



Spatial variation in the phylogenetic structure of flea assemblages across geographic ranges of small mammalian hosts in the Palearctic



Boris R. Krasnov^{a,*}, Shai Pilosof^a, Georgy I. Shenbrot^a, Irina S. Khokhlova^b

^a Mitrani Department of Desert Ecology, The Swiss Institute for Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel

^b Wyler Department of Dryland Agriculture, French Associates Institute for Agriculture and Biotechnology of Drylands, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel

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ABSTRACT

We investigated spatial variation in the phylogenetic structure (measured as a degree of phylogenetic clustering) of flea assemblages across the geographic ranges of 11 Palearctic species of small mammalian hosts and asked whether the phylogenetic structure of the flea assemblage of a host in a locality is affected by (i) distance of this locality from the centre of the host's geographic range, (ii) geographic position of the locality (distance to the equator) and (iii) phylogenetic structure of the entire flea assemblage of the locality. Our results demonstrated that the key factor underlying spatial variation of the phylogenetic structure of the flea assemblage of a host was the distance from the centre of the host's geographic range. However, the pattern of this spatial variation differed between host species and might be explained by their species-specific immunogenetic and/or distributional patterns. Local flea assemblages may also, to some extent, be shaped by environmental filtering coupled with historical events. In addition, the phylogenetic structure of a local within-host flea assemblage may mirror the phylogenetic structure of the entire cross-host flea assemblage in that locality and, thus, be affected by the availability of certain phylogenetic lineages.

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1. Introduction

Spatial variation in the composition of plant and animal communities is a central theme in ecological biogeography. Thousands of publications have been dedicated to patterns of spatial variation in species richness and diversity such as latitudinal gradients (e.g., Rohde, 1992), distance decay of similarity (e.g., Nekola and White, 1999) or species–area relationships (e.g., Rosenzweig, 1995). The vast majority of these studies have dealt with free-living species, while parasites have received less attention despite forming a large if not the largest proportion of the diversity of life (Windsor, 1998; Poulin and Morand, 2000, 2004). Nevertheless, the last decade and a half has witnessed a burst of studies on spatial patterns in species diversity and composition in parasite communities (e.g., Poulin and Morand, 1999; Carney and Dick, 2000; Rohde, 2002; Poulin and Valtonen, 2002; Poulin, 2003; Calvete et al., 2004; Krasnov et al., 2005; Oliva and González, 2005; Vinarski et al., 2007; Pérez-del-Olmo et al., 2009), although some pioneering studies were carried out earlier (e.g., Kisielewska, 1970; Kennedy and Bush, 1994). Many spatial patterns found initially for free-living species have been supported by data on parasites. However, some

parasite-specific patterns have also been revealed due to the intimacy of their relationships with their hosts (e.g., Poulin, 2010; Krasnov et al., 2004, 2012).

Recently, phylogenetic information has started to be introduced into community ecology and biogeography and has proven to be a powerful tool allowing better understanding of evolutionary processes involved in the assembly of plant and animal communities and their spatial variation (Webb et al., 2002; Cavender-Bares et al., 2009; Morlon et al., 2011). Unsurprisingly, the studies combining phylogenetic data with community ecology and biogeography have been carried out on free-living species, while the role of phylogeny in determining spatial variation of parasite assemblages remains to be studied, although some initial steps have already been taken (Poulin, 2010; Krasnov et al., 2012).

The species composition of a community in a locality is shaped by a variety of ecological and evolutionary factors (Vuilleumier and Simberloff, 1980; Ricklefs, 1987). The parasite assemblage of a particular host in a particular locality is determined by two main components. One part of an assemblage is due to host identity, while another part is due to the host's biotic and abiotic environments (Kennedy and Bush, 1994). Some of the parasite species on a host may be inherited from its ancestors, whereas other parasites can switch from other hosts that occupy the same habitat as the focal host (e.g., Paterson and Gray, 1997). In addition, the abiotic envi-

* Corresponding author. Tel.: +972 8 6596841; fax: +972 8 6596772.
E-mail address: krasnov@bgu.ac.il (B.R. Krasnov).

ronment may act as a filter that excludes some species from a parasite assemblage due to their environmental requirements (Lebrija-Trejos et al., 2010). This is especially important for parasites that spend some part of their life cycle as free-living (e.g., Krasnov et al., 2001). Thus, processes that shape the parasite assemblage of a host in a locality have a historical component (associated with parasites inherited from ancestors), an abiotic environmental component (associated with parasites for which the environment offered by a host is favourable) and a biotic environmental component (associated with parasites that switch from co-occurring hosts). Considering the variation in phylogenetic structure of parasite assemblages may allow us to disentangle these components and to identify the predominant force behind assemblage composition.

Here, we investigated spatial variation in the phylogenetic structure of flea assemblages across the geographic ranges of 11 Palearctic species of small mammalian hosts. Fleas are characteristic insect ectoparasites of small mammals. Imagos of these insects are holometabolous obligatory haematophages. Their larvae are usually not parasitic, feed on various kinds of organic matter and reside in the host's burrow or nest. Abiotic conditions (temperature, humidity, and substrate texture) strongly affect the survival, longevity and reproductive performance of fleas (Krasnov et al., 2001, 2002a,b). Furthermore, there is a substantial difference in abiotic environmental preferences among flea species (see Krasnov, 2008 for review).

We used a recently proposed index of phylogenetic species clustering (Helmus et al., 2007; see details below; see Section 2.4) and asked whether the phylogenetic structure of the flea assemblage of a host in a locality is affected by (i) distance of this locality from the centre of the host's geographic range, (ii) geographic position of the locality (that is, latitude; measured as distance to the equator) and (iii) phylogenetic structure of the entire flea assemblage of the locality (that is, flea species recorded on all host species inhabiting the locality). The relationships between the phylogenetic structure of a host's flea assemblage in a locality and the centre of the host's geographic range are likely to reflect historical processes involved in the shaping of flea assemblages. In many species, the centre of a geographic range is an area where a species attains its highest abundance, while abundance decreases toward the periphery of the range (Hengeveld and Haeck, 1982; Hengeveld, 1990). Although this pattern is not universal (Sagarin and Gaines, 2002; Gaston, 2003; Sagarin, 2006), it is rather widespread (Hengeveld, 1990). Among several explanations of the "abundant-centre" hypothesis (e.g., Carson, 1959; Brown, 1984; Kirkpatrick and Barton, 1997), the most parsimonious one is that conditions for survival and reproduction are most favourable at the centre of the range, and become gradually poorer toward the periphery (Hengeveld, 1990). The decline in abundance away from the centre of the range is often accompanied with increased patchiness and isolation in peripheral populations (Lawton, 1993). Small and isolated populations of both hosts and parasites may be subjected to random evolutionary forces such as inbreeding and drift (Holt, 1990), experience genetic bottlenecks (Brussard, 1984) and thus be characterised by low genetic diversity. We expected that flea assemblages of peripheral host populations would be more phylogenetically diverse than those of the central populations because (i) a host may acquire new parasites from different phylogenetic lineages at the periphery of its range (Hoberg and Brooks, 2008a,b), (ii) hosts in isolated populations may be less immunocompetent than those in the core populations (Whiteman et al., 2006), and (iii) parasites in the isolated populations may eventually speciate (Banks and Paterson, 2005).

Relationships between the phylogenetic structure of a host's flea assemblage in a locality and its geographic position (distance to the equator) may mirror environmental processes affecting flea assemblages. Successful development of pre-imaginal fleas takes

place at air temperatures greater than 10–15 °C but lower than 30 °C, and relative humidities greater than 60% (Marshall, 1981; Krasnov, 2008). As a result, their geographic distribution in the Palearctic is characterised by peaks of species richness in the temperate and steppe zones, with a decrease to the north (tundra and boreal forests) and south (deserts) (Yudin et al., 1976; Medvedev, 1996). Given that the southernmost localities in our study did not include hyperarid areas and desert host species (Krasnov et al., 2010; see Section 2), we expected an increase in phylogenetic clustering of flea assemblages with increasing latitudes because (i) the occurrence of phylogenetically distant lineages is more probable in richer assemblages and (ii) environmental filtering may restrict flea assemblages in the coldest localities to a certain phylogenetic subset. The association between phylogenetic structure of the local flea assemblage of a host with that of the entire flea community on all flea-supporting host species may be expected if a host's flea assemblage represents a random sample from the surrounding species pool (Krasnov et al., 2004), so that phylogenetic structure of within-host assemblages correlates positively with that of across-host assemblages.

2. Materials and methods

2.1. Selection of data on fleas and small mammals

We used data from our database compiled from published surveys of fleas parasitic on small mammals (Soricomorpha, Erinaceomorpha, Rodentia and Lagomorpha) across the Palearctic (60 surveys in 52 localities). These surveys reported the number of fleas of each individual species found on a given number of individuals of each mammalian species. The complete list and geographic location of surveys can be found elsewhere (Krasnov et al., 2010; see also Supplementary Fig. S1). We selected host species that were recorded in at least six localities, harboured at least six flea species per locality, and for which at least 10 individuals per locality were examined. This resulted in datasets of local flea assemblages for 11 host species (10 rodents and one shrew; see Supplementary Fig. S1) occurring in six to 20 localities situated at latitudes from 38°N to 68°N.

2.2. Phylogenetic information

The phylogenetic tree of fleas was based on the only available molecular phylogeny of fleas recently constructed by Whiting et al. (2008). This tree includes 128 flea species (ca. 6% of the global fauna) belonging to 83 genera (ca. 34% of the entire number of flea genera). Most genera in our dataset were represented by the tree published by Whiting et al. (2008), but this was not the case for species. Consequently, the positions of the species which were not represented in the original tree of Whiting et al. (2008) were determined using their morphologically-derived taxonomy (see details in Krasnov et al., 2011). All branch lengths were set equal to 1.0. The tree was ultrametrised using the option "chronopl" in the package "ape" (2.8) (Paradis et al., 2004) implemented in the R 2.15 statistical environment (R Development Core Team, 2011, <http://www.R-project.org>).

2.3. Geographic information

To estimate the geographic range of a host species, we applied species distribution modelling based on occurrence records and environmental data (see details in Shenbrot and Krasnov, 2005; Shenbrot, in press). In brief, records of occurrences of a species were obtained from the Global Biodiversity Information Facility (GBIF; <http://data.gbif.org>), museum collection databases and pub-

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