

Evolution and adaptation of insects and mites to vegetation systems

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Plant living insects and mites provide biologists with excellent material to study the dependence of herbivores on the plants they consume. There are two strategies used by these organisms. The first is to exploit as wide a range of plants as possible (polyphagy). An insect such as the peach potato aphid (*Myzus persicae*) is a good example of this strategy¹. It can colonise hundreds of different types of plants from many families and species. This path leads to competition from other insects, but has the advantage of offering plentiful food sources throughout the year. The second strategy is to become a specialist. This occurs by an organism becoming more and more adapted to the vegetation system i.e. the seasonal, physiological and ecological conditions of a host plant and its environment. In this second scenario, increased specialisation over evolutionary time is expected to lead to ever increasing selection pressure on the herbivore. It is forced to adapt to any changes in the plant, further restricting its ability to make use of alternative food sources, thus reinforcing the specialisation.

In the last decade, work at SCRI has started to use the highly sensitive techniques of molecular biology to examine the molecular ecology and evolution of

groups of arthropods in vegetation systems. Where these are pests, it is important to understand how they have become so, whether they are generalists or specialists, how related they are, what their virus transmitting capabilities are and how readily they will be able to adapt to control measures, particularly plant resistance genes transferred between plant species.

This article describes work on two groups of arthropod pest, one insect and one mite, which has provided new insights to their evolution. The insect species belong to the byturid beetles. This is an interesting group that contains the important raspberry pests; *Byturus tomentosus* and *B. unicolor*. The mite species belong to the genus *Cecidophyopsis*, amongst which the most important pest species is the blackcurrant gall mite, *C. ribis*. However, other species of both groups are found on many other crop and non-crop plants. The host range of individual species in both groups is believed to be restricted to one or two related host plant species, but it was not clear how many species there are, or their exact host ranges. In addition to their use in applied research, the methodologies also contribute information to help identify and conserve endangered organisms, such as the byturids in tropical vegetation systems.



Species	Origin	Host plant	Pest
<i>B. unicolor</i>	N. America	Raspberry	Yes
<i>B. tomentosus</i>	Europe	Raspberry	Yes
<i>B. ochraceus</i>	Europe	Wood Avens	No
<i>B. affinis</i>	Asia	Japanese Rose?	No

Table 1 Hosts, location and pest status of byturid beetles.

The byturid beetles that have been included in this study are shown in Table 1. There are more species, but these are very rare in nature. In Figure 1, the life cycle of the European raspberry beetle is represented. The larvae of this beetle are only associated with two plant species, *Rubus idaeus* (raspberry) or *R. fruticosus* (bramble). There are a large number of physiological 'locks and keys' that are required for this beetle to complete its life-cycle. Firstly, it must emerge at the right time of year and find flowers on which to feed and develop its ovaries/testes (hawthorn), and then find flowers of wild or cultivated raspberry or blackberry on which to mate and lay its eggs. With only one generation a year, the adults get no feedback as to the success of their offspring, as they only live for a few weeks. Therefore, the attraction to plant chemicals must be 'hard wired', i.e. innate. In addition to finding host plants, the beetles must find mates of the same species, another critical step requiring recognition processes. Knowledge of these recognition processes can be particularly useful for developing control strategies². For the beetles, their life cycle is aided by the relatively stable vegetation system with which they are associated. Specifically, their wild hosts are perennial, propagate through their roots and are associated

with climax vegetation, remaining in the same area for a long time. Other byturids, where the life cycle is known, have a restricted number of plants on which the larvae can develop (Table 1). *B. ochraceus* has the narrowest range of all, as the larvae only develop on *Geum urbanum* - the wood avens. From these observations, it is clear that any biochemical and evolutionary modifications made by their host plant, including speciation, would need to be matched by the insect. Thus, over extended periods of time, beetle evolution would be driven by their host plant's evolution and, where different species are found on two closely related plants, they should reflect the relationships of the plant, i.e. be two closely related species.

A similar situation is encountered with *Cecidophyopsis* mites. These tiny creatures can form galls on plants, hence the common name - gall mites. However, not all species form galls (Table 2). These mites are also believed to be highly host specific and, like the byturids, this specialism is likely to have been positively reinforced. One major difference between the mites and the beetles is in their sexual reproduction. The mites are haplo-diploid, with males developing from unfertilised (haploid) eggs, like bees and wasps, and the female is in control of their production. This

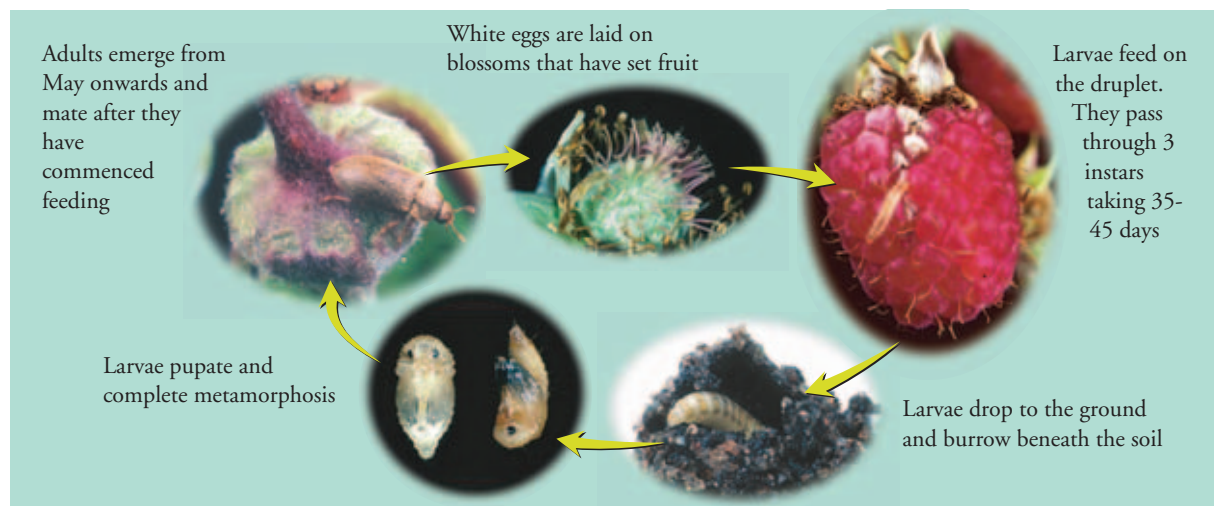


Figure 1 Life cycle of raspberry beetle.

Species	Host	Molecular ID	Morphological ID	Damage
<i>C. aureum</i>	Golden currant	Yes	Amrine	Galling
<i>C. alpinum</i>	Alpine currant	Yes	Amrine	Galling
<i>C. grossulariae</i>	Gooseberry / Blackcurrant	Yes	Collinge	Leaf browning
<i>C. ribis</i>	Blackcurrant	Yes	Westwood	Galling
<i>C. selachodon</i>	Red currant	Yes	Eyndhoven	Galling
<i>C. WC (new species)</i>	Red currant	Yes	No	Leaf surface
<i>C. spicata</i>	Red / Blackcurrant	Yes	No	Galling

Table 2 Hosts, descriptions and damage caused by the known *Ribes* infesting *Cecidophyopsis* species.

means that she can alter the sex ratio in her offspring, laying unfertilised eggs that develop into males when the timing is right. Therefore, unlike a byturid beetle, a *Cecidophyopsis* mite does not have to search for a partner. The single founder of a colony will generate both males and females. However, the other processes of adaptation to the vegetative system, i.e. seasonal movement, host finding and recognition, selection and biochemical adaptation, will be present alongside, in some cases, an ability to alter plant growth to form protective structures.

Classical study has long considered that host-specialised organisms will have co-evolved with their vegetative system. It is now possible to examine objectively the extent of this inter-dependence between arthropods and host plants using molecular and classical phylogenetic methods. The evolution of gene sequences is a classical and accepted method of tracking the evolution of the whole organism. In two

populations which have undergone, or are undergoing speciation, changes in DNA sequences accumulate. The greater the time that passes, the more different the sequences become. Speciation will occur some time after a barrier to gene flow develops. The number of sequence changes allows the time-scale, and order of evolutionary events, to be estimated. Having done this for the insect or mite, it is then possible to compare the results to those of their host plants with the same or classical methods and determine the extent of parallel evolution.

In the byturids, there are beetles in both the old and new worlds, colonising European (*Rubus idaeus idaeus*) or American (*R. idaeus strigosus*) raspberry. The two raspberry species are inter-fertile. They, or a common ancestor, are likely to have been distributed over both continents prior to the separation of N. America from Europe. This distribution is termed holarctic and is mirrored by many other plant and animal species including the Rosaceae (which includes raspberry) and beetle families. Therefore, it is a reasonable starting hypothesis that the two raspberry beetles on the two continents should be closely related, or even sub-species, like their hosts. However, we found that this was not the case³, as shown in Figure 2. Instead, the American raspberry beetle is more related to an Asian species than the ecological equivalent from Europe. There is another important difference in that the America beetles have at least three distinct genetic lineages, whereas *B. tomentosus* is genetically uniform on an equivalent geographical scale, i.e. from Japan to Scotland.

In the case of the raspberry beetle pests of Europe and America, it appears that they have two distinct origins and that those of America may have colonised America from Asia. Asia is the main source of byturid diversity with 12/16 species present in this region. *B. unicolor* is also more diverse, perhaps due to the lack of competition from other closely related byturids. This genetic diversity probably renders the American beetle more adaptable as a pest.

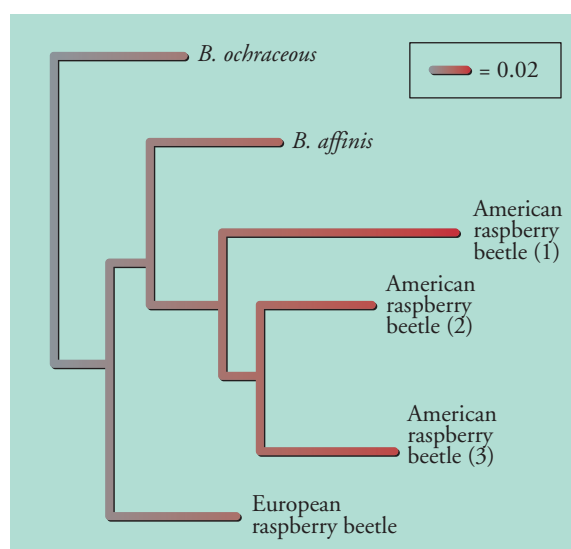


Figure 2 A representative phylogenetic tree constructed from a maximum likelihood analysis of rDNA and mitochondrial sequences of byturid beetles. The American raspberry beetle had three biotypes indicated 1, 2, and 3.

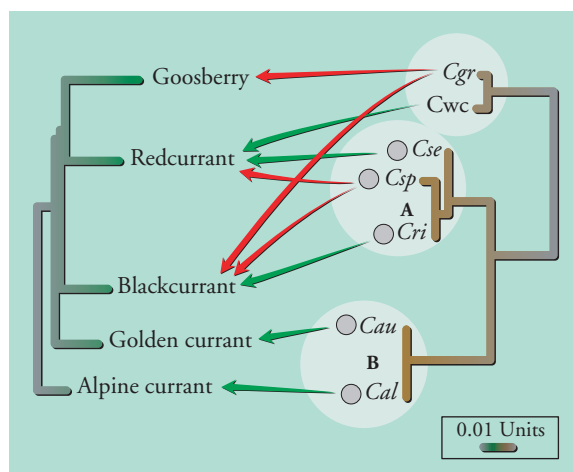


Figure 3 The phylogenetic trees constructed from maximum likelihood analyses of the rDNA sequences of *Cecidophyopsis* mites and their host plants. The shaded circles represent those species which cause galls on the plant. The green arrows indicate the host plant for mites with single hosts and the red arrows those for mites with two hosts.

For the *Cecidophyopsis* mites, the phylogenetic analysis was taken one step further, as an assessment was also made of the genetic diversity of their host plants⁴. Therefore, it was possible to subject samples of host DNA to exactly the same analysis as the mites. This provided two molecular phylogenetic trees, which could then be compared directly (Fig. 3) to give detail about how the two groups of organisms related to each other. The main points can be summarised as follows: 1) The *Ribes* host plants appeared to have undergone a rapid diversification early in their evolutionary history and since then there has been relative stability. 2) The mites have undergone continuous evolution, with very recent diversification events giving rise to three groups. 3) There is little correlation (phylogenetic tracking) between the mite's evolutionary history and those of

the host plants. 4) There is correlation in the gall forming character with the two non-gall forming mites being closely related, yet their host plants are not. 5) Two mite species appear to have more than one host, whilst the rest have a single *Ribes* host.

This work has discovered that three of the main soft fruit pests of the world have not been evolving along with their hosts, and so are likely to be able to adapt to new challenges. This is based on the following observations: 1) Host switching, such as when *C. aureum* colonises *R. aureum* in Europe although the plant originated in America. 2) Two mite species have more than one host. 3) The byturids have colonised raspberry at least twice to give rise to the European and American raspberry beetle lineages. 4) The American raspberry beetles contain three genetic lineages, which are likely to indicate extended phenotypic capabilities. This information can now be used to test new control strategies on the full range of pest potential, providing more durable pest resistance in the long term. One major aim of SCRI is sustainable agriculture using pest-resistant crops to decrease dependence on pesticides. Other benefits of this fundamental research are: 1) Information for deployment strategies (and models) for resistant crops. 2) Arthropod-plant interactions can now be studied on ecological and evolutionary time scales and we can therefore compare the effects of intensive agricultural selection with longer-term effects.

References

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