

# Linking patterns and processes of species diversification in the cone flies *Strobilomyia* (Diptera: Anthomyiidae)

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## Abstract

Phytophagous insects provide useful models for the study of ecological speciation. Much attention has been paid to host shifts, whereas situations where closely related lineages of insects use the same plant during different time periods have been relatively neglected in previous studies of insect diversification. Flies of the genus *Strobilomyia* are major pests of conifers in Eurasia and North America. They are specialized feeders in cones and seeds of *Abies* (fir), *Larix* (larch), and *Picea* (spruce). This close association is accompanied by a large number of sympatric *Strobilomyia* species coexisting within each tree genus. We constructed a molecular phylogeny with a 1320 base-pair fragment of mitochondrial DNA that demonstrated contrasting patterns of speciation in larch cone flies, as opposed to spruce and fir cone flies; this despite their comparable geographic distributions and similar resource quality of the host. Species diversity is the highest on larch, and speciation is primarily driven by within-host phenological shifts, followed by allopatric speciation during geographical expansion. By contrast, fewer species exploit spruce and fir, and within-host phenological shifts did not occur. This study illustrates within-host adaptive radiation through phenological shifts, a neglected mode of sympatric speciation.

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## 1. Introduction

The study of species concepts and speciation has undergone many developments since Darwin (Pigliucci, 2003). In the 1930s, research shifted away from the study of natural selection as the driving force of speciation, and highlighted the fundamental role of geographical reproductive isolation in population differentiation (Bush, 1975; Coyne and Price, 2000; Mayr, 1963). Sympatric speciation was long considered impossible because the conditions required were thought unlikely to occur in nature (Bush, 1994). In the past few years, however, ecological shifts have been shown to play a major role in the process of speciation. They are at the heart of the mechanism of ecological speciation (Orr

and Smith, 1998; Rundle and Nosil, 2005; Schluter, 2001; Wiens, 2004); according to which, populations living in different environments or using different resources face contrasting selection pressures on traits that can ultimately lead to reproductive isolation and the formation of new species. Because of their tremendous biodiversity, phytophagous insects have been particularly well studied with respect to sympatric or ecological speciation (Berlocher and Feder, 2002; Roderick and Gillespie, 1998). Much attention has focused on host shifts and the evolution of host races into new species (Abrahamson et al., 2003; Drès and Mallet, 2002; Emelianov et al., 2004; Filchak et al., 2000; Thomas et al., 2003; Via, 1999), but other interesting situations arise when insect clades specialize in different anatomical parts of the same hosts, or use the same resource during different time periods (Groman and Pellmyr, 2000).

For example, the tephritid flies of the genus *Blepharoneura* are highly host specific, and some species also specialize

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on different organs within a single host-plant species: male flowers, female flowers, or seeds (Condon and Steck, 1997). Field data and molecular phylogenetics show that organ shifts have occurred many times during the evolution of the *Andricus* gallwasps (Cook et al., 2002; Stone et al., 2002). Allochronic speciation has been demonstrated in the periodical cicadas of the genus *Magicicada* (Cooley et al., 2003; Marshall and Cooley, 2000; Simon et al., 2000). Divergence in the timing of development and reproduction at a seasonal scale has also been documented. The North American aphid *Pemphigus obesinymphae* forms galls on the same host as *Pemphigus populi-transversus*, but has a truncated life cycle without egg diapause (Sokal et al., 1991). It is suspected that this divergence arose sympatrically without host shift (Abbot and Withgott, 2004). Three cases of species divergence by change in ovipositor length and phenological shift have been demonstrated in the *Apocryptophagus* parasitic fig wasps (Weiblen and Bush, 2002). A similar mechanism has been proposed to explain the origin of three closely related sympatric species of *Megarhyssa* parasitoid wasps (Gibbons, 1979; Ramadevan and Deakin, 1990). Three adaptive syndromes have been described on the fig-breeding flies *Lissocephala*, corresponding to correlated morphological, behavioral, and ecological traits, including differences in the oviposition time and site on the fig (Harry et al., 1998). Finally, phylogenetic analyses of the *Chiastocheta* flies, pollinators, and seed predators of the globeflower *Trollius* (Ranunculaceae), have shown that host shifts cannot explain all speciation events (Després et al., 2002). Several sister-species can be found on one host-plant species, differing only in their timing of oviposition (Després and Jaeger, 1999; Pellmyr, 1989). At the genetic level, laboratory experiments on the daily locomotive activity of *Drosophila* show that mutations on clock genes can lead to allochronic isolation (Tauber et al., 2003).

Adaptive radiation, the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Gavrilets and Vose, 2005), can be observed in several of the preceding examples (Condon and Steck, 1997; Després and Jaeger, 1999; Gibbons, 1979; Harry et al., 1998; Weiblen and Bush, 2002). It produces a concentration of speciation events soon after the evolution of key innovation or colonization of unoccupied habitats. Practically this results in speciation bursts at the base of molecular phylogenies, which can be used to reveal the historical factors underlying these adaptive radiations (Gavrilets and Vose, 2005; Lovette and Bermingham, 1999).

The objective of this study is to test the relative roles of three mechanisms of speciation in one particular insect genus: speciation by geographical isolation (vicariance), speciation by host shift, and speciation by phenological shift within a single host-plant. The cone flies of the genus *Strobilomyia* are excellent candidates for studying such mechanisms because of their wide geographic distribution and their extensive adaptive radiation (Michelsen, 1988; Turgeon et al., 1994). Molecular phylogenies are a widely used tool to understand the patterns and processes of speci-

ation (Barraclough and Nee, 2001), and here we present results inferred from the sequence-analysis of a 1320 base-pair (bp) fragment of mitochondrial DNA. We compared this phylogeny with the taxonomy, distribution range and ecology (host-plant, phenology, and oviposition behavior) of the species to test the relative roles of geographical isolation, host shifts, and phenological shifts in driving speciation (Barraclough and Vogler, 2000; Berlocher and Feder, 2002; Losos and Glor, 2003). If geographical isolation is the primary condition for speciation, then most sister-species should be distributed across non-overlapping ranges; if host shift is the main mechanism of speciation, then most sister-species should occur on different host-plants. Finally, if phenological shift within a host-plant is the main mechanism of speciation, sister-species should occur on the same host-plant but with divergence in the seasonal timing of reproduction and development.

## 2. Biology and taxonomy of *Strobilomyia* cone flies

Cone flies of the genus *Strobilomyia* Michelsen (Diptera: Anthomyiidae) are among the most serious cone-and-seed pests of conifers (Turgeon et al., 1994). They are taxonomically close to the genus *Chiastocheta* (Pellmyr, 1989), but they are strict parasites and do not contribute to the pollination of their hosts. Their larval instars develop exclusively in cones of various genera of Pinaceae, namely fir, larch, and spruce (Michelsen, 1988). Until the 1980s, precise knowledge of the specific distribution and life cycle of *Strobilomyia* species was limited by taxonomic uncertainties; for instance, most cone-fly damage on larch across Eurasia was erroneously attributed to a single species, *Lasioomma* (*Strobilomyia*) *laricicola* (Roques et al., 2003). The genus *Strobilomyia* was created in 1988 following a revision of cone-fly taxonomy by Michelsen, based on morphological (especially genitalic) features. So far, 20 *Strobilomyia* species are recognized (Michelsen, 1988; Roques et al., 1996), of which 12 have been recorded on larch (*Larix* Miller), 5 on fir (*Abies* Miller), and 3 on spruce (*Picea* Ditr). Several species groups have been defined by Michelsen (1988) using morphology (Table 1). The geographic distribution of the genus is large, including boreal forests and alpine regions of the Palearctic and the Nearctic.

The biology of the different species is similar. In spring, the eggs are laid on developing cones, and the larvae tunnel into the cone, feeding on both cone tissues and seeds. Full-grown third-instar larvae drop to the ground where they pupate and over-winter. Larval development is closely synchronized with the phenology of their host's cones (Brockhoff and Kenis, 1997; Roques et al., 1984, 2003). One noteworthy feature of the genus *Strobilomyia* is the number of sympatric species that infest the same host, especially those species exploiting larch. Three species that colonize larch have been identified in the French Alps, and six in Northern China (Table 1). A single cone can contain up to four larvae, often belonging to different species (Roques et al., 1984, 2003). Several ecological and behavioral traits

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