



# Editorial overview: Ecology: Ecological adaptation in agroecosystems: novel opportunities to integrate evolutionary biology and agricultural entomology

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Entomologists have long puzzled over how insect herbivores rapidly adapt to agroecosystems. As early as 1865, Benjamin Walsh wondered where the ‘New Potato-bug’, later named the Colorado potato beetle, came from as it started ravaging potato plants in the Midwestern USA [1]. Walsh also hypothesized in 1867 that the apple maggot, now *Rhagoletis pomonella* Walsh, attacking apples was ‘only a local race of the species that has acquired the habit’, and proceeded to describe host race formation. Although many early observations on rapid evolution focused on insects adapting to agroecosystems, the fields of evolutionary biology and agricultural entomology have unfortunately remained widely separated over time. In this Special Issue on ‘Ecological Adaptation in Agroecosystems’, we highlight how the study of rapid evolution of insects to agroecosystems can lead to new insights in both fields. Insect pests are under distinct and strong selection pressures in agroecosystems compared to natural systems, which provide not only important case studies of natural selection in ‘real time’, but also new perspectives on mechanisms underlying rapid evolution for evolutionary biologists. For agricultural entomologists, a major challenge is to understand how to manage the ability of insect pests to rapidly evolve in response to pest control measures and to develop novel pest control tactics based on this knowledge.

Compared to natural habitats, agroecosystems are ecologically novel systems because they support abiotic and biotic conditions that are clearly extreme based on the ecological history of a particular place [2]. The earliest crop plants were domesticated as early as ~13 000 years ago [3], at the end of the Pleistocene in several discrete geographical regions [4–6]. As early farmers migrated to new territory, they brought crops with them, setting in motion the dispersal processes that led to the current global distribution of crop plants [7,8]. Agroecosystems are distinct from natural ecosystems because: first, human selection during domestication and breeding results in crop phenotypes that do not occur in nature [9–11], second, humans have modified the selective environments of agroecosystems through cultivation and management [12], and third, major crops are grown far from their region of origin in novel abiotic and biotic conditions [13].

The individual evolutionary histories of insect pests can be influenced by crop cultivation, human-mediated migration, hybridization, and host shifts [14,15]. Insect herbivores become pests in agroecosystems via two major modes of evolution, either through a previous association with the wild crop ancestor or by host shifts from native plants onto introduced crops [15]. In

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this Special Issue, Bernal and Medina [16] discuss how the origins of insect pests in agriculture are closely linked with human history. For example, the population genetic structure of the corn leafhopper, *Dalbulus maidis*, likely expanded its geographic range with the expansion of maize cultivation [17]. This can have important implications for how patterns of pest genetic diversity are shaped, and research has shown that some pests recruit considerable genomic diversity as they shift into agroecosystems [18]. Studying historical demography remains a critical component of understanding how insect pests rapidly evolve [19–26].

Although agroecosystems select insect pests and natural enemies, it is surprising how limited research has been on insect evolution in agriculture. Using the keywords (insect and (evol\* or adapt\*) and (agriculture\* or agroeco\* or domestic\*)), but excluding diseases, resistance to insecticides, and transgenic crops, we were surprised to find a short list of only 300 studies. A notable exception can be found in the edited volume, 'Evolution of Insect Pests: Patterns and Variation' [27] in which contributing authors discussed how variation in agriculture at different scales, such as geographic, environmental, habitat, and host plant, influences patterns of evolution. Most studies on adaptation of insect pests to agriculture have focused on the evolution of resistance to both insecticides and insecticidal transgenes. Broadening search terms yielded some of the most well-known cases of rapid evolution in insect pests, such as sympatric speciation of the apple maggot fly, *Rhagoletis pomonella* [28] and crop rotation resistance in the western corn rootworm, *Diabrotica virgifera virgifera* [29]. By using the terms (evol\* or adapt\*) and insect and (insecticide\* or transgenic or Bt), we found a total of 1764 studies. While not exhaustive, the results from our search suggests that our collective research effort and understanding of ecological adaptation in agroecosystems needs to grow.

Compared to insect herbivores in natural systems, crop pests that attack globally-traded crops have more opportunities to invade new geographic regions [30], where they are exposed to new selective forces in the form of climate or environmental variation, host plants, and management practices [22,31,32]. Given their economic importance, agricultural entomologists have been monitoring many pest populations since their emergence as pests across broad cropping areas, yielding a wealth of temporal and spatial data. Such data could be enormously useful for understanding temporal and spatial dynamics of evolution, questions that would be difficult to approach in natural systems. Pélissié *et al.* [33] argue that spatial and temporal variation in pest populations provide unique opportunities to develop hypothesis-driven population genomic research on adaptive evolution. While Pélissié *et al.* discuss opportunities to examine historical selective processes, there is still the puzzle of explaining how contemporary selection results in rapid adaptive processes. Brevik *et al.* [34] offer a new hypothesis on the possible role of transgenerational epigenetic effects in contributing to evolution of new insecticide-resistant phenotypes.

Aphids have been particularly successful in rapid phenotypic evolution within agroecosystems, and new research provides insight on the biological basis for their success. Figueroa *et al.* [35] provide evidence that obligate parthenogenesis, in combination with phenotypic plasticity and host plant abundance, are key drivers mediating aphid invasions. Following invasion, Simon and Peccoud [36] discuss how aphids employ multiple mechanisms to facilitate adaptation, ranging from a high mutation rate to the critical role of facultative endosymbionts. A remarkable range of evolutionary mechanisms has led to aphid success in exploiting new host plants, resisting insecticides,

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