# Rapid evolution in insect pests: the importance of space and time in population genomics studies

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Pest species in agroecosystems often exhibit patterns of rapid evolution to environmental and human-imposed selection pressures. Although the role of adaptive processes is well accepted, few insect pests have been studied in detail and most research has focused on selection at insecticide resistance candidate genes. Emerging genomic datasets provide opportunities to detect and quantify selection in insect pest populations, and address long-standing questions about mechanisms underlying rapid evolutionary change. We examine the strengths of recent studies that stratify population samples both in space (along environmental gradients and comparing ancestral vs. derived populations) and in time (using chronological sampling, museum specimens and comparative phylogenomics), resulting in critical insights on evolutionary processes, and providing new directions for studying pests in agroecosystems.

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## Introduction

Insect agricultural pests are responsible for substantial economic losses annually and are a threat to global food security [1]. Implementing effective and efficient management strategies to control pest outbreaks is very challenging, as it relies on comprehensive knowledge of the pest's biology and ecology, as well as anticipating evolutionary changes that exacerbate pest management problems. To address these challenges, agricultural research has increasingly incorporated fundamental research in population genomics to understand the processes driving adaptive change and the genetic architecture of pest traits [2].

For more than two decades, population genetics approaches have been used to trace insect pest histories [3] and understand how genetic variation contributed to the success of pest populations [4]. An important step in controlling nascent pest outbreaks is to reconstruct the pest's expansion routes and describe its demography, in order to restrain further migration and the influx of additional genetic variability. For example, the spotted wing Drosophila (*Drosophila suzukii*) was discovered in the USA in 2008 [5], and it took less than a year to spread from California northwards along the West coast, and then subsequently from Florida north to the Midwest and East Coast [6]. Model-based phylogeographic studies provide a way to test hypotheses about the geographical origin(s) of pest populations. They are also well-suited to assess the role of recurrent introductions and admixture between populations [7], which can be crucial in determining the probability that a pest will continue to expand its range. In addition, identifying the pest's geographical origin and recovering its invasion history can lead to the identification of potential agents of biological control [8].

An important remaining challenge is to understand the evolutionary changes species undergo to become pests, particularly the mechanisms underlying niche shifts that result in economically damaging pest outbreaks [9]. This is especially relevant for managing insect pests in agricultural environments that are often (in comparison to natural environments) homogeneous, widespread, predictable and composed of host plants with relatively low genetic diversity [10], which facilitates species' rapid adaptation because of a simplified landscape of selection pressures [11]. In the case of insect pests, selection pressures include host plant traits, climatic conditions and human-imposed stressors like pesticides or crop rotation. Whether pest species (and invasive species) have properties that facilitate adaptation to novel selection pressures (or environmental stress in general) is still under debate [9,10,12], but there is little doubt that some pest species exhibit a high potential for rapid evolution. For example, while the European corn borer (*Ostrinia nubilalis*) [13] and U.S. populations of the pink bollworm (*Pectinophora gossypiella*) [14] have remained susceptible to transgenic Bt toxins for many generations, western corn rootworm (*Diabrotica virgifera virgifera*) developed resistance within a few years of exposure to the toxin [15]. Some pests

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**Glossary**

*De novo* **mutation:** A mutation that appears in a population for the first, creating *de novo* (as opposed to standing) genetic variation.
**Standing genetic variation:** The presence of several alleles at a locus in a population before a selective event, one or more of which confer an advantage under selection.
**Hard selective sweep:** A rare beneficial mutation increases rapidly in frequency in a population, due to selection. Genetic hitchhiking reduces genomic diversity around the selected mutation, leaving a marked signature of selection in the population.
**Soft selective sweep:** A previously neutral or nearly-neutral mutation, present in several genomic backgrounds (haplotypes) in a population, that becomes beneficial after a change in the organism's environment. Its increase in frequency due to the effect of selection carries several haplotypes toward fixation, and therefore results in a subtle hitchhiking effect that is often difficult to detect.
**Polygenic adaptation:** Selection causes changes in allele frequencies at several (possibly many) loci. It may result in soft selective sweeps at some of these loci.
**Gene family expansion:** An increase in the number of genes in a gene family due to duplication. New genes can accumulate mutations (including regulatory changes) to gain new function. Expanding gene families represent good candidates to detect selective events that are specific to the evolutionary lineages they belong to.

species show an extreme capacity to develop resistances to pesticides, like the Colorado potato beetle (*Leptinotarsa decemlineata*), which is a global potato pest and resistant to more than 50 different pesticides, covering all modes of action [16]. Understanding how such species can evolve so rapidly is important in pest management, where such knowledge can be used to predict population dynamics and spread, or develop more efficient control strategies. Ultimately, this research will also address fundamental questions, such as how a species becomes a pest in the first place, shedding light on the processes and constraints to biological adaptation, and not only in pests, but in any biological system.

However, detecting and quantifying selection in pest species is not an easy task (Box 1). The range of approaches include comparing phenotypic distributions of ancestral and derived populations [17], conducting experimental evolution assays [18], modeling the response to selection of specific traits [19], and looking for genetic signatures of selection [20,21,22•,23,24]. Although potentially very powerful, the latter approach has long been constrained to model systems [10], due to the difficulty of obtaining genomic data and to the analytical challenges inherent in discerning genetic evidence of adaptation. Most research in non-model species has instead focused on candidate traits or genes, or simplified laboratory experiments. Recently, these constraints have been removed by the development of inexpensive high-throughput sequencing methods [25,26], of sophisticated population genomics approaches [10], and of collective efforts like the i5K initiative, dedicated to increasing the number of sequenced arthropod genomes [27]. The real challenge now lies in making sense of this sudden flood of genomic information by developing knowledge of

**Box 1 Studying adaptive processes in pest species: questions, challenges and solutions.**

*Asking fundamental questions for applied solutions:*

Some central evolutionary questions are crucial to understanding adaptive mechanisms at play in pest species. For example, the relative role of selection on standing genetic variation versus *de novo* mutations is of prime importance [55,58]. Although new mutations are often assumed to be rare, pest populations are large and mutation might not be limiting [59]. Then, is standing genetic variation necessary for invading pests to rapidly evolve? Similarly, the debate on the monogenic versus polygenic nature of adaptation in pest insects has important implications, especially for the management of insecticide resistance [60]. Management practice typically assumes that resistance evolves from monogenic changes of large effect, but increasing evidence suggests polygenic adaptation is common [61].

Disentangling the relative importance of adaptive mechanisms could improve our integrated pest management practices, but it is a challenging problem in many cases. It relies on our ability to detect signatures of natural selection, including soft selective sweeps which are statistically difficult to distinguish from neutral variation [58]. Soft sweeps are expected under both selection from standing variation (because adaptive alleles are associated with multiple haplotypic backgrounds) and polygenic selection (as multiple loci of varying effect size and initial frequency are selected upon).

Another very exciting area of research explores how phenotypic traits such as host–plant breadth provides standing genetic variation that enables rapid adaptation to human-imposed stressors like pesticides or crop rotations [62]. For example, are polyphagous insects more likely to become pests than monophagous species? Do species feeding on relatively toxic plants possess genetic variation in detoxifying mechanisms allowing them to evolve pesticide resistance more rapidly than species relying on less toxic hosts [63]?

*Disentangling the effect of neutral versus adaptive processes:*

Reconstructing the demographic history of pest populations is crucial to distinguishing between neutral and adaptive processes underlying their genomic changes. Tests of selection are more accurate when null models incorporate demographic history [64], and sites and regions under selection tend to bias demographic reconstructions. One approach is to separate neutral sites from selected loci *a priori*, for example by assuming synonymous sites in protein coding regions and all non-coding regions are neutral. Although removing non-synonymous sites is feasible in almost any system, parsing sites in coding regions requires (often unavailable) knowledge of the genome composition (i.e. the availability of a official gene set — OGS), and even non-coding regions can be indirectly affected by selection if they contain regulatory elements or are linked to selected sites. Therefore, careful data curation, including the use of methods that separate neutral and selected loci, are important for unbiased estimates of demographic history, which might include population size change or admixture events.

*Leveraging known patterns of adaptive divergence among populations:*

Although neutral processes shape the distribution of phenotypes within and between populations via the combined action of mutation, migration, and genetic drift, adaptive processes do so under selective pressures that can act divergently across heterogeneous environments or in parallel across environmentally similar, but geographically isolated habitats.

*Local adaptation* occurs when genotypes have reciprocally higher fitness in their local habitat than they do in other habitats [34]. Local adaptation relies on selection acting differentially across landscapes, where biotic (e.g. host plant condition, competitors, or the presence of predators and pathogens) and abiotic (e.g. climatic variation and