



Convergent herbivory on conifers by *Choristoneura* moths after boreal forest formation

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ABSTRACT

Mitogenomes are useful markers for phylogenetic studies across a range of taxonomic levels. Here, we focus on mitogenome variation across the tortricid moth genus *Choristoneura* and particularly the spruce budworm (*Choristoneura fumiferana*) species complex, a notorious pest group of North American conifer forests. Phylogenetic relationships of Tortricidae, representing two subfamilies, four tribes and nine genera, were analyzed using 21 mitogenomes. These included six newly-sequenced mitogenomes for species in the spruce budworm complex plus three additional *Choristoneura* species and 12 previously published mitogenomes from other tortricids and one from the Cossidae. We evaluated the phylogenetic informativeness of the mitogenomes and reconstructed a time-calibrated tree with fossil and secondary calibrations. We found that tortricid mitogenomes had conserved protein and ribosomal regions, and analysis of all protein-coding plus ribosomal genes together provided an efficient marker at any taxonomic rank. The time-calibrated phylogeny showed evolutionary convergence of conifer feeding within *Choristoneura*, with two independent lineages, the Nearctic spruce budworm complex and the Palearctic species *Choristoneura murinana*, both shifting onto conifers about 11 million years ago from angiosperms. These two host-plant shifts both occurred after the formation of boreal forest in the late Miocene. Haplotype diversification within the spruce budworm complex occurred in the last 4 million years, and is probably linked to the initial cooling cycles of the Northern Hemisphere in the Pliocene.

1. Introduction

Mitogenomes, which represent the separate DNA system for mitochondria, are receiving increasing attention in phylogenetic and evolutionary research on insects. Their small molecular size and absence of introns have made mitogenomes convenient and useful markers for phylogenetic studies across insects (Cameron, 2014), with 3679 full mitogenome sequences now published for 1514 insect species (GenBank, accessed May 2017; Clark et al., 2016). However, few studies have used complete mitogenomes to determine evolutionary patterns within a family level clade, particularly within the Lepidoptera (e.g. Cameron and Whiting, 2008; Ramírez-Ríos et al., 2016; Tian et al., 2012; Timmermans et al., 2014; Wu et al., 2016; Yang et al., 2015).

Leafroller moths (Tortricidae) are a diverse family of about 11,000 currently recognized species (Gilligan et al., 2014a). They include several economically significant species (Brown et al., 2008), as well as major modulators of temperate forest dynamics (Cooke et al., 2007; Nealis, 2015) that have cyclic outbreaks and use wind currents for long-distance dispersal (Sturtevant et al., 2013). Various molecular studies have focused on the evolution, phylogenetic relationships and origin of this family (e.g. Gilligan et al., 2014b; Razowski and Tarcz, 2014; Regier et al., 2012). Recently, Fagua et al. (2017) estimated a time-calibrated tree for all recognized tribes of Tortricidae (*sensu* Horak and Brown, 1991), using six genes and fossil calibrations. However, tortricid evolution has not yet been studied with full mitogenome sequences. Of the 22 tribes and three subfamilies recognized within the Tortricidae (see

Abbreviations: ESS, effective sample size; Ma, million years ago; PSRF, potential scale reduction factor; SBW, spruce budworm; smy, substitution per site per million years; UFBS, Ultra-Fast Bootstrap support

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Regier et al., 2012; Fagua et al., 2017), mitogenomes have been published for eleven species to date (Wu et al., 2016) from four tribes in the two largest subfamilies: Olethreutinae (tribes Eucosmini and Grapholitini) and Tortricinae (tribes Archipini and Tortricini).

Within the tribe Archipini, *Choristoneura* Lederer, 1859 is one of the most economically and ecologically important tortricid genera (Silk and Eveleigh, 2016). The only mitogenome available for this genus is from *Choristoneura longicellana* (Walsingham, 1900), a generalist orchard pest from temperate East Asia (Byun et al., 1998; Wu et al., 2016). No mitogenome has been published yet for the well-studied species of Archipini, several of which are in the *Choristoneura fumiferana* (Clemens, 1865) species complex, also known as the spruce budworm (SBW) species complex. The SBW complex includes eight (Brunet et al., 2017; Dupuis et al., 2017) or nine (Brown, 2005; Gilligan et al., 2014a) coniferophagous species of *Choristoneura* in North America. In addition to major impact on forestry by the SBW complex (Alfaro and Fuentealba, 2016), *Choristoneura murinana* (Hübner, 1799) is an important conifer pest in Europe (Sarı́kaya and Avcý, 2005), while *Choristoneura rosaceana* (Harris, 1841) and *Choristoneura confictana* (Walker, 1863) are pests in orchards and aspen forest in North America (Holsten and Hard, 1985; Reissig, 1978). Consequently, understanding of diversification processes in *Choristoneura* has implications for both evolutionary biology and resource management.

Several mitochondrial genes have been widely used in phylogenetics due to their ease of amplification and high rate of evolution compared to nuclear genes (Cameron, 2014; Fagua et al., 2017). Insect mitogenomes are usually composed of 37 genes (13 protein-coding, 22 tRNAs, and two rRNAs), a few short non-coding regions, and a long and highly variable control region (Babbucci et al., 2014; Cameron, 2014). Cytochrome c oxidase I (COI) is the most frequently used gene (Mandal et al., 2014), but few studies have compared phylogenetic informativeness among all mitochondrial genes (Cameron and Whiting, 2008; Nelson et al., 2012). The variability and accessibility of short mitochondrial DNA sequences of COI have led to their use in several studies on the SBW species complex. Sperling and Hickey (1994, 1995), followed by Lumley and Sperling (2010, 2011a,b), found 169 mitochondrial haplotypes clustered into five major lineages (named f, p, o, b β , and o β) distributed among the species of the SBW complex. Most SBW species were non-monophyletic with respect to these mitochondrial lineages but the f and p lineages each had most of their haplotype variation restricted to a single species: *C. fumiferana* and *Choristoneura pinus* (Harris, 1841), respectively (Lumley and Sperling, 2011a).

Despite the economic importance of *Choristoneura*, its diversification remains poorly studied, with only general comments in taxonomic and phylogenetic studies of the genus or Archipini (Razowski, 1987, 1992, 2002, 2008; Dang, 1992; Jinbo, 2000; Wang and Yang, 2008; Dombroskie and Sperling, 2013). However, work on species origins in the SBW complex has generated contrasting hypotheses. Volney (1985) proposed that the current distribution of western and eastern species is due to recent changes in the composition and distribution of boreal forests during the Holocene. Powell and De Benedictis (1995) proposed a similar hypothesis for the western species but attributed their divergences to changes in forest distribution during the Pliocene, more than 2.5 million years ago (Ma). No rigorous time estimates were available for *Choristoneura* or the SBW complex to test these competing hypotheses.

In this study, we examine mitogenomes across Tortricidae, emphasizing *Choristoneura* and the SBW complex, to estimate: (i) phylogenetic relationships based on single mitochondrial genes compared to whole mitogenomes; (ii) rates of mitochondrial DNA evolution in Tortricidae, and (iii) divergence times of coniferophagous species of *Choristoneura* and major mitochondrial lineages in the SBW complex. We sequenced new mitogenomes for three non-SBW species of *Choristoneura* and all five major mitochondrial lineages of the SBW complex, then estimated phylogenetic relationships and divergence times using fossil and secondary calibrations.

2. Material and methods

2.1. Samples, library preparation, and sequencing

Mitogenomes for 12 lepidopteran species were obtained as accessions in GenBank (Clark et al., 2016), including these 11 Tortricidae: *Acleris fimbriana* (Thunberg & Becklin, 1791), *Adoxophyes honmai* Yasuda, 1998, *Adoxophyes orana* (Fischer von Röslerstamm, 1834), *Choristoneura longicellana*, *Cydia pomonella* (L.), *Epiphyas postvittana* (Walker, 1863), *Grapholita dimorpha* Komai, 1979, *Grapholita molesta* (Busck, 1916), *Spilonota lechriaspis* Meyrick, 1932, *Retinia pseudotsugaicola* Liu & Wu, 2001, and *Rhyacionia leptotubula* Liu & Bai, 1984 and a member of the Cossidae as outgroup: *Eogystia hippophaecolus* (Hua, Chou, Fang & Chen, 1990) (Gong et al., 2014; Lee et al., 2006; Niu et al., 2016; Son and Kim, 2011; Shi et al., 2013; Timmermans et al., 2014; P.F. Wu et al., 2013; Q.L. Wu et al., 2013; Wu et al., 2016; Zhao et al., 2011, 2016; Zhu et al., 2012). Nine additional mitogenome sequences of *Choristoneura* were obtained via library preparation and high-throughput sequencing (Roche 454[®]; TruSeq[™]/HiSeq[™] and Nextera[™]/NextSeq[™] from Illumina[®]), four of them prepared at the Institut de Biologie Intégrative et des Systèmes (IBIS) at Laval University and the McGill University and Genome Quebec Innovation Centre (*C. fumiferana* [East] f lineage, *C. occidentalis occidentalis* Freeman, 1963, o lineage, *C. occidentalis biennis* (Freeman 1967) b β lineage, and *C. pinus* p lineage) and five prepared at the Molecular Biology Service Unit at the University of Alberta (*C. fumiferana* [West] f lineage, *C. occidentalis occidentalis* o β lineage, *C. confictana*, *C. murinana* and *C. rosaceana*). Collection information associated with each specimen and accession are presented in the online Supplementary data (Appendix A).

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Sequence data for the *C. fumiferana* (East) mitogenome was obtained from DNA extracted from a pool of male pupae (Insect Production Services, Natural Resources Canada, Sault Ste. Marie, Canada). This DNA was used to generate both a shotgun and a 6 kb paired-end library for sequencing on a Roche 454 GS-FLX sequencer. *Newbler* version 2.6 (Roche) was used for genome assembly. The eight other new mitogenome sequences were generated from ethanol precipitated DNA samples extracted from entire thoraces using DNeasy Blood & Tissue Kits (Qiagen[®]). DNA quantity and quality were assessed using the Qubit[®] dsDNA BR Assay and Nanodrop[®] 1000 protocols

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