



## Different space preferences and within-host competition promote niche partitioning between symbiotic feather mite species



Sofía Fernández-González<sup>a,\*</sup>, Antón Pérez-Rodríguez<sup>a</sup>, Iván de la Hera<sup>a</sup>, Heather C. Proctor<sup>b</sup>, Javier Pérez-Tris<sup>a,\*</sup>

<sup>a</sup> Departamento de Zoología y Antropología Física, Universidad Complutense de Madrid, Spain

<sup>b</sup> Department of Biological Sciences, University of Alberta, Edmonton, Canada

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### ABSTRACT

Obligate symbionts (including parasites, commensals and mutualists) often share host species and host-based food resources. Such symbionts are frequently distributed unequally among hosts with different phenotypic features, or occupy different regions on a host. However, the processes leading to distinct within-host symbiont distributions remain obscure. We aimed to test whether distinct in-host symbiont distributions arise as the outcome of species-specific habitat preferences or interspecific competition, and how host phenotype influences such processes. To this end, we studied the distribution within and among individual bird hosts of two feather mites (*Proctophylloides sylviae* and *Trouessartia bifurcata*) of migratory and sedentary European blackcaps, *Sylvia atricapilla*, wintering in sympatry. *Trouessartia bifurcata* was mostly restricted to resident blackcaps, while *P. sylviae* was abundant on both host types. Within hosts, each species tended to settle on different feather sectors (proximal or distal, respectively), which they filled by spreading on the wing following ordered but opposite patterns, thereby supporting the view that spatial segregation was primarily the outcome of dissimilar space preferences. However, we also found evidence of competition finely tuning mite distributions: when *P. sylviae* increased abundance and expanded onto the range of *T. bifurcata*, abundances of the two species were negatively correlated in the shared areas. In addition, the presence of *T. bifurcata* on a host was associated with a more restricted distribution of *P. sylviae*. Our results show that both species-specific preferences and interspecific interactions contribute to shaping mite distributions among and on individual hosts, a situation likely mirrored by other host-multi-symbiont systems.

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## 1. Introduction

The ecological niche of a species can be defined as the combination of conditions of the physical environment, resource requirements and biological interactions (with competitors, mutualists, predators and pathogens) that allow its existence (Hutchinson, 1978; Chase and Leibold, 2003). In theory, the various species that live in the same place cannot occupy the same ecological niche because the slightest advantage for one competitor will eventually drive others to extinction (MacArthur and Levins, 1967; Amarasekare, 2003; Schoener, 2009). Therefore, to make

coexistence possible, ecologically similar species are expected to partition their niches, showing differences in some niche dimensions such as diet, spatial distribution or phenology (Schoener, 1974; Chesson, 2000). Niche specialization is thus central to the evolution and maintenance of biological diversity (Chesson, 2000; Schluter, 2000; Pfenning and Pfenning, 2010).

For obligate symbionts (those that live permanently in close association with their hosts, such as many parasites, commensals and mutualists), the host population represents the fundamental niche (i.e., the habitat that provides conditions and resources for the species to exist in the absence of competitors, predators and pathogens; Hutchinson, 1978; Soberón and Peterson, 2005). This is divided into patches (the individual hosts) that in many cases are shared by different types of symbionts, which may then overlap in their niches and spatial distribution. In these cases, the realised distribution of each symbiont species within a shared host may be the outcome of both species-specific habitat preferences

\* Corresponding authors at: Departamento de Zoología y Antropología Física, Universidad Complutense de Madrid, Calle José Antonio Nováis 2, E-28040 Madrid, Spain. Tel.: +34 913944949; fax: +34 913944947.

E-mail addresses: [sofia.fernandez@bio.ucm.es](mailto:sofia.fernandez@bio.ucm.es) (S. Fernández-González), [jperez@bio.ucm.es](mailto:jperez@bio.ucm.es) (J. Pérez-Tris).

and interspecific interactions (Holmes, 1973; Sousa, 1994; Pulliam, 2000; Nicholls and Racey, 2006; Jeglinski et al., 2013). However, within-host symbiont distributions, and the way these vary in relation to host characteristics, changes in species' abundance, or symbiont co-occurrence among individual hosts, are poorly known for most host-symbiont systems (Choe and Kim, 1988). Filling this knowledge gap is important to our understanding of the processes that promote and maintain the diversity of symbiotic organisms, and ultimately configure their distributions at different spatial scales (Poulin, 2007).

Similar to their free-living relatives, obligate symbiotic animals may behaviourally adjust their distributions depending on habitat characteristics (host phenotype), local population size (within the host), and the presence or absence of potential competitors. Competition among coexisting species may depend on the degree of overlap of micro-distributions, which in turn could vary due to changes in population size. At low densities, all individuals of a species may aggregate in the preferred habitat patches (those with the best conditions of food availability, temperature, humidity, etc.). But when population density increases in these patches, some individuals could be forced to poorer habitats, where fitness may be lower (Pulliam, 1988; Rodenhouse et al., 1997). The dynamics of space occupation may then create a "buffer effect" (Brown, 1969), in which population size fluctuates greatly in low quality sites (which are typically occupied only when population abundance is high), but is buffered in high quality sites (which typically are the first to be occupied and remain occupied in the face of population fluctuation; Brown, 1969; Gill et al., 2001). When different species occupy nearby areas, individuals of one species that are forced into poor habitat by conspecific competitors may end up interacting closely with heterospecific competitors, if the less preferred habitats for the first species are favoured by others. Therefore, the cost of being pushed into poor habitats may depend on the presence and numbers of coexisting species, and this in turn could affect local demography by impairing the buffering effect of these habitats (Gill et al., 2001).

We studied the distribution of two feather-dwelling mite species (Acari: Astigmata), *Proctophylloides sylviae* Gaud (Proctophylloidae) and *Trouessartia bifurcata* (Trouessart) (Trouessartiidae) on the wings of European blackcaps *Sylvia atricapilla* (L.) (Aves: Sylviidae). *Proctophylloides sylviae* and *T. bifurcata* are the most common mites on blackcaps and often coexist on the same individual host (Fernández-González et al., 2013). *Trouessartia bifurcata* has been found on several hosts of at least four bird families (Santana, 1976), while to our knowledge *P. sylviae* has only been found on blackcaps. These mites feed upon the uropygial gland secretions that cover the feathers, also consuming entrapped particles and microorganisms such as bacteria and fungi (Proctor, 2003). In southern Europe, resident blackcaps coexist during winter with migratory individuals from further north (Pérez-Tris and Tellería, 2002), and mite species show a different distribution among individual hosts according to their migratory behaviour. Whereas both mite species reach intermediate abundance on resident blackcaps, *P. sylviae* is more abundant and *T. bifurcata* is rare on migratory blackcaps (Fernández-González et al., 2013). Such differences may be associated with phenotypic divergence between migratory and resident blackcaps, which differ in wing morphology (migratory blackcaps possess a greater wing surface area) and potentially also availability of food for the mites (resident blackcaps have larger uropygial glands and therefore may produce more abundant oil secretions; Fernández-González et al., 2013).

Spatial partitioning is evident at a gross level because *P. sylviae* occupies the ventral side of the wing feathers, while *T. bifurcata* lives on the dorsal side (Fernández-González et al., 2013).

Specialization in relation to within-host microhabitat and spatial segregation in relation to host phenotype may reduce direct competition between *P. sylviae* and *T. bifurcata*. Still, there is evidence of negative interactions between both mite species when they coexist on the same host: *P. sylviae* tends to have a lower abundance when *T. bifurcata* is present on the host, although the opposite is not true (Fernández-González et al., 2013). Previous research has found that feather mites are not randomly distributed across the host's plumage (Jovani and Serrano, 2004), and coexisting mite species may show distinct distributions on the wing surface (Choe and Kim, 1989; Mestre et al., 2011). However, we do not know what processes create these patterns, if variation in mite abundance in the presence of competitors is associated with changes in mite distribution on the host, or whether the degree of overlap between the distributions of different mite species may influence the outcome of competition.

We set out to test two alternative, yet not mutually exclusive, behavioural mechanisms that could account for mite spatial distributions: species-specific habitat preferences or within-host interspecific competition. Aggregation of each mite species in distinct areas of the plumage might be a result of species-specific habitat preferences, which would by itself decrease the likelihood of interspecific competition (Holmes, 1973; Morand et al., 1999). Alternatively, both species could have similar habitat preferences but different realised distributions when they coexist on the same host, as a consequence of competition for the same space. However, even if each species has particular preferences, an increase in population density of one species in its preferred habitat might cause its spread over the plumage to overlap with the range of the other species, increasing the opportunity for competition on shared wing space. To investigate these processes, we first examined the features of mite distributions by testing whether *P. sylviae* and *T. bifurcata* follow a random or regular distribution on the wing, and whether they tend to crowd in distinct wing sectors. These could be the same or different between species, as would be expected if they partitioned the available wing space as a consequence of ongoing competition or different microhabitat preferences. Then we tested specific predictions stemming from habitat preferences or competition as alternative hypothetical mechanisms underlying mite distributions. If habitat preferences drive the pattern of mite distribution, a nested pattern of filling of the available areas of the wing is expected, according to which the best habitat patches will be the first to be occupied at low mite densities, and habitats of progressively poorer quality will be occupied only when better habitats are already filled. Therefore, a nested order of wing filling would imply that the distribution of mites on wings at a given abundance is contained in the distribution when their abundance is higher. We tested whether *P. sylviae* and *T. bifurcata* followed nested patterns of wing filling, and whether or not these patterns differed between species. To test whether competition occurs in habitat patches that may be occupied by both species, we analysed whether a negative correlation between the numbers of the two species could be detected, controlling for variation in the population size of each mite species across the host's wing. In all of these analyses, we took into account the host's migratory behaviour, as migratory and sedentary hosts have divergent phenotypes that may influence the patterns of distribution of the two mite species and the outcome of their interactions. From a broader perspective, this study will contribute to understanding the ecology and evolution of host-multi-symbiont systems by (i) distinguishing between habitat preferences or competition as putative mechanisms of niche partitioning in obligate symbionts, and (ii) identifying ecological scenarios (created by variation in host phenotype or symbiont abundance) that may promote one mechanism above the other.

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