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Current Opinion in
Insect Science

Role of dispersal in resistance evolution and spread

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Gene flow via immigration affects rate of evolution of resistance to a pest management tactic, while emigration from a resistant population can spread resistance alleles spatially. Whether resistance detected across the landscape reflects ongoing *de novo* evolution in different hotspots or spread from a single focal population can determine the most effective mitigation strategy. Pest dispersal dynamics determine the spatio-temporal scale at which mitigation tactics must be applied to contain or reverse resistance in an area. Independent evolution of resistance in different populations appears common but not universal. Conversely, spatial spread appears to be almost inevitable. However, rate and scale of spread depends largely on dispersal dynamics and interplay with factors such as fitness costs, spatially variable selection pressure and whether resistance alleles are spreading through an established population or being carried by populations colonizing new territory.

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Current Opinion in Insect Science 2017, **22**:xx–yy

This review comes from a themed issue on **Social insects**

Edited by **Amy Toth** and **Adam Dolezal**

<http://dx.doi.org/10.1016/j.cois.2017.04.005>

2214-5745/Published by Elsevier Inc.

Introduction

Insect dispersal plays a pivotal role in both the evolution of resistance to an insecticide or other management tactic at a location, and in the rate and pattern of its spatial spread [1,2]. Dispersal by individual insects is the fundamental process by which resistance genes move across a landscape. Consider a population where resistant individuals are favored by local selection. At its simplest level, immigration of susceptible individuals decreases the frequency of resistance alleles in the receiving population and thus slows the local rate of resistance evolution. Conversely, immigration of resistant individuals increases

resistance allele frequency and thus increases the rate of resistance evolution in that population. Immigration in one population presupposes emigration from another, and the rate of emigration of individuals from a resistant source population affects the rate of resistance spread in the landscape (Figure 1). The relative roles of *de novo* resistance evolution vs. subsequent spread can be of great practical importance because it determines the most appropriate mitigation strategy to be employed. The spatial scale at which mitigation tactics must be applied within the larger landscape to contain or reverse resistance that has evolved in a local ‘hotspot’ depends on dispersal dynamics of the species. As critical as these rates of inflow and outflow are to all aspects of insect resistance management (IRM), they are poorly understood for most species. Accordingly, the complex dynamics of resistance evolution and spread are likewise difficult to characterize.

A distinction can be made between dispersal that moves resistance genes between existing populations by gene flow, and dispersal that moves resistance genes into new territory as the insect colonizes previously unoccupied habitat. The first involves a process that can be likened to an invasion of resistance alleles into parts of the larger metapopulation that originally had none. The second, colonization of new habitat by insects carrying resistance alleles conflates the spatial invasion of alleles via gene flow with the genetic consequences associated with geographic invasion by a species, such as bottlenecks. The evolutionary ecological outcomes of both processes can be quite interesting.

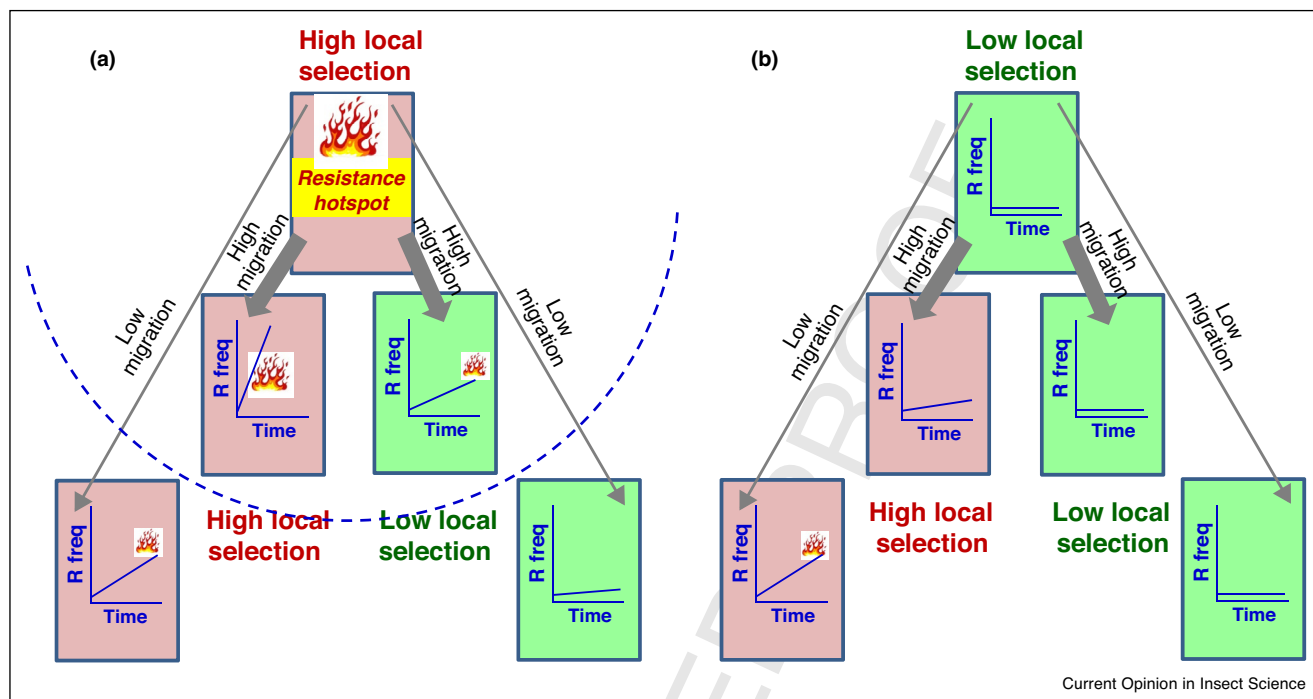
Spread of resistance among existing populations

Case study: *Culex pipiens* resistance allele clines

An especially well studied case of the spatial and temporal distribution of resistance alleles in established populations comes from the mosquito *Culex pipiens* in the south of France [3–6]. In this case, the dynamics of resistance were studied at a small geographical scale relative to dispersal distances. Consequently, alleles have usually been observed at migration-selection equilibrium. In this region there is an annual program of mosquito control whereby breeding sites within approximately 20 km of the Mediterranean coast are treated with insecticides every breeding season. This program relied heavily on organophosphate insecticides (OPs) until the mid 2000s, when they were replaced with *Bacillus thuringiensis*. Resistance by southern French populations of *C. pipiens* to OPs involves both mutations that render the OP target, acetyl cholinesterase, less sensitive to the insecticide, and that increase expression of detoxifying

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Figure 1



Schematic conceptualization of the effects of rate of migration from (a) a hotspot of resistance, or (b) a wild-type susceptible population, into receiving populations of high or low selection for resistance on relative rates of increase in resistance allele frequency (R freq) over time (generations). The dashed arc indicates the region around the resistance hotspot within which mitigation tactics must be implemented to slow the spread of resistance alleles through the larger landscape. Determining the spatial scale at which mitigation will effectively contain spread of resistance from a hotspot depends in part on the insect's dispersal rate and distance, and on spatial variation in selection pressure across the landscape. In practice, this scale can be very difficult to determine. If it extends beyond the dimensions of a farm, implementation of coordinated mitigation tactics by growers across an area may be necessary, with all the difficulties that implies. Thus, rapid implementation of mitigation around a still-localized hotspot offers the best hope of containment (see Andow *et al.* [22**] for discussion in the case of *D. v. virgifera*).

92 esterases that degrade the insecticide. Both forms of
 93 resistance entail significant fitness costs in the absence
 94 of insecticide. The interplay of gene flow mediated by
 95 mosquito dispersal, selection for resistance near the coast,
 96 and fitness costs further inland produces clines in
 97 resistance allele frequencies. A joint analysis of the clines
 98 in target-site insensitivity and esterase overproduction
 99 produced an estimate of the standard deviation in
 100 parent-offspring dispersal of 6.6 km [3]. This rate of
 101 dispersal was sufficient to rapidly reestablish selection-
 102 migration equilibrium each year at both loci [4]. In the
 103 case of the *Ester* locus in southern France, the *Ester*²
 104 resistance allele increased in frequency between 1999 and
 105 2002 but did not replace *Ester*⁴ despite a higher level of
 106 resistance, because it also imposed a higher fitness cost
 107 in the absence of insecticide [5]. After the use of OPs was
 108 discontinued in 2007, the *Ester*² allele was rapidly lost
 109 from the population. The *Ester*⁴ allele persisted but the
 110 cline in *Ester*⁴ frequency, while still significant, flattened
 111 markedly [6], presumably due to a combination of
 112 reduced selection at the coast and gene flow between
 113 the coast and inland.

Case study: spread of *Diabrotica virgifera virgifera* rotation resistance

114
 115
 116 Resistance to crop rotation in the western corn rootworm,
 117 *Diabrotica virgifera virgifera*, provided an opportunity to
 118 observe resistance spreading over a wide area as it
 119 occurred. Thus, the spatiotemporal dynamics of
 120 resistance were observed at a much larger geographical
 121 scale relative to adult dispersal distance than in the case of
 122 *C. pipiens* described above, so that alleles were not at
 123 migration-selection equilibrium during their years-long
 124 invasion of the surrounding metapopulation. The basic
 125 biology and history of adaptation to crop rotation by *D. v.*
 126 *virgifera* was comprehensively reviewed by Gray *et al.* [7].
 127 Resistance to crop rotation is almost certainly based on a
 128 reduced preference for cornfields by females as oviposition
 129 sites. Thus in landscapes dominated by corn-soybean
 130 rotated crop fields, eggs (the overwintering stage) laid
 131 outside of corn have a better chance of hatching in a
 132 cornfield the following year than those that were laid in
 133 corn. In contrast to OP resistance in *C. pipiens*, the precise
 134 genetic basis of adaptation to crop rotation is not known.
 135 Recent research has focused on adaptations that allow

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