

# Generation and maintenance of species diversity in leaf cone moths (*Caloptilia*) feeding on maples (*Acer*)

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## Summary

Herbivorous insects are remarkably species diverse and comprise over one-third of the described biodiversity on earth. The traditional explanation for the huge diversity of herbivorous insects is that high host specialization, as the result of coevolution between plant chemical defenses and insect detoxifying ability, provided opportunities for host-shift-driven speciation and thereby increased their speciation rate. However, recent phylogenetic studies found that the evolution of herbivory is not necessarily accompanied with increased diversification, prompting the need to better examine the role of host shifts during the process of speciation. An alternative view of herbivorous insect diversity is that diversity is saturated through time, and the factors that affect the upper limit on species richness, such as the number of locally coexisting species or mean range size, are the more likely determinants of current species richness. Thus, the process that *generates* diversity (i.e., speciation mode) and the factors that *maintain* diversity (i.e., determinant of limit on species richness) are both critical for our understanding of herbivorous insect diversity.

In this thesis, I focused on the relationship between leaf cone moths (*Caloptilia*) and their maple hosts (*Acer*) because, among the species of *Caloptilia*, the diversity of species using maples as hosts is notably high. By thoroughly sampling *Caloptilia* moths throughout Japan, I clarified detailed geographic distributions and host ranges of 14 maple-feeding *Caloptilia* species, including three species that are newly found. Phylogenetic analysis of 58 *Caloptilia* species collected from diverse angiosperm hosts,

including the above 14 maple-feeding species, indicated that 13 of the 14 maple feeders form a clade together with a *Toxicodendron*-feeding species and thus diversified primarily on maples. Statistical test of speciation by host shift indicated that host shifts occurred more frequently in the early stage of the diversification. Thus, contrary to traditional views that host shifts promote speciation, not all *Caloptilia* speciation events were accompanied by host shifts.

I then determined the patterns of host use by locally coexisting *Caloptilia* species in the University of Tokyo Chichibu Forest and Ashiu Forest Research Station of Kyoto University. There were 7 *Caloptilia* species co-occurring at the Chichibu Forest and 10 *Caloptilia* moths co-occurring at the Ashiu Forest Research Station. Co-occurring *Caloptilia* species generally had non-overlapping host ranges, and each *Caloptilia* species used one to several phylogenetically related hosts, which shared similar leaf chemistry (tannin content and/or C/N ratio) and mechanical property (leaf thickness). This indicates that the number of co-occurring *Caloptilia* species is a function of the phylogenetic diversity of maples at each site. In addition, as many as three species with similar host ranges coexisted at both sites; however, species with similar host ranges did not necessarily have different phenology or parasitoid community.

Overall, the current thesis presents an alternative view on species diversity of herbivorous insects. In the temperate forests of Japan, the genus *Acer* is usually the largest woody plant genus. Thus, the diversity of maple-feeding *Caloptilia* may not be the result of high diversification rate, as traditionally been assumed, but a consequence of extensive local coexistence, which is brought about by the high phylogenetic diversity of locally co-occurring maple species. Therefore, to better understand the species diversity of herbivorous insects, it is important to consider not only the

diversification process but the factors that determine the upper limit on species richness.