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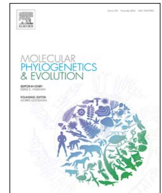

Cophylogenetic analyses reveal extensive host-shift speciation in a highly specialized and host-specific symbiont system

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ABSTRACT

Host-shift speciation and cospeciation are the two major processes driving symbiont macroevolutionary diversification. Cospeciation is expected to be frequent in vertically transmitted and host-specific symbionts, and leads to congruent host-symbiont phylogenies. However, the cophylogenetic dynamics of many groups of highly specialized host-specific symbionts is largely unstudied. Thus, the relevance of cospeciation vs. host-shift speciation remains largely unknown. Here, we investigated this question by performing the largest cophylogenetic study of feather mites to date, using both distance and event-based cophylogenetic methods. For these analyses, we inferred phylogenies based on all protein coding genes of the mitochondrial genome of *Proctophyllodes* and *Trouessartia* feather mite species living on European passerine birds. Results show high incongruence among bird and feather mite phylogenies, because of extensive host-switching. We conclude that host-shift speciation, rather than cospeciation, may be the main driver of symbiont diversification even for highly specialized symbionts with low host-switching potential.

1. Introduction

Understanding the evolutionary diversification of symbiont species remains a challenge, with most symbiont groups unstudied (Althoff et al., 2014; Ricklefs et al., 2014; Clayton et al., 2016), albeit with major implications for relevant areas such as emerging infectious diseases (Hoberg and Brooks, 2015), biological invasions (Dunn, 2009; Traveset and Richardson, 2014) and climate change (Carlson et al., 2013). Macroevolutionary events, such as host-shift speciation, cospeciation, sorting (i.e. extinction and "missing the boat"), and duplication events are the drivers of most of the current diversity of symbiont species (Janz, 2011; de Vienne et al., 2013; Clayton et al., 2016). Cospeciation (symbiont speciation following host speciation) and host-shift speciation (symbiont speciation following a host-switch) are the main alternative modes involved in generating diversity in most symbiont lineages (de Vienne et al., 2013; Clayton et al., 2016). However, the relative importance of these processes is highly variable among host-symbiont systems, and although strongly linked to particular ecological and evolutionary traits (Jousselin et al., 2009; Ricklefs et al., 2014; Clayton et al., 2016), we still lack a solid understanding of which scenarios favor one mechanism over the other.

Host-switches can lead to diversification (i.e. host-shift speciation) when a symbiont species moves to a new host species, successfully colonizes it, and eventually speciates (Johnson and Clayton, 2004; Giraud et al., 2010; Janz, 2011; de Vienne et al., 2013). Host-switches are more likely in symbionts with high dispersal potential (Clayton et al., 2016), such as those with free-living stages (e.g. Platyhelminthes; Braga et al., 2015), those that use vectors for transmission (e.g. avian malaria parasites; Ricklefs et al., 2004, 2014), or ectosymbionts dispersing attached to other symbionts (i.e. phoresis, e.g. *Brueelia* feather lice; Johnson et al., 2002; Bush et al., 2016). Host-switches are pervasive and are considered to be the main driver of symbiont diversification (Janz, 2011; de Vienne et al., 2013), to the extent of being reported as the most relevant drivers of the diversification process, in 93% of the cophylogenetic studies reviewed by de Vienne et al. (2013).

However, cospeciation is expected to be the main driver of diversification in vertically transmitted and host-specific symbionts, in which symbiont reproduction is strongly tied to host reproduction (McCoy et al., 2003; Thompson, 2005; Clayton et al., 2016). Examples of systems with extensive cospeciation include viruses, bacteria,

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nematodes, and mites (reviewed in Clayton et al., 2016). However, the cophylogenetic dynamics of most of highly specialized, host-specific symbionts is largely unstudied, so the relevance of cospeciation vs. host-shift speciation among host-specific symbionts remains an open question.

Feather mites (Acari: Astigmata: Analgoidea and Pterolichoidea), the most diverse and abundant ectosymbionts of birds, are an interesting model system to tackle this question (Gaud and Atyeo, 1996; Proctor and Owens, 2000; Proctor, 2003; Dabert, 2004; Doña et al., 2016). Plumage-dwelling feather mites (hereafter, feather mites) are host-specific and highly specialized mites that spend their entire lifecycle on their host's flight feathers (Proctor, 2003). Feather mites cannot survive off of their host (Dubinin, 1951; Proctor, 2003), and have developed several adaptations for this obligate lifestyle: flattened bodies, sucker-like pretarsi (ambulacra), and various clasping and seizing mechanisms on their bodies and legs to avoid becoming dislodged out of the host (Mironov, 1999), and also behavioral adaptations such as avoiding feathers that are about to be molted (Jovani and Serrano, 2001). Feather mites only leave the host during transmission, mainly when they pass from parents to offspring (i.e. vertical transmission) (Mironov and Malyshev, 2002; Doña et al., 2017). In addition, feather mites are not transmitted by phoresy (Jovani et al., 2001), as opposed to some dermicolous epidermoptid mites, which do (Jovani et al., 2001; Proctor, 2003). Feather mites are thus an excellent highly specialized, vertically transmitted symbiont model to test whether (as expected) cospeciation is predominant over host-shift speciation (Proctor and Owens, 2000; Dabert, 2004; Agosta et al., 2010). In fact, studies of feather mites of the families Avenzoariidae (Analgoidea) and Freyanidae (Pterolichoidea) associated with non-passerine avian orders support cospeciation as the dominant process (Mironov and Dabert, 1999; Ehrnsberger et al., 2001; Dabert et al., 2001). However, most feather mite taxonomic groups remain unstudied in a cophylogenetic context, and there are no studies using the recently developed analytical and methodological tools.

Here, we present the largest cophylogenetic study of feather mites to date by using both distance and event based cophylogenetic methods to study species of the genera Proctophyllodes and Trouessartia living on European passerine birds. Proctophyllodes and Trouessartia are the most speciose genera among all feather mites, and are generally associated with passerine birds (Atyeo and Braasch, 1966; Santana, 1976; Mironov, 2012; Doña et al., 2016). Within *Proctophyllodes* analyses we also included two species from the genus *Monojoubertia* and one from *Joubertophyllodes*. This is because their genus status is unsupported by recent phylogenetic studies, suggesting they belong to the genus *Proctophyllodes* as part of the glandarinus and pinnatus species groups, respectively. Hereafter they are treated as *Proctophyllodes* for the sake of text clarity (Knowles and Klimov, 2011; Klimov et al., 2017a).

For the analyses, we generated phylogenies based on all protein coding genes of the mitochondrial genome. Our results show high incongruence among bird and feather mite phylogenies because of extensive host-switching. We conclude that host-shift speciation, rather than cospeciation, may be the main driver of symbiont diversification even for highly specialized symbionts with low host-switching potential.

2. Materials and methods

2.1. DNA libraries preparation

Illumina libraries for 64 feather mites were constructed using the DNA extracts from Doña et al. (2015a), covering a great fraction of mite species from these genera in European passerines; see Table S1 Supporting information in Doña et al. (2015a) for voucher details. A total amount of 1.0 μg genomic DNA per sample was used as input for the DNA sample preparation carried out at Novogene (China). Sequencing libraries were generated using Agilent SureSelect Human All ExonV5 kit (Agilent Technologies, CA, USA) following the manufacturer's recommendations. Index codes were added to each sample. Briefly, fragmentation was carried out by hydrodynamic shearing system (Covaris, Massachusetts, USA) to generate 180–280 bp fragments. Remaining overhangs were converted into blunt ends via exonuclease/polymerase activities and enzymes were removed. After adenylation of 3′ ends of DNA fragments, adapter oligonucleotides were ligated. DNA fragments with ligated adapter molecules on both ends were selectively enriched in a PCR reaction. After the PCR reaction, libraries were hybridized with Liquid phase with biotin labelled probe, then magnetic beads with streptomycin were used to capture exons. Captured libraries were enriched in a PCR reaction to add index tags to prepare for hybridization. Products were purified using AMPure XP system (Beckman Coulter, Beverly, USA) and quantified using the Agilent high sensitivity DNA assay on the Agilent Bioanalyzer 2100 system. The clustering of the index-coded samples was performed on a cBot Cluster Generation System using TruSeq PE Cluster Kit v4-cBot-HS (Illumina, San Diego, USA) according to the manufacturer's instructions. Then, we applied whole-genome shotgun sequencing using the Illumina HiSeq 4500, generating 150 bp paired-end reads. In total, the sequencing of the 64 libraries produced 64 Gb of data (~1 Gb per library).

2.2. Mitochondrial genome assembly

FASTQ files were quality-trimmed at a base call error probability limit of less than 0.05 in Geneious 9.1.5 (http://www.geneious.com, Kearse et al., 2012). Mitochondrial genomes were assembled by using the quick option of MITObim (Hahn et al., 2013). For each mite library, we ran two assemblies: 1) using the COI sequence from the same individual mite (Doña et al., 2015a) as starting seed; and 2) using a feather mite mitochondrial genome as reference. *Trouessartia kratochvilli* was the first genome assembled by the first approach, and was used as reference for the second approach. In addition, we checked that there were no differences in assembly success depending on the reference used. After running both assemblies, we visually inspected the genomes, and only kept the longest assembled contig for further analyses (Table S1, Supporting information).

2.3. Assembly quality check

All mitochondrial genomes were annotated using MITOS (Bernt et al., 2013). We then remapped raw reads from each library against the corresponding annotated genome to verify that reads mapped correctly. We used the Geneious read mapper with Medium-Low sensitivity and default parameters. The results of the map-to-reference analyses were inspected manually. Feather mite mitochondrial genomes have the same 13 protein coding genes (PCGs) as dust mites (Dermauw et al., 2009) and other arthropods. In this study, all PCGs were assembled, but only those individual PCGs assembled with high coverage (~20X) were kept for later analyses. Lastly, we translated each gene sequence into amino acids (into each of six possible reading frames) and removed those sequences with stop codons.

2.4. Phylogenetic analysis

We aligned each gene separately from each feather mite genus using MAFFT v7.222 (Katoh et al., 2002). Taxa with less than 3000 bp (n = 24) were removed from the alignment for the backbone phylogenetic tree (see below) because of their presumed lower phylogenetic information content as a result of extensive missing data (Gómez-Rodríguez et al., 2015). We then made an additional COI alignment to posteriorly place the initially removed taxa into the tree based now only on COI sequences from Doña et al. (2015a) (see below) (Zhou et al., 2016). All the alignments were trimmed with Trimal v1.2 (Capella-Gutiérrez et al., 2009) and checked by eye in Geneious. We also checked for saturation of our marker (Fig. S7). We concatenated the 13

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