Fundamental and specialized questions on host race formation and speciation — an introduction

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Abstract

Host race formation and speciation are at the core of the enormous insect diversification. Insect–host relationships can take many forms, ranging from parasitic to mutualistic. Despite its long history of study, many questions remain about host race formation and speciation. They are addressed in eight original papers of this special issue, including two review-type articles. In line with the scope of Entomologia Experimentalis et Applicata, they include both fundamental and applied studies. They reveal that host race formation and speciation can take many forms and that they are still active topics of entomological research.

Introduction

No species evolves in a vacuum. The power of host-associated differentiation in insect evolution is evident in how it generated some of the most species-rich groups. These mega-diverse radiations represent many different types of insect–host relationships (Mayhew, 2018). They can be adversarial in nature, such as the parasitoids and parasites with their hosts, and phytophagous insects with their host plant. In contrast are the mutually beneficial partnerships between pollinators and flowering plants. There are also ambiguous cases with less easily defined interactions, as with insects that habitually co-habituate with specific plants or animals for unclear reasons.

An important aspect of host race formation is what selective pressures cause populations to diverge. For insects, this may involve novel adaptation to different host plants or prey species, introduction to a new geographic range (e.g., for invasive species or biological control agents), or divergence in their biology for other reasons (e.g., climate change, genetic drift). As association with specific hosts increasingly differentiates populations within species, their genetic backgrounds, morphologies, and behaviors will become more distinct. Through this greater specialization on a host type, new ecological niches will develop and biotypes become more reproductively isolated from each other. Even if some gene flow remains, host race formation is an important force that drives sympatric speciation (Butlin, 1987; Bush, 1994).

Entomologia Experimentalis et Applicata has a long history in publishing studies on host race formation and speciation. The number of articles on this topic exceeds 300 over the period 1968–2021 including seminal reviews by Feder & Filchak (1999) and Matsubayashi et al. (2010) as well as several case studies in the last few years (e.g., Saint Jean et al., 2018; Tadeo et al., 2018; Fogliata et al., 2019; Hensen et al., 2020). It becomes clear from these publications that many questions remain concerning host race formation. Just as there has been debate and ambivalence on species concepts, the same applies to host races — what exactly constitutes a distinct host race? How can this be tested and how can races be delimited? Are host races indicative of speciation events in action or are they reflective of phenotypic plasticity of host range use? How do factors that work converse to host race formation, for example, genetic recombination or increased admixture, influence its effects? Does identification or application of the wrong host race have consequences for practical matters of conservation, insect-vector disease control, and agricultural pest control? Such questions are at the heart of this special issue.

This special issue

Several articles explore the fundamental nature of host race formation itself. In a quantitative assay, Harrison et al.
Jadera haematoloma

soapberry bug
to a new host. Another textbook example is the phenotypic changes occur in insects following adaptation to a new host. What if the insect itself has moderate dispersal ability? A study on the herbivorous ladybird beetle Henosepilachna pustulosa (Kono) (Coleoptera: Coccinellidae) and its thistle host Cirsium boreale Kitam (Asteraceae) investigates these questions (Fujiyama et al., 2022). It finds that host race formation can occur just as strongly under these circumstances as immobile insects on heterospecific hosts. Intuitively, it is expected that specialized groups have strongly defined population structure in relation to their hosts. By investigating Tometoplagia flies (Diptera: Tephritidae) specialized on Asteraceae flower hosts, Leal et al. (2022) demonstrate that geographic and genetic structure can be absent even in groups with highly specialized host association.

The role of invasive species in host race formation is a topic of current interest. As there can be repeated introductions of a single species, how consistent are host-shift events for different introductions? How do they assist with or detract from that species’ host specialization or survival in a new environment? And how does this affect host use of native species? To answer this, Mattson et al. (2022) compare a newer Pacific Northwest establishment of English pea aphid, Sitobion avenae (Fabricius) (Hemiptera: Aphididae), adapted to different grains. In doing so, they implicate the significance of chemical physiology in host race formation.

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Another major aspect of host race formation is what phenotypic changes occur in insects following adaptation to a new host. Another textbook example species is the soapberry bug Jadera haematoloma (Herrick-Schäffer) (Hemiptera: Rhopalidae). Its adaptation to Mexican buckeye, Ungnadia speciosa Endl. (Sapindaceae), represents a host shift to a species with highly dissimilar biology to previously recorded hosts. Comerford et al. (2022) tested for corresponding changes in morphology and behavior and found differentiation in mouth parts, reflecting changes in feeding traits. Herbivorous insects must be able to contend with the chemical defenses of their plant. Zhang et al. (2022) detect variation in the expression of genes important for breaking down secondary metabolites in biotypes of English pea aphid, Sitobion avenae (Fabricius) (Hemiptera: Aphididae), adapted to different grains. In doing so, they implicate the significance of chemical physiology in host race formation.

In line with the fundamental as well as applied research scope of Entomologia Experimentalis et Applicata, other articles examine the applied implications of host races. Gene drives have been proposed as a means to suppress pests. By introducing a genetic sterilizing element that rapidly spreads in a population, problematic insects can potentially be controlled quickly and even permanently. However, host races may complicate gene drive efficiency. Medina (2022) reviews the ways that the presence of multiple host races can dampen gene drives, ranging from slowing down its spread to ecologically and geographically isolating its effects. Parasites both divert resources from their hosts and can also transmit disease. Their strength of association with their environment and different species will affect the degree of detriment they inflict on each of their host classes, because preferred hosts may be more susceptible. For example, the American dog tick, Dermacentor variabilis (Say) (Acar: Ixodidae), includes humans in its host range and is a carrier for multiple pathogens. Tietjen et al. (2022) execute a genetic study to detect host-associated differentiation for different mammal classes and a surprising free-living race on vegetation. They discuss what this may mean for the epidemiology of tularemia and Rocky Mountain fever.

Overall, this special issue provides new insights on how the many forms of host race formation in insects and allies come about. The presented studies reflect a multitude of outcomes in both fundamental and applied settings.

Author contributions
Kelley Leung: Conceptualization (equal); Formal analysis (lead); Methodology (lead); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (supporting). Leo W Beukeboom: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (lead); Validation (supporting); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (lead).

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