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Review

Evolutionary consequences of long-distance dispersal in mosquitoes

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Long-distance dispersal (LDD) provides a means for mosquitoes to invade new regions and spread adaptive alleles, including those conferring insecticide resistance. Most LDD takes place on human transport vessels and will typically be rarer and more directionally constrained than active flight but can connect populations and regions that are otherwise mutually inaccessible. These features make LDD worthy of specific consideration in mosquito research. This paper reviews recent evolutionary research on LDD and its consequences for mosquito populations and mosquito control. LDD is the main source of mosquito range expansions, and genomic methods can now trace the origins of new invasions to specific towns or cities. Genomic methods can also give a rough indication of the number of invaders, which if very small may lead to the stochastic loss of advantageous alleles during invasion bottlenecks. Once invasions are established, LDD spreads adaptive alleles between populations. Emerging insights into insecticide resistance evolution indicate that LDD has repeatedly spread resistance mutations across global species ranges, but these broad patterns are convoluted by two other evolutionary processes: parallel adaptation at the same gene or gene cluster and polygenic adaptation at different genes in different populations. Together, these processes have produced patterns of similarity and dissimilarity at resistance genes that are decoupled from geographical distance. LDD within cities is less well studied but is important for planning and evaluating local control efforts. Urban investigations of LDD may help identify areas experiencing weaker selection pressures from insecticides and isolated areas to target for control.

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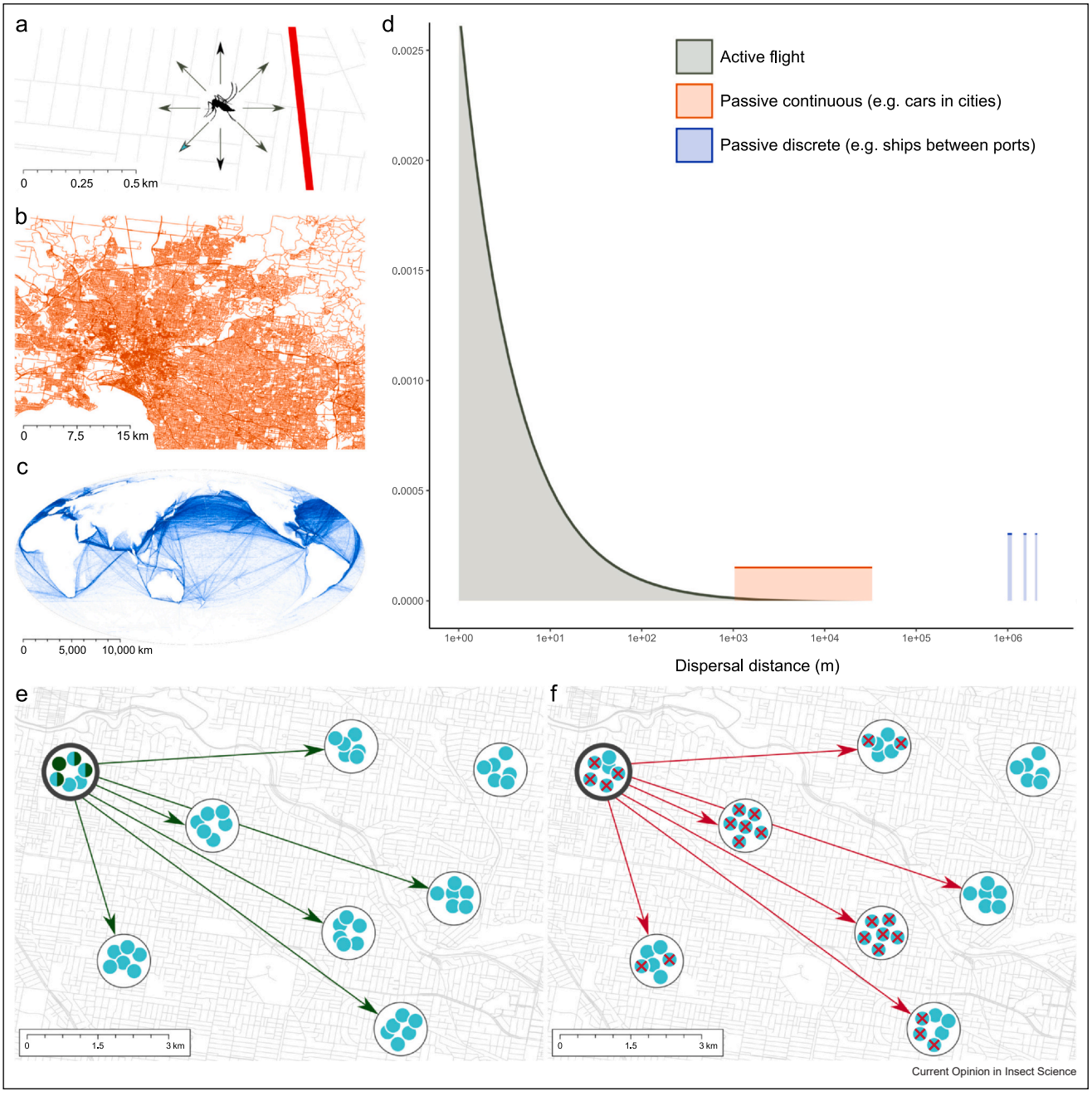
Introduction

Mosquitoes are internationally notorious vectors of human disease. Notably, only a small subset of the >3500 species of mosquito transmit human disease, and disease transmission is often taxon specific, including malaria (*Anopheles* spp.), dengue (*Aedes* spp.), and West Nile virus (mostly *Culex* spp.). Some globally distributed mosquito diseases are spread by different local taxa in each country [1], but others are more taxon specific [2]. For instance, almost all dengue is transmitted by two mosquitoes, *Aedes aegypti* and *Ae. albopictus*, yet dengue is one of the most geographically widespread threats to human health worldwide. When disease transmission is species specific, disease risk is limited by the geographical range of the vector.

Most mosquitoes disperse weakly by active flight (Figure 1a). Although flight distances of 2–3 km have been reported in some *Aedes* [3,4], *Culex* [3,5], and *Anopheles* [6], anthropophilic species like *Ae. aegypti* may fly only 10s–100s of metres in a lifetime [7,8]. Underlying the global distributions of many mosquitoes is an additional dispersal process, that of passive, long-distance dispersal (LDD). LDD usually occurs through accidental human transportation on air, road, and shipping networks (Figure 1b,c), but wind-driven dispersal of *Anopheles* spp. [9] is also an LDD mechanism. LDD is rarer than active flight but allows mosquitoes to expand their geographical ranges by invading new areas. Mosquitoes from any life stage can undergo LDD [10,11], though transportation of adults may be through different mechanisms than eggs, larvae, and pupae.

As well as expanding mosquito ranges, LDD connects mosquito populations that receive little to no gene flow through active dispersal. This migration may result in genome-wide admixture [12,13] or introgression of selectively advantageous alleles, such as those conferring insecticide resistance [12,14]. Mosquito LDD is thus a critically important issue for biosecurity and human health, as it introduces mosquito disease to new locations while making the vectors harder to control with insecticides. LDD is also an important consideration in rear-and-release mosquito control programmes such as those using *Wolbachia* bacteria [15] or gene drives [16], where LDD may reduce the effectiveness of these strategies.

Figure 1



Modelling dispersal within and between urban environments. **(a)** Active flight within a city. Dispersal is directionally unconstrained (isotropic) apart from a road barrier (red line). **(b,c)** Passive dispersal networks that are roughly continuous within cities (**b**, road network) but discrete between them (**c**, shipping network). Passive dispersal along these networks will be more directionally constrained than active dispersal. **(d)** Active and passive dispersal kernels. Active flight follows a near-Gaussian distribution with a slightly longer tail. Passive continuous follows a uniform distribution between minimum and maximum distances of urban car travel. Passive discrete models dispersal between three seaports or airports. The y-axis is not to scale for the passive dispersal kernels. **(e,f)** Spatial heterogeneity across a large urban population following LDD into a single subregion or neighbourhood. Black rings enclose sampling areas, and the heavy black ring indicates the site of LDD. Circles indicate sampled individuals. Arrows indicate subsequent LDD into other subregions. **(e)** A large LDD propagule leads to local genome-wide admixture (dark green) around the site of LDD, but this does not spread to other subregions. **(f)** LDD introduces a large-effect allele (red cross). Subsequent LDD spreads the allele into other subregions where it occasionally fixes. The absence of the allele from other subregions may be due to different selective pressures or isolation from other subregions. Mosquito image credit: Ana Ramirez.
(b) Data from https://mapcruzin.com/. (c) Data from Halpern et al. [62]

This review considers the evolutionary consequences of LDD in mosquitoes. Specifically, I consider the consequences of LDD in relation to (i) the establishment of mosquito invasions; (ii) gene flow between populations, including the spread of insecticide resistance; and (iii) urban mosquito management, including rear-and-release programmes.

Long-distance dispersal in mosquitoes

Mosquitoes disperse by active flight and passive transportation. This review focuses on LDD as an outcome of passive transportation specifically, most of which takes place over 10s–10 000s km. Operationally, dispersal can be defined as both the act of movement [17] or the evolutionary outcome of this movement (i.e. 'effective dispersal' [18]), and here I leave this definition open. This broad definition thus covers both individuals intercepted at borders after moving but before reproducing [10,11,19] and unobserved movement inferred from shared genetic variation [12,20]. While intercepted individuals will be evolutionarily irrelevant, each interception represents an observation of long-distance movement that can help inform our understanding of LDD if treated appropriately.

Dispersal at the population level can be represented as a *dispersal kernel*, a probability density function of the distribution of dispersal distances (Figure 1d). For active flight, kernels can follow a Gaussian or near-Gaussian distribution and may be directionally unconstrained (*isotropic*) except for dispersal barriers such as roads [7] (Figure 1a). Passive transportation may have a very different kernel, differing not just in scale but also in shape and degree of directional constraint. For instance, movement by land vehicle within a metropolis may take place over distances of 1–10s of km, may be non-Gaussian in shape, and may be directionally constrained towards city centres or other common destinations (Figure 1b). Car transport was estimated to provide 10 000s of daily passive transportation opportunities for *Ae. albopictus* within Barcelona, Spain (human metropolitan population ~5–6M) [21].

Movement between cities will mostly follow trucking, shipping, or airline routes, where dispersal is constrained in direction and distance between specific locations, such as loading bays, seaports, and airports (Figure 1c). For instance, mosquitoes disperse between international airports [10,11,22], with dispersal following the specific times and bearings of air travel. Overall, kernels that are more *leptokurtic* (with more LDD) tend to produce spatially heterogeneous patterns of dispersal [23]. LDD will also lead to correlated dispersal among individuals dispersing passively together, though in many cases, only a single individual will be transported.

Mosquito dispersal can be modelled with a single composite kernel reflecting the contributions of all passive and active movements. However, it will often be more appropriate to model active and passive dispersal separately, given differences in scale, kernel shape, directional constraint, and interindividual correlation (Figure 1d). This is particularly important when considering that some populations and regions are only accessible by LDD.

Long-distance dispersal and new mosquito invasions

Many mosquito species are undergoing current range expansions, driven in part by the tripartite anthropogenic processes of climate change, increased global supply chain complexity, and increased global urbanisation [24,25]. When a mosquito expands its range into a new country or across a sufficiently large distance, it is typically called a biological invasion, and current genomic methods can trace invasion origins to a high degree of specificity [26–28] including to specific islands in an archipelago [27] or cities within a state [27,29]. Certain traits may enable mosquitoes to be more likely to move or better survive movement over long distances, including cold tolerance [30,31], desiccation resistance [28], diapause [30], insecticide resistance [12,28], and degree of anthropophilia [32]. Regions with many LDD options may also be the source of more LDD propagules, such as large cities [33], shipping ports and tourist destinations [34], and regions with appropriate wind dispersal patterns [9].

Biosecurity detections of exotic mosquitoes at airports and seaports indicate that incursions of single mosquitoes are common [10,11,19,22,34]. Some of these will be mated females. A single-mated female is theoretically capable of establishing an invasion, provided the population remains competitive following the subsequent strong inbreeding and drift. Assuming the population grows rapidly after establishment, these effects will be manifest as a strong reduction in allelic richness, though genome-wide heterozygosity may remain at 60–70% of that of the source population [35]. While the likelihood of establishment may be reduced, it seems plausible that some mosquito invasions are started from very small propagules. A recent example is in Tennant Creek, Australia, where *Ae. aegypti* established an invasion in 2021. Immediately after establishment, the invasion was confined to a single suburban block where a single land vehicle had recently returned from the invasion source ~1500 km away [27]. Within months, the population had spread across the entire town. The stark genetic patterns of drift and inbreeding suggest a small genetic propagule, and the distance and remoteness are such that multiple introductions are unlikely. Similarly, strong drift was not observed in a comparable analysis of

reinvasion in California [29], suggesting a larger propagule was involved.

While LDD leads the mosquitoes that establish these invasions to evolutionary success, there will be many instances where a single male or unmated female undergoes transportation. This LDD will almost certainly fail to establish an invasion, as the second transportation event required to bring a potential mate is unlikely to occur in the first mosquito's lifespan.

Long-distance dispersal between mosquito populations

Genome-wide admixture

Once a mosquito invasion establishes, population size and density will grow rapidly if unhindered by local abiotic and biotic factors. This process and its outcomes can be modelled with an evolutionary application of Founder Takes All theory [36]. First, the specific genetic composition of the population will be established from a combination of founder effect (sampling error from the source population) and subsequent strong drift (sampling error from the founders). The population then rapidly grows to high density. High density helps maintain the specific genetic composition of the population, as the fecundity of new migrants will be dwarfed by the number of local offspring. Under this model we expect genome-wide gene flow resulting from LDD after the initial establishment phase of invasion to be minimal, and observations of population admixture from a second or third population to be rare.

How does this match the emerging data? There is reported admixture among *Ae. albopictus* in Europe [13] and in Papua New Guinea [12], but these appear to be from multiple proximate invasion backgrounds blending into each other after establishment, rather than from LDD. This process may be analogous to the crystallisation model of competing soft sweeps, in which admixture is only possible provided both genetic backgrounds establish in different locations before one becomes regionally dominant [37]. By comparison, admixed *Ae. aegypti* in New Caledonia are likely the product of LDD from the Americas into an established West Pacific population [12]. This break from model expectations could reflect an atypically large LDD propagule, such as during New Caledonia's time as a WWII naval base, or a low local mosquito density, such as from a strong tropical dry season or a sparse human population. Within *Anopheles* subspecies, there is often insufficient population structure to detect admixture [38,39], but hybridisation and introgression are common between subspecies and ecotypes [40,41]. Admixture can also be confounded by cryptic taxa incorrectly assigned as hybrids [42]. This pitfall is common across population genetic analyses in which uncertainty in assignment is mistaken for admixture [43].

The above model suggests that admixture from LDD may often be too faint to observe once it has diffused through a city. However, recent admixture may be detectable by sampling across multiple genetic neighbourhoods (Figure 1e). A genetic neighbourhood is the number of potential breeding individuals within a given dispersal radius (σ) [44], making this a key parameter for urban mosquito populations where active flight occurs over much smaller scales than the total population area. Mosquito neighbourhood sizes are much smaller than N_e of large urban populations, on the scale of 100–1000 individuals [4,7,45], and small neighbourhood size and large N_e are both predicted by small σ [46]. Accordingly, while population-scale admixture resulting from LDD may be rare, it may be more common for local admixture pockets to emerge within large urban mosquito populations, where stochastic processes underlying LDD lead to local introduction of novel genetic backgrounds that remain local due to the low σ of active dispersal (Figure 1e). Detecting this 'neighbourhood admixture' would require comprehensive sampling across urban areas, and such admixture may be quickly overwhelmed by local gene flow. Analogous processes have been observed in *Wolbachia* invasions of *Ae. aegypti* [47].

Introgression of adaptive alleles

Although genome-wide admixture by LDD requires a relatively large number of migrants, introgression of adaptive alleles can be initiated by any propagule size. Here, LDD drives rapid evolutionary change by transporting adaptive alleles into new populations. The best studied adaptive alleles in mosquitoes are those conferring insecticide resistance (hereafter: 'resistance'). A functional evaluation of resistance evolution is beyond the scope of this review; it is sufficient to specify that there are a range of resistance phenotypes (e.g. metabolic resistance, target-site resistance: Box 1), produced by a range of allele types (e.g. *SNPs*, *CNVs*), which confer a range of selective advantages (large- or small-effect loci: Box 2) that may be chemically specific or general (e.g. target-site or metabolic resistance).

Continuing with our previous case of LDD involving small propagules (e.g. $n < 10$), we now consider a small propagule of dispersers migrating to a distant population, bringing with them selectively advantageous alleles not found in the new population (Figure 2). As advantageous alleles will be at very low frequency in the F0 (Figure 2a) and F1 (Figure 2b) generations, stochastic effects may eliminate some alleles from the new population despite them conferring an advantage, with alleles conferring greater selective advantage more likely to be retained (Figure 2c). These advantageous alleles will then rise in frequency, producing selective sweep

Box 1 Target-site and metabolic resistance.

A common finding across *Aedes* and *Anopheles* is that genetic backgrounds at genes conferring target-site resistance, which is associated with a specific gene or gene family (though see Ref. [67]), are often distributed across multiple populations, while metabolic resistance backgrounds are geographically restricted [12,14]. These observations accord with a model of LDD in which alleles with a large, specific effect will confer such a strong selective advantage they require only a small propagule to spread into new populations, but small propagules of alleles with a small, general effect may be lost to drift if they do not confer a sufficient advantage over local resistance alleles (Figure 2). While metabolic resistance genes have previously been thought to follow this latter model [68], recent work in mosquito genomics has identified strong exceptions to this at glutathione S-transferase epsilon class (GSTe) genes [12,14,69,70] and certain specific cytochrome P450 [61,71,72] and alpha-esterase genes [73]. Alleles at these genes appear to confer large selective advantages and have spread rapidly across large geographical ranges. Local fixation of resistance backgrounds appears to be rare. This aligns with observations that partial sweeps in *Anopheles* are more common than completed sweeps [74]. It is possible this reflects a fitness cost of these backgrounds, similar to the well-characterised costs of knockdown resistance (*kdr*) mutations in the voltage-sensitive sodium channel (VSSC) [75]. However, local fixation of VSSC mutations has been observed in regions where GSTe backgrounds are segregating at intermediate frequencies [12]. Another explanation is that GSTe and P450 sweep backgrounds do not fix due to redundant resistance mutations at other loci [37], though this hypothesis remains to be tested.

Box 2 Large-effect and small-effect loci.

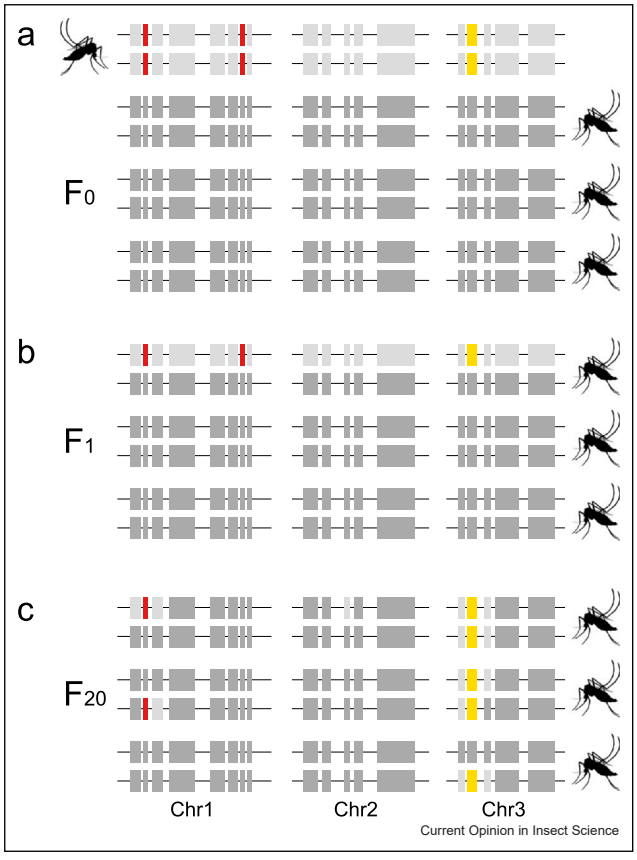
Although classifying selectively advantageous alleles as large-effect and small-effect presents a false binary, it can serve as a useful shorthand for evaluating evolutionary hypotheses. For instance, population genomic studies of mosquito resistance evolution can help evaluate the longstanding hypothesis that wild pest populations will tend to only evolve resistance at large-effect loci, while small-effect loci will be favoured in laboratory experiments [76]. This is because wild populations experience such heavy insecticidal pressure that large-effect loci are necessary for survival, while laboratory population sizes are too small to reliably have large-effect mutations available for selection and thus have to be exposed to lower insecticidal concentrations to prevent colony extinction. Recent mosquito genomic studies appear to contradict this hypothesis [12,14,48,77]. One explanation put forth by Lucas et al. [14] was that once large-effect loci are at sufficiently high frequency in wild populations, small-effect loci can then build upon those backgrounds. An additional explanation is that the large N_e in wild populations makes selection more efficient, allowing small-effect loci to escape the nearly neutral zone, while the same loci in small laboratory populations would be shaped more by drift than by selection. A final explanation is that urban mosquito environments are far more spatiotemporally heterogeneous than agricultural environments, with fine-scale variation in insecticidal intensity, frequency, location, and chemistry (Figure 1f). Thus, while agricultural pests may all experience high doses of insecticide, mosquitoes in urban environments may experience a wide range of doses and selection pressures. Effects of local environmental variation on mosquito resistance have been recently demonstrated [52].

patterns in the new population (Figure 2c). Notably, selective sweeps produced by LDD will generally be *hard sweeps*, even if they occur as *soft sweeps* in their original population, as the small propagule size and infrequency of LDD make establishment of multiple sweep backgrounds unlikely [37].

In the absence of additional mutations, LDD should eventually establish the same single resistance background at every population connected by transport networks (Figure 1c) and experiencing the same insecticidal selection pressures. However, this is confounded by two other evolutionary processes: *parallel adaptation* at the same gene or gene cluster [37]; and polygenic adaptation at different genes in different populations (Box 2). Hard sweeps initiated by LDD can be differentiated from those initiated by parallel *de novo* mutation through the linked genetic background that hitchhikes along with the allele. For LDD, this background will be identical by descent with the source population (Figure 2) but highly differentiated from local wild type and *de novo* sweep backgrounds at that locus. Recent population genomics research has explored these linked regions to identify the number of times resistance has evolved at a locus, which populations share which resistance backgrounds, and how resistance alleles across the genome combine to produce resistance phenotypes. Two recent studies on *Aedes* [12] and *Anopheles* [14] are particularly informative here. These used patterns of linkage among resistance alleles [12] or genotype–phenotype associations [14] to detect positive selection at multiple gene families where resistance has repeatedly evolved and spread across populations. These large-effect loci were supplemented by polygenic adaptation at other gene clusters, with geographically heterogenous selection patterns, indicating that different populations had taken different evolutionary pathways to reach their present resistance statuses. Parallel adaptation can occur even among adjacent populations with high gene flow [48], likely facilitated by high local population densities [37].

Future genomics work will help clarify how resistance alleles of different effect sizes evolve under different selection regimes (Box 2). An intriguing extension of this line of research concerns how this evolution is affected by changes in population size, particularly those from invasion bottlenecks. These bottlenecks may occur during invasion (i.e. inbreeding on ships during transport) or immediately after establishment and later may be iterated at the edges of an invasion as it spreads spatially [49]. At these times and spaces, low N_e may lead to the loss of advantageous alleles due to drift, with small-effect loci lost before large-effect loci. If resistance alleles are lost in this manner, they may be replenished

Figure 2



Outcomes of LDD between populations. Rows indicate genotypes across three chromosomes, and rectangles indicate genes. Light and dark grey rectangles indicate genetic backgrounds of source and recipient populations, respectively. Red rectangles indicate alleles that are slightly advantageous, and yellow rectangles are strongly advantageous. **(a)** A small number of dispersers (light grey) reach a new population (dark grey), carrying three alleles with a selective advantage. **(b)** Mating produces a small number of admixed individuals. These are heterozygous for the advantageous alleles, which are in perfect linkage disequilibrium through admixture. **(c)** After several generations of mating, the strongly advantageous allele is sweeping to high frequency along with a linked 'hitchhiking' region. One slightly advantageous allele has been lost, the other is at intermediate frequency. The remaining advantageous alleles are in strong linkage disequilibrium. Most of the neutral genetic background of the dispersing individuals has been lost, apart from hitchhiking regions. Future migration from the same source population may replenish any lost advantageous alleles. Mosquito image credit: Ana Ramirez.

by future LDD into the invasive population, creating additional problems for management termed 'genetic invasions' [50].

Long-distance dispersal within cities

Dispersal within cities will be a combination of active flight and LDD, with the latter following roads and other transport networks (Figure 1b). As LDD is comparatively rare, urban populations of weakly dispersing mosquitoes can exhibit genome-wide patterns of isolation by distance at fine scales [7,51]. However, even rare LDD may be sufficient to spread adaptive alleles across a city (Figure 1f). Following the above dynamics of introgression across populations, LDD of single individuals should be sufficient to spread advantageous alleles across opposite sides of a city, though these subregions will still show isolation by distance at other loci. Spatially explicit studies of these combined processes are currently lacking, though these would be highly informative for indicating regions of cities disconnected from LDD networks or regions that are connected but lack advantageous alleles (Figure 1f). This latter finding could provide evidence of spatial heterogeneity in insecticidal selection pressures, which could help fine-tune local control efforts [52] (Box 2). Such studies would ideally involve sampling that is spatially continuous and temporally cross-sectional (c.f. [53]), where spatial patterns of genome-wide differentiation can be contrasted with the geographical distribution of advantageous alleles.

LDD within cities has major implications for the local eradication of mosquito populations, whether through insecticides [29,54], *Wolbachia* bacteria [15], gene drives [16], or other suppression mechanisms [55]. Here, when a species has been completely eradicated from a target region, such as an island or town, LDD into the region will enable recolonisation, making LDD a key determinant of how frequently eradication must be repeated. LDD will further confound rear-and-release strategies (e.g. *Wolbachia*, gene drives) that require released mosquitoes to be at high concentrations at target regions, as some proportion of these will end up far from the release point due to incidental LDD.

An additional issue of LDD concerns rear-and-release strategies that aim to introgress *Wolbachia* bacteria into wild mosquito populations [56]. Here, *Wolbachia*-carrying mosquitoes have a positive frequency–dependent fitness advantage over mosquitoes without *Wolbachia*. This leads to a fitness advantage for mosquitoes remaining near release sites, while those undergoing LDD are at a disadvantage and are effectively wasted [57]. This reduces the likelihood and speed of successful establishment and spread, which requires high local *Wolbachia* frequencies (e.g. >0.35 [58]), though stochastic processes can also drive local establishment in isolated areas [47].

Models of *Wolbachia* dynamics can effectively ignore LDD and focus wholly on active flight [59]. While the total composite (active and passive) dispersal kernel of a mosquito population may be highly leptokurtic and have $\sigma >> 1\,\text{km.gen}^{-1/2}$ [59], *Wolbachia* dynamics can be

modelled using a Gaussian dispersal kernel with lower σ. Wave width and speed in early *Wolbachia* releases into *Ae. aegypti* indicated $\sigma \approx 100\,\text{m.gen}^{-1/2}$ [58], which aligns well with fine-scale genomic estimates [7,60].

Conclusions and future directions

In the absence of LDD, mosquitoes would have more limited distributions, would pose a lower disease threat, and would be easier to control with insecticides. LDD in mosquitoes has been investigated with a wide range of methods, including intercepting live mosquitoes at biosecurity checkpoints [19,27] and identifying identical genetic backgrounds in distant populations [12,20,61]. Biosecurity data can be very helpful for understanding pest dispersal [62] as they provide specific observations of the passive transportation process, including the origin, destination, vessel type, time of transport, and development stage of the transported pest. Combining these data with genomics presents a powerful emerging tool for understanding LDD and will be aided by new reference genomes for broadly distributed species such as *C. quinquefasciatus* [63] and *An. aquasalis* [64].

Urban environments present a complex but compelling direction in mosquito dispersal research, in which active and passive dispersal co-occur and where environmental heterogeneity should influence both dispersal connectivity and local selection regimes. Understanding how urban environments can be conducive to the spread of mosquitoes, mosquito disease, and resistance mutations is vital, given the importance of urban environments for mosquito disease transmission [65,66]. While we expect variation among mosquito species to influence LDD, such as differential levels of anthropophilia [32] and ability to undergo diapause [30], some general patterns are emerging into how LDD operates across mosquito genera. Mosquitoes are thus becoming a useful model for understanding the evolutionary consequences of passive LDD, which can assist with biosecurity and management strategies for a wider range of pest taxa.

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Data Availability

No data were used for the research described in the article.

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- • of special interest
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Glossary

dispersal kernel: A probability density function of the distribution of dispersal distances. This may encompass all dispersal processes or specific active or passive processes.

isotropic: Proceeding equally in all directions.

leptokurtic: Compared with a Gaussian distribution, a leptokurtic distribution has more scores near the mean and more scores far from the mean (i.e. a 'fat-tailed' distribution).

SNP: Single nucleotide polymorphism. A mutational change of a single nucleotide to a different nucleotide.

CNV: Copy number variant. A gene or gene region where the number of copies varies across individuals.

hard sweeps: Selective sweeps in which the advantageous allele is only observed on a single genetic background.

soft sweeps: Selective sweeps in which the advantageous allele is observed on multiple genetic backgrounds.

parallel adaptation: The recurrent evolution of the same adaptive phenotype via multiple, independent mutations. Phenotypes can be quantified by degree of parallelism.