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Relationships among different facets of host specificity in three taxa of haematophagous ectoparasites

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ABSTRACT

Host specificity is a fundamental trait of a parasite species. Recently, multiple aspects of host specificity have been recognized, but the relationships between these facets are still poorly understood. Here, we studied pairwise relationships between basic, structural, phylogenetic and geographic host specificity in three taxa of haematophagous ectoparasitic arthropods that differ in tightness of their association with the host. We asked which metrics of host specificity are correlated within each parasite taxon and whether the patterns of the association between different facets of host specificity are similar among parasite taxa. Data on bat flies were taken from published surveys across the Neotropics while data on fleas and mites parasitic on small mammals were compiled from multiple published surveys across the Palaearctic. Basic, structural, phylogenetic and geographic specificity indices were calculated for 18 bat fly species recorded on 40 host species from 15 regions, 109 flea species recorded on 120 host species from 51 regions and 34 mite species recorded on 67 host species from 28 regions. Then, we tested for the correlation between any two measures of host specificity using model II regressions. We found that structural and basic specificity, as well as structural and geographic specificity, exhibited a positive association in all three taxa. However, basic and geographic specificity, as well as basic and phylogenetic specificity, were significantly positively associated in fleas but did not correlate in bat flies or mites. In addition, we found a significant negative association between structural and phylogenetic specificity in bat flies but no association in the remaining taxa. Moreover, geographic and phylogenetic specificity were not associated in any parasite taxon. Our results suggest that different facets of host specificity were shaped differently by natural selection in different taxa.

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1. Introduction

Host specificity is a fundamental trait of a parasite species. In the most general terms, host specificity of a parasite reflects the extent to which it is able to utilize different host species. Traditionally, host specificity of a given parasite has been measured as the

number of host species in or on which this parasite has been recorded (i.e. basic specificity; [Lymbery, 1989](#)). Implementation of the mere number of host species as a measure of host specificity inherently assumes that (i) a parasite uses all hosts equally both in a given locality and across its geographic range and (ii) these hosts are equivalent from a parasite's perspective. In reality, however, a parasite exploits some hosts more intensely than other hosts ([Rohde, 1994](#)), the pattern of exploitation of different hosts may vary across space ([Krasnov et al., 2011a](#)) and may depend on host relatedness ([Khokhlova et al., 2012](#)). From an ecological perspective, host specificity should define the breadth and position of a parasite's niche. In other words, host specificity can be measured

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as (i) the diversity of host species that a parasite utilizes and (ii) variation of host use by a parasite across its geographic range (Futuyma and Moreno, 1988). From an evolutionary perspective, host specificity should define not only the number of host species utilized, but also their identity and how closely related they are or, in other words, the historical association among hosts (Poulin and Mouillot, 2003). Therefore, the modern understanding of host specificity recognizes that this trait is complex and represents a combination of different facets (Poulin et al., 2011).

Recently, Poulin et al. (2011) proposed definitions of multiple aspects of host specificity and tools to quantify those. In particular, structural specificity reflects distribution of a parasite (via abundance or prevalence) across host species (Rohde, 1994). For example, two parasite species, A and B, use the same number of host species. However, abundance or prevalence of parasite A varies depending on the host species it utilizes, whereas parasite B attains similar relative abundance or prevalence in all host species. Phylogenetic or taxonomic specificity represents phylogenetic or taxonomic diversity of host species used by a parasite (Poulin and Mouillot, 2003). For example, two parasite species, A and B, use the same number of hosts and achieve similar relative abundances across host species. However, host species used by parasite A are more closely related (e.g. belong to the same genus) than those of parasite B. Recently, Krasnov et al. (2011a) introduced geographic specificity which measures consistency in host use across a parasite's geographic range. For example, two parasite species, A and B, use the same number of host species, attain similar relative abundances across host species and use host species that are phylogenetically equally related. However, the species composition of host assemblages of parasite A varies across locations, whereas host assemblages of parasite B are the same across its entire geographic range. It is important to note that all of these measures, except structural specificity, are actually inverse indicators of host specificity.

Relationships among different facets of host specificity are still poorly known. One of the reasons for this is that different facets of host specificity have rarely been quantified simultaneously in the same host-parasite association across the same geographic space (see Krasnov et al., 2011a). However, understanding these relationships may provide us with important insights into host-parasite ecology and evolution by elucidating either similar or entirely different selective forces that shape patterns of host use in a given parasite taxon. For example, a correlation between host specificity indices would suggest that at least some of the different facets of specificity are driven by similar forces. In contrast, no association among specificity metrics would indicate that different facets of host specificity are shaped by different factors. Furthermore, patterns of the relationships among different facets of host specificity may differ among parasite taxa due to multiple and independent origins and evolutionary pathways of parasitism in different phylogenetic lineages (Poulin, 2006). To the best of our knowledge, the relationships among different facets of parasite specialization (= host specificity) have never been specifically explored, although some patterns could be gleaned from the results of somewhat related studies (e.g., Krasnov et al., 2011a, 2015; Rosas-Valdez and de León, 2011).

Here, we studied and compared pairwise relationships between different aspects of host specificity in three taxa of haematophagous ectoparasitic arthropods, namely fleas (Insecta: Siphonaptera) and gamasid mites (Acari: Mesostigmata) in the Palearctic and bat flies (Insecta: Diptera) in the Neotropics. We calculated basic, structural, phylogenetic and geographic specificity of each species across all regions where it was recorded (i.e., global specificity) and asked which metrics of host specificity correlated with each other within each parasite taxon and whether the patterns of the association between different facets of host specificity were similar among the three parasite taxa. Obviously, all metrics of host specificity

are equally low in strictly host-specific parasites with narrow geographic distributions. However, this may not be the case for less host-specific species. Nevertheless, relationships between basic/structural and phylogenetic specificity could be expected because as more species compose a parasite's host spectrum, the probability that these species belong to different phylogenetic lineages increases (Poulin and Mouillot, 2003; Krasnov et al., 2006). Furthermore, an association between geographic and phylogenetic specificity can be expected if, for example, a parasite utilizes (i) many distantly-related hosts locally and the compositions of local host spectra vary greatly across space or (ii) a few closely-related hosts both locally and across its geographic range (see Krasnov et al., 2011a). If a parasite attains similar abundances in a given number of closely related hosts and in the same number of distantly related hosts then a negative relationship between structural and phylogenetic specificity will arise (Poulin et al., 2011).

The three ectoparasite taxa considered in this study differ in the tightness of their association with the hosts. Both bat flies and fleas are obligate haematophages. However, bat flies spend almost all their life on bodies or the wing membranes of their hosts. Female bat flies leave the host only for a short time to deposit prepupae in roost substrate (Dick and Dittmar, 2014). Adult fleas of the majority of species alternate periods spent on the bodies of their small-to-medium sized mammalian hosts and in their nests/burrows, whereas non-parasitic immature stages are mostly found off-host (see Krasnov, 2008). In contrast, gamasid mites vary substantially in their feeding habits, ranging from obligatory to facultative haematophagy to predation on nidicolous arthropods. Mites spend most of their life off-host (some of them are purely phoretic) although a few species are more intimately associated with the host (Radovsky, 1985, 1994). We hypothesized that the difference in the typical pattern of association among bat flies, fleas and gamasids could be manifested in different patterns of relationships among different facets of host specificity. In particular, we predicted a predominantly positive correlation between (i) basic/structural and phylogenetic specificity and (ii) geographic and phylogenetic/structural specificity in fleas and bat flies but not in mites. In addition, we expected stronger associations among different facets of host specificity in bat flies and fleas than in mites because the former are much more dependent on the resource provided by a host (e.g., blood) than the latter.

2. Materials and methods

2.1. Parasite and host species

Data on bat flies were taken from published surveys across the Neotropics (see [Supplementary Data S1](#)). Data on fleas and mites parasitic on small mammals (Soricomorpha, Erinaceomorpha, Rodentia and Lagomorpha) across the Palearctic were compiled from multiple published surveys (see Krasnov et al., 2010 for references and details). We selected only surveys that reported the number of parasites of a given species found on a given number of individuals of a given host species. Then, we selected parasite species that were recorded in at least three regions and from at least three host species across the entire data set. This resulted in 18 bat fly species recorded on 40 host species from 15 regions, 109 flea species recorded on 120 host species from 51 regions and 34 mite species recorded on 67 host species from 28 regions (see [Supplementary Data S2](#)).

2.2. Host specificity indices

2.2.1. Basic specificity

Basic specificity represents the number of host species used by a parasite species. However, rare host species might be overlooked

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