using package "ape" implemented in the R software environment (Paradis et al. 2004)]. Abundances were calculated as mean numbers of individual fleas per individual host of a preferred species in a region, averaged across regions and corrected for unequal sampling effort (see text for explanations).

Supplementary material Table S2 and S3). Among three regional and the continental (Palaearctic) assemblages for which significant phylogenetic signal for the degree of host specificity was detected, it was supported by all three metrics for a single regional assemblages (Moyyunkum) and by two metrics for one regional (Akmolinsk) and the continental assemblages.

In all assemblages for which significant phylogenetic signal for abundance was detected, values of Blomberg et al.'s (2003) *K* were lower than 1 (Supplementary material Table S3). The same was true for phylogenetic signal in the degree of host specificity.

Discussion

We found evidence for similarity among related flea species in abundance and host specificity mainly at a continental rather than at a regional scale. Furthermore, the phylogenetic signal in the number of hosts exploited was found for Palaearctic but not Nearctic fleas. Whenever a significant phylogenetic signal was detected it was positive, except for the number of host species in fleas of Adzharia, though this particular result was supported by only one of three metrics. Moreover, when Abouiheif/Moran's test was used for abundance, a positive standard deviate of the observed statistics from the mean null expectation was found in 16 out of 19 regions (Table 1), although it was non-significant for the majority of regions. This trend was weaker for host specificity with positive standard deviates from the mean null expectation found in 12 of 19 regions (Table 1).

The geographic range of a flea species within a continent can be rather large, but the distribution of the majority of flea species considered in this study is continentally restricted (Shenbrot et al. 2007). Therefore, continental estimates of abundance and host specificity for a flea calculated from a number of local estimates can likely be considered as fundamental characters of flea species that are shaped during flea evolution. In simple words, continental-scale estimates represent what fleas can really do over a large gradient of abiotic and biotic conditions; that is, their realized niches which are similar to their potential niches at this large scale. In contrast, local estimates of abundance and host specificity reflect what fleas actually do locally and thus only represent their truncated niches which are far from their potential niches.

The results of this study suggest that closely-related fleas exhibit a tendency to be similar in their abundance and host specificity on an evolutionary, but not an ecological, scale. This could mean that the realized niche of a flea species (or at least some of its dimensions) at a large spatial scale is subject to a strong phylogenetic signal, whereas its locally truncated niche is not. In contrast, the abundance or host specificity values computed across an entire continent, because of the way they are calculated here, come closer to the average ecological potential inherent to each flea species independent of whether or not it can be achieved in a particular locality. Only such species-specific traits are likely to be determined by phylogeny. This finding is consistent with Silvertown et al. (2006) who showed that plant β and γ niches (habitat and large scale environments, respectively) are affected by phylogenetic conservatism while α niches (within-habitat scale) are not.

Whenever values of Blomberg et al.'s *K* were found significant, they were <1. This suggests that the effects of phylogeny on trait evolution in fleas are weaker than expected from a model of Brownian motion (Freckleton et al. 2002). In other words, this indicates substantial evolutionary lability in abundance and host specificity among fleas (Blomberg et al. 2003). This may be because these traits are strongly affected by a variety of factors (e.g. Krasnov et al. 2004a for host specificity in fleas) that mask their evolutionary trajectories. In addition, as noted by Blomberg et al. (2003), deviation from Brownian motion may cause *K*-values to be <1. For example, adaptation to a particular environmental or host-related factor could occur only in some rather than all species in a clade. Another reason for $K<1$ may be measurement errors in the tip data, branch lengths, or tree topology (Blomberg et al. 2003). In our data set, branch lengths were unavailable, so they were arbitrarily set to 1 (see Methods). Errors in tree topology are also possible because only a single study on flea phylogeny has been carried out (Whiting et al. 2008). However, these errors tend to reduce rather than inflate phylogenetic signal (Blomberg et al. 2003).

Closely-related fleas are not similar in their abundance and host specificity at an ecological scale

The lack of phylogenetic signal in flea abundance and host specificity at an ecological scale (that is, in a region) may have at least three non-mutually exclusive reasons. First, a regional flea assemblage within a continent may consist of distantly related fleas which are characterized by lineage-specific values of certain traits. In other words, there may be too few closely-related species in a regional assemblage for a phylogenetic signal to be revealed. For example, there were only 1.51 species per genus in regional assemblages. However, this explanation is substantially weakened by the fact that there was no difference in the number of species per higher taxonomic unit (genus, tribe, subfamily) between regions where significant phylogenetic signals for abundance or host specificity were found and regions for which this was not the case (e.g. 1.55 versus 1.50, respectively).

Second, local biotic and abiotic conditions may modulate the species-specific level of abundance or the degree of host specificity. For example, the local abundance of a flea is affected by the microclimate of host burrows (Krasnov et al. 2001), host density (Krasnov et al. 2002, Stanko et al. 2006), and the abundance and diversity of co-occurring fleas (Krasnov et al. 2005). The reasons for the effect of the local environment on the level of host specificity in fleas are less clear, but this effect has been shown to be strong (Krasnov et al. 2006). However, the same environmental factor may have different effects on different flea species (Krasnov et al. 2001), whereas the same flea may exhibit different abundance or host specificity in different regions. This may be the reason behind the absence of phylogenetic signal in some regions and the existence of this signal in other regions, even when flea assemblages in these regions are composed of the same or closely-related taxa. For example, the Novosibirsk and Volga-Kama regions share 13 species and 14 genera, and yet they are characterized by different patterns (see Table 1 and Supplementary material Table S3). In other words, the local environment may modulate not only the values of a trait per se, but also the relationship between phylogenetic relatedness and species similarity (Anderson et al. 2004).

Third, as shown by Kelly et al. (2008), the phylogenetic structure of a community above the genus level seems to be irrelevant to its ecological structure. This is because interaction-dependent characters such as abundance are directly regulated by ecological interactions (which should be strongest between, say, congeneric rather than confamilial species) rather than phylogenetic relatedness.

Closely-related fleas are similar in their abundance and host specificity at an evolutionary scale

Phylogenetic dependence in abundance and the size of the host spectrum of flea species may arise if 1) there are some life history features that determine limits of the two traits and 2) these features are subjected to natural selection. Lower limits of flea abundance can be affected by species-specific mating systems and/or the relationship between mating and blood feeding, whereas upper limits of abundance can be set by species-specific reproductive outputs, generation times, and/or morphological constraints of the female reproductive system (see Krasnov 2008 and references therein). The level of host specificity of a flea species is affected by the range of host-related conditions that this species is adapted to tolerate, such as the structure of host skin, the physical and chemical properties of host blood and the microclimate of the host burrow (Krasnov 2008). This, in turn, may be determined by the species-specific morphology of the flea's mouth apparatus, the physiology of its digestive system as well as its tolerance of microclimatic fluctuations. For example, fleas with heavily armed lacinia (the apex of the maxilla) (e.g. *Xenopsylla cheopis*) are usually less host-specific than fleas with weakly armed lacinia (e.g. *Letopsylla segnis*).

Although the evolution of any of the above-mentioned life history or morphological features in fleas is completely unknown, similarity in some of them among congeneric or confamilial flea species suggests that they may well be inherited from common ancestors. For example, Darskaya et al. (1965) proposed classifying fleas into three groups according to their daily egg output. The majority of fleas assigned to the group with the lowest daily egg production appeared to belong to the same family (Hystrichopsyllidae), whereas fleas with medium daily egg output belonged either to the genus *Nosopsyllus* or to the genus *Xenopsylla* (although these genera belong to different families). Indeed, as can be seen in Fig. 1, some fleas of these genera are characterized by relatively higher levels of mean abundance than many other fleas. The phylogenetic dependence of these features may be the reason behind the phylogenetic dependence of abundance and host specificity found in our study. This further supports and explains our earlier results that abundance and host specificity (in terms of number of hosts exploited but not of their taxonomic distinctness) of fleas belonging to the same genus, tribe, or subfamily are more similar to each other than expected by chance (Krasnov et al. 2004a, 2006) and that sister flea species exploit similar numbers of hosts (Mouillot et al. 2006).

An additional reason for the occurrence of positive phylogenetic signals in both abundance and host specificity, at least on one of the continents, is that in fleas these traits are interrelated. Fleas capable of exploiting many host species achieve higher abundance on those hosts than do specialist fleas on their more restricted sets of host species (see details in Krasnov et al. 2004c). Consequently, if, for instance, closely related flea species inherit the ability to attain high or low abundance from a common ancestor, this may cause also the inheritance of the ability to exploit either large or small numbers of host species, respectively.

The phylogenetic dependence of host specificity in fleas from the Palaearctic but not the Nearctic suggests that evolution of this trait in parasites may be affected by the history of parasite-host associations. The higher number of flea species in the Palaearctic than in the Nearctic (Medvedev 1996) and the fact that flea-host interactions in the Palaearctic are relatively specialized compared with those in the Nearctic, so that each flea species interacts with relatively fewer host species in the former (Krasnov et al. 2007), suggest a relatively short history of flea-host associations in the latter. This could have resulted in the re-distribution of fleas among new hosts, thus confounding the relationship between phylogeny and host specificity. Therefore, the detection of phylogenetic signals may depend not only on the spatial scale of the study, but also on its temporal scale.

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