

## GUEST EDITORIAL



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### **Centrifugal Phylogeny as a Basis for Non-Target Host Testing in Biological Control: Is it Relevant for Parasitoids?**

Practitioners of biological control need to conduct nontarget host testing prior to field release of exotic organisms. The determination of which organisms to test has been criticized as “*a matter of tradition, expediency, and convenience*” (5). In fact, there is currently no robust or intellectually satisfying framework for identifying the range of potential nontarget species.

Weed biocontrol has historically entailed more rigorous nontarget testing than biocontrol of arthropods. Principles and protocols for testing weed agents have been effectively implemented for 50 years, whereas those for arthropod agents are in their infancy. We who work with parasitoids could benefit from the experience of weed biocontrol practitioners.

Central to the practice of specificity testing in weed biocontrol is the concept of centrifugal phylogeny, where the agent is exposed to a sequence of plants from those most closely related to the target weed to progressively more distantly related plants, until the host range has been circumscribed (9). There are several reasons why this may not be the best available framework for testing the host range of parasitoids.

Arthropod species often outnumber plant species in communities by an order of magnitude, and many arthropods remain undescribed. In Hawaii, there are only about 1,000 species of native plants, but over 10,000 species of native arthropods. Approximately 99% of these plants have been described, whereas only 50% of the arthropods even have names. In New Zealand the situation is similar, with ~2,000 native plants and ~20,000

native insects. Again, only half of the arthropods are described. The trend in other island and continental ecosystems is undoubtedly similar. While it is difficult to quantify the confidence we have in proposed phylogenies for these taxa, it would likely be proportional in a broad sense to our overall knowledge of the species pools.

This lack of knowledge of arthropod phylogeny is not restricted to obscure families. Tephritid flies have been extensively studied around the world because of their importance as agricultural pests and their usefulness as biocontrol agents against weeds. Yet, there is no generally accepted higher classification of the tephritids (10). Many of the nontarget tephritids that might be at risk from parasitoids in Hawaii fall into what taxonomic experts acknowledge is an 'ill-defined tribe' (the Tephritini), which contains exotic and endemic species; gall-formers and flower-head feeders; endangered species and beneficial biocontrol agents. With no further knowledge of the phylogeny, how do we circumscribe the range of species requiring testing?

While herbivore specificity reflects the outcome of evolutionary strategies to solve compatibility problems (host finding, nutrition, defense mechanisms) primarily for one trophic level, parasitoids must routinely adapt to an arthropod host, a plant host, and the interaction of the two. In fact, many parasitoids are known for which host range is characterized in large part by microhabitat characteristics rather than by the hosts themselves.

Eulophid parasitoids in the genus *Pnigalio* attack widely divergent hosts in the Hymenoptera, Coleoptera, Lepidoptera, and Diptera. The organizing principle is that all hosts are leafminers – there is no relation to phylogeny. Another eulophid, *Chrysocharis gemma*, parasitizes lepidopterous larvae on evergreen oak and dipterous larvae on holly – the defining element is the fact that the plants retain leaves through the winter. Other parasitoids restrict their hosts to those that occur on certain plant taxa, or to plants of a certain height, or even to those on only the upper or lower leaf surface (1). Parasitoids in the genera *Pachycrepoides*, *Spalangia* (Pteromalidae) and *Dirhinus* (Chalcididae) attack tephritid pupae in the soil, ignore related tephritids in nearby galls or flower-heads, but parasitize housefly and dung fly pupae – the defining factor being the location of hosts in the soil.

Phylogenetic disjunction in host range is not unique to parasitoids. Some herbivores also attack non-related hosts that share certain chemicals. Certain *Papillio* swallowtails feed on unrelated plants in the Umbelliferae and Rutaceae because they contain similar flavonoids. However, in parasitoids the disjunctions appear to be the rule, rather than the exception.

Wapshere (9) outlined several additional criteria for selecting hosts to test in weed biocontrol, in order to safeguard against failure using the centrifugal method. However, these criteria focus on cultivated plants of economic importance whereas parasitoids, in contrast, are usually indicted for impacting rare or endemic, non-economic hosts (4).

In a biocontrol project against medfly (*Ceratitis capitata*) in Hawaii, we have imported several opiine braconid parasitoids from Africa and Australia that successfully attack the target. However, there are at least 31 non-target tephritids that are potentially at risk from new parasitoids, including five introduced species used for biocontrol of weeds, and 26 species endemic to Hawaii, some of which are candidates for inclusion on the Federal Rare and Endangered Species list. Potential nontarget effects are one of the main obstacles to improved fruit fly biocontrol (6).

After ascertaining that parasitoids attack the target (medfly, tribe Ceratitinae), we move out to related Dacine flies. Here, host suitability is irregular: melon fly (*Bactrocera cucurbitae*) and oriental fruit fly (*B. dorsalis*) encapsulate the parasitoids, while the closely related solanum fly (*B. latifrons*) is a suitable host. Thus, we are compelled to move further out into the subfamily Tephritinae, where a cluster of genera (*Eutreta*, *Neotephritis*, *Ensina*, *Procecidochares*, *Trupanea*) are, to the best of our knowledge, equidistant in relatedness to *Ceratitis*. Here, again, the pattern of host suitability is not clear; the endemic flowerhead feeder *Trupanea dubautiae* is not suitable, whereas the lantana gall fly, *Eutreta xanthochaeta*, and two other gall-forming weed control agents (*Procecidochares alani* and *P. utilis*) are suitable.

We are then faced with a daunting question: since the parasitoid's host range is not yet clearly circumscribed within the Tephritidae, must we conduct host testing further afield? . . . perhaps in other families of Diptera related to tephritids? Again, phylogeny cannot give us unambiguous guidelines regarding proximity among families. Furthermore, the situation rapidly becomes untenable: there are 50 other families of acalypterate muscoid flies in Hawaii. The Drosophilidae family alone contains 600 known species, and an additional 200 species that have been collected and are in museum trays awaiting description. Clearly, they cannot all be tested.

If one dissects suitable medfly larvae from fruit and presents them to braconid parasitoids in a petri dish, the wasps will walk right over the larvae without stinging. Apparently visual, tactile and olfactory cues from the fruit are necessary to elicit oviposition in the wasps. Lockwood (5) argued that we should define nontargets as ecological processes, rather than as species or material entities. Many parasitoids respond neither to the insect host itself nor to the plant itself, but to the interaction of the two, a process which often generates unique sets of stimuli. These are manifest in several forms, such as frass (insect-digested plant tissue) or semiochemicals (emitted by plants in response to herbivory and insect saliva) (8).

Since the opiine braconids introduced into Hawaii are adapted to oviposit into small, round, reddish-colored fruit (coffee berries) which vibrate from internal larval feeding, we might expect that wasps would also attack small, round, reddish-tinged galls that vibrate from internal feeding by the lantana gall fly. In fact they do (2). In contrast, flower-heads containing nontarget flies are not recognized as suitable host-habitats, and are generally ignored by the wasps (3). Orientation in the wasps is also strongly influenced by fruit odors (7).

Phylogeny is still the best starting point for predicting the host range of parasitoid biological control agents, but it must be used with circumspection. New criteria should be developed that take into account findings in parasitoid behavioral ecology which show that host range is related to the interaction of stimuli from several trophic levels and ecological sources.



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