

REVIEW

Rapid adaptation in a fast-changing world: Emerging insights from insect genomics

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Abstract

Many researchers have questioned the ability of biota to adapt to rapid anthropogenic environmental shifts. Here, we synthesize emerging genomic evidence for rapid insect evolution in response to human pressure. These new data reveal diverse genomic mechanisms (single locus, polygenic, structural shifts; introgression) underpinning rapid adaptive responses to a variety of anthropogenic selective pressures. While the effects of some human impacts (e.g. pollution; pesticides) have been previously documented, here we highlight startling new evidence for rapid evolutionary responses to additional anthropogenic processes such as deforestation. These recent findings indicate that diverse insect assemblages can indeed respond dynamically to major anthropogenic evolutionary challenges. Our synthesis also emphasizes the critical roles of genomic architecture, standing variation and gene flow in maintaining future adaptive potential. Broadly, it is clear that genomic approaches are essential for predicting, monitoring and responding to ongoing anthropogenic biodiversity shifts in a fast-changing world.

KEYWORDS

adaptive potential, climatic shifts, deforestation, ecosystem change, genomic architecture, human-driven evolution, standing genetic variation

1 | INTRODUCTION

Under the fast-changing conditions of the Anthropocene (Lewis & Maslin, 2015), many species lacking phenotypic plasticity must adapt, disperse or else potentially face extinction (Berg et al., 2010; Halsch et al., 2021). However, the extent to which wild populations may be able to adapt to their rapidly shifting environments remains an outstanding question for much of the planet's biodiversity (Catullo et al., 2019; Hendry et al., 2017; McGill et al., 2015; Sih et al., 2011). For instance, while recent temporal surveys appear to indicate that diverse insect assemblages are suffering substantial declines across many regions of the globe (e.g. Baranov et al., 2020; Hallmann et al., 2017; Thomas et al., 2019; Wagner, 2020, but see van Klink et al., 2022), relatively little is

known about their adaptive capacity (see Table 1 for glossary of terms). This dearth of knowledge is particularly concerning given that insects comprise such a vast proportion of the earth's biodiversity (Stork, 2018).

Prior to the molecular revolution, our understanding of evolution in wild populations rested heavily on phenotypic analyses of a handful of well-studied species (e.g. Cain & Sheppard, 1954; Clarke et al., 1985; Daday, 1954; Kettlewell, 1973). By contrast, the recent application of genomic approaches is now enabling researchers to revisit long-standing hypotheses of human-driven adaptive shifts (e.g. Van't Hof et al., 2016). Building on classic phenotypic studies, recent genomic analyses are now beginning to illuminate new cases of rapid insect adaptation in response to large-scale human impacts such as deforestation, translocation and climate change.

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TABLE 1 Glossary of terms

Term	Definition
Adaptive potential	The capacity of a population to respond to changing selection pressures
Adaptive shift	An evolutionary change in a population due to natural selection.
Convergent evolution	The independent evolution of similar phenotypes in unrelated lineages, typically via distinct genetic mutations
<i>De novo mutation</i>	A new mutation in the genome that was not inherited from a parent
Genomic architecture	The arrangement of functional elements (e.g. genes and regulatory regions) in the genome
Genomic islands of differentiation	Small regions of the genome that are tightly associated with adaptation, and resistant to gene flow
Inversion	A structural variant that involves a segment of a chromosome breaking off and reattaching in the reverse direction
Parallel evolution	The independent evolution of similar traits in related lineages
Polygenic	A trait controlled by two or more genes
Reverse evolution	The reacquisition of a phenotypic trait by a population or species after it has been lost
Standing genetic variation	Pre-existing genetic variation within a population
Structural variation	Major variations in chromosomal structure, including deletions, duplications, insertions, and inversions
Transposable element	A 'mobile' sequence of DNA that can move to different locations within a genome

While numerous researchers have questioned the adaptive capability of natural populations (Davis et al., 2005; Nogués-Bravo et al., 2018), recent genomic studies are revealing startling evidence for rapid adaptation over ecologically relevant timeframes in response to global change issues such as deforestation and translocation. Here we synthesize genomic insights emerging from diverse systems, including genetic studies of both 'natural' and 'pest' insect populations, to highlight strong evidence for rapid evolution in response to human pressure. In particular, we highlight emerging evidence of rapid evolution in response to deforestation and other previously little-studied anthropogenic pressures, focussing particularly on the most recent studies. While it is not our intention to provide an *exhaustive* review of the myriad studies of insect evolution, we point interested readers to several helpful recent reviews (e.g. Garnas, 2018; Hoffmann, 2017; Pélessié et al., 2018).

2 | JUMPING GENES AND ADAPTIVE RESPONSES TO POLLUTION

The classic case of shifting frequencies of British peppered-moth (*Biston betularia*) phenotypes (Clarke et al., 1985; Cook &

Saccheri, 2013; Kettlewell, 1973) during the industrial revolution continues to represent the most widely-known example of anthropogenic evolution (Figure 1). A recent genomic analysis concluded that the black phenotype which emerged in the mid 19th century (in response to industrial pollution) is underpinned by a transposable element inserted in the intron of the gene *cortex* (Van't Hof et al., 2016). Statistical analysis of recombined haplotypes suggests that this insertion occurred around 1820 (Van't Hof et al., 2016), consistent with historical records which indicate melanic moths were first identified in 1848 (Kettlewell, 1973). This research thus provides a novel example of the increasingly recognized role of jumping genes in mediating rapid adaptive shifts in wild insect populations (Gilbert et al., 2021; Schrader et al., 2014; Woronik et al., 2019).

Ideally, studies inferring evolutionary change in response to anthropogenic environmental gradients should be replicated, either geographically (within species) or phylogenetically (across species) (Johnson et al., 2018; Majerus, 1998; Santangelo et al., 2018), to help account for potential alternative non-adaptive explanations such as drift. In the case of moths, similar phenotypic shifts linked to pollution have been observed in more than 100 additional species across Britain (Kettlewell, 1973), with recent research suggesting that mutations in the *cortex* gene may underpin melanism in at least two of these species (Van't Hof et al., 2019). However, linkage analysis indicates the mutation causing melanism in these two species likely arose prior to the industrial revolution, suggesting the rapid phenotypic shifts in these species were the result of selection on standing genetic variation, rather than via more recent *de novo* mutations (Van't Hof et al., 2019). These results illustrate how seemingly similar phenotypic shifts may be underpinned by distinct genomic mechanisms.

3 | ADAPTING TO DEFORESTATION

Globally, deforestation has led to the fragmentation of countless natural populations (Alberti, 2015; Hanski et al., 2007; Karlsson & Van Dyck, 2005), and thus represents a highly replicated natural experiment (Vitousek et al., 1997). Remarkably little is known, however, about the *evolutionary* impacts of this forest loss (Foster, McCulloch, Ingram, et al., 2021; Willi & Hoffmann, 2012). Polymorphic taxa provide ideal models for testing *the role of widespread deforestation* in driving rapid and repeated evolutionary change in wild populations. Here we highlight new evidence emerging from comparative analyses of polymorphic insects in New Zealand, which together reveal the dramatic evolutionary effects of deforestation.

Recent analyses of New Zealand stonefly (Plecoptera) populations have revealed sharp clines in flight loss with increasing elevation, typically delineated by the alpine treeline (Figure 2; Foster, McCulloch, Ingram, et al., 2021; McCulloch, Foster, Dutoit, et al., 2019; McCulloch, Foster, Ingram, et al., 2019). These data support Darwin's long-standing hypothesis that insects in wind-exposed 'insular' habitats evolve flight loss to maintain local recruitment (Darwin, 1859, see also Leihy & Chown, 2020). These findings

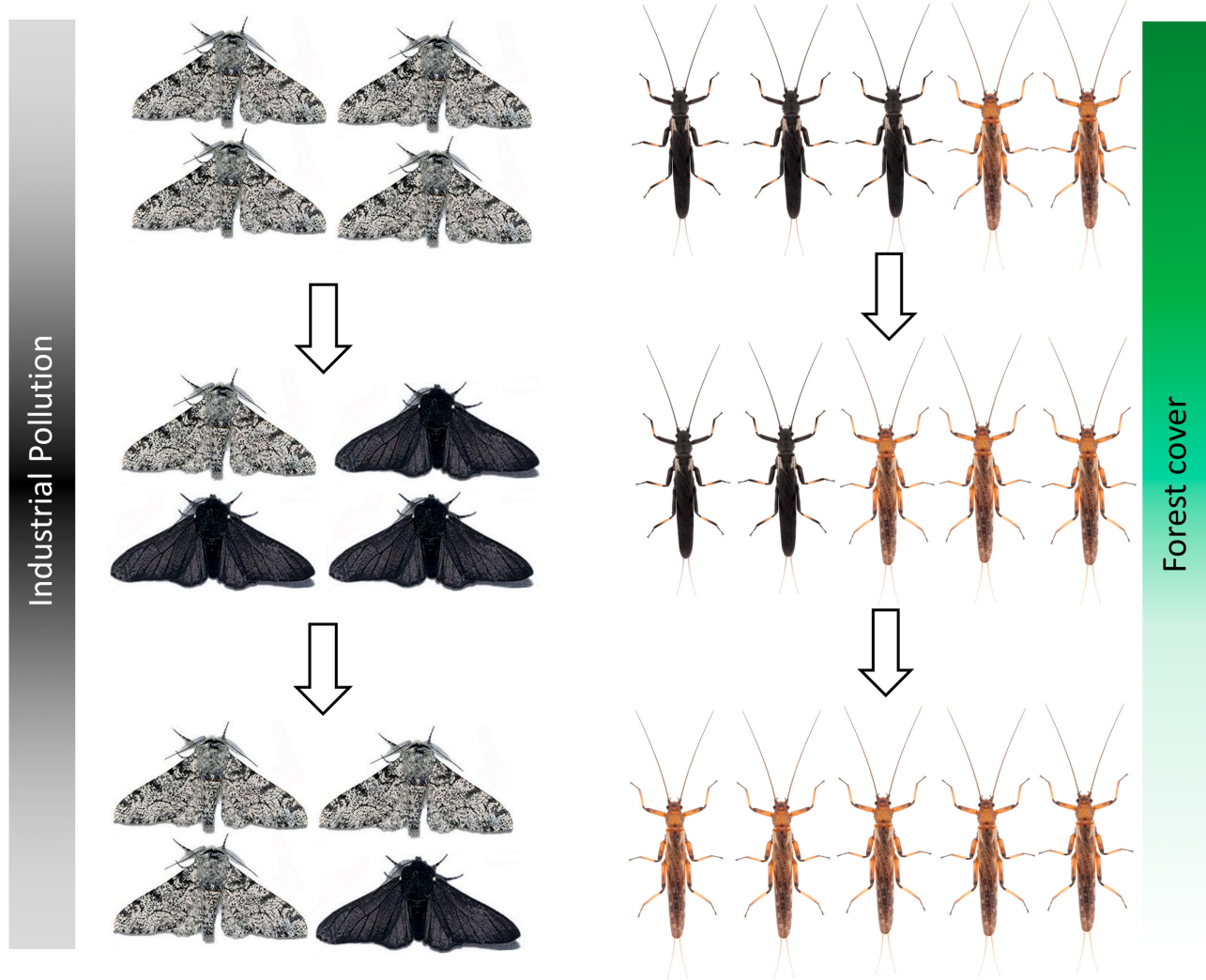


FIGURE 1 Human-driven shifts in insect colouration. The recently-evolved melanic morph of the peppered moth *Biston*, controlled by a transposable element in the intron of *cortex* (van't Hof et al., 2016), was selectively favoured by industrial pollution (Kettlewell, 1973), but has since declined in frequency (Clarke et al., 1985). Dark morphs of New Zealand *Zelandoperla*, underpinned by a mutation in the insect melanism gene *ebony* (Foster et al., 2022), mimic the noxious, forest-dwelling stonefly *Austroperla* (Foster, McCulloch, & Waters, 2021; McLellan, 1997, 1999). We hypothesize that anthropogenic deforestation has driven widespread reductions in both the abundance of *Austroperla* and the frequency of melanic *Zelandoperla* mimics (see Foster et al., 2022).

echo montane flight loss events detected across many regions of the globe (e.g. Hendrickx et al., 2015; Suzuki et al., 2019). In the case of *Zelandoperla*, genomic analyses have revealed genome-wide divergence among alpine/lowland ecotype pairs across different mountain ranges, with this divergence potentially underpinned by mutations in the developmental supergene *doublesex* (McCulloch et al., 2021). By contrast, full-winged and wing-reduced ecotype pairs in some heavily deforested subalpine regions of New Zealand show no such genome-wide divergence (Figure 2), implying that wing reduction has evolved only in recent centuries (Foster, McCulloch, Ingram, et al., 2021), likely in response to anthropogenic deforestation soon after human arrival 750 years ago (McWethy et al., 2010). These data highlight the potential for rapid insect evolution in response to environmental shifts over ecologically relevant timeframes. Future genomic analyses promise to shed additional light on

the parallel versus convergent origins of wing reduction across these recently deforested subalpine regions, and the potential capacity for reacquisition of flight in reforested regions.

In addition to the increased fragmentation and exposure experienced by populations in deforested habitats (see above), associated shifts in community composition are predicted to alter the evolutionary dynamics of surviving taxa. This possibility is highlighted by a melanic polymorphism in *Zelandoperla* stoneflies (Figure 1) that underpins Batesian mimicry of an unrelated, noxious stonefly *Austroperla* (Foster et al., 2022; McLellan, 1997, 1999). Specifically, melanic mimics of the aposematic 'model' have high frequencies in forested habitats of southern New Zealand where *Austroperla* is abundant (Foster et al., 2022), but low frequencies in deforested habitats (where *Austroperla* is rare; Nyström et al., 2003). Genomic analyses reveal that this colour-polymorphism variation is controlled by

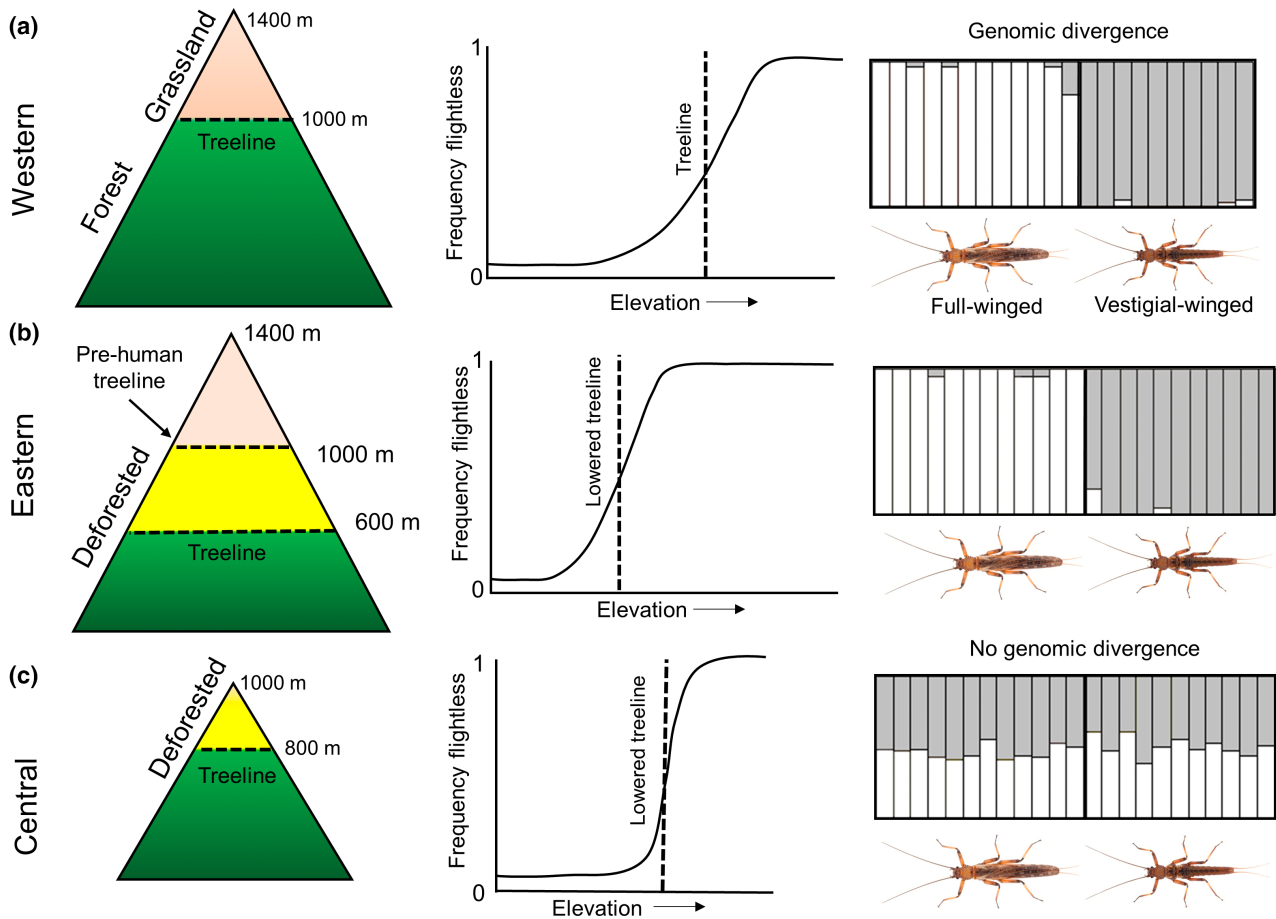


FIGURE 2 Anthropogenic shifts in elevational wing-reduction clines in subalpine *Zelandoperla* stoneflies. While flight loss is a widespread adaptation to New Zealand's alpine conditions (e.g. western South Island; a), recent deforestation has selected for flightless ecotypes also in many subalpine habitats (yellow; b, c) (McCulloch et al., 2021; McCulloch, Foster, Dutoit, et al., 2019). Wing reduction clines are consistently linked to the alpine treeline (Foster, McCulloch, Ingram, et al., 2021), but occur at lower elevations in recently deforested regions (b), suggesting shifts in ecotype distribution in response to exposure (see also Darwin, 1859; Leihy & Chown, 2020). While flighted and flightless lineages in alpine regions show genome-wide divergence predating human impacts (a, b), the absence of such ecotype divergence in recently deforested subalpine habitats (c) suggests that flight loss in these regions is entirely anthropogenic (Foster, McCulloch, Ingram, et al., 2021; McCulloch et al., 2021).

the well-known insect melanism gene *ebony* (Wittkopp et al., 2002), and is likely maintained by frequency-dependent selection linked to variation in model abundance (Foster et al., 2022). Given the context of recent deforestation in New Zealand (McWethy et al., 2010), this system may thus present an evolutionary parallel to the peppered moth (Kettlewell, 1973; Van't Hof et al., 2016, 2019) as a 'textbook case' of rapid human-driven evolution in insect melanism (Figure 1).

4 | ADAPTING TO CLIMATIC SHIFTS

Under rapid anthropogenic climate change, numerous insect populations will be forced to shift or adapt (Halsch et al., 2021). Indeed, climate change has already caused significant distributional shifts across a range of insect species (Parmesan, 2006; Sánchez-Guillén et al., 2013), which in some cases has resulted in rapid adaptation (Sánchez-Guillén et al., 2016). For example, the recent

climate-induced range expansion of the blue-tailed damselfly across Sweden has led to significant physiological shifts in populations at the leading edge of the range expansion (Lancaster et al., 2015, 2016). Recent genomic analyses indicate that these shifts may be linked to positive selection on heat shock proteins, which are typically involved in coping with thermal stress (Dudaniec et al., 2018).

Migration represents a key adaptation facilitating response to environmental change, and anthropogenic pressures are thus expected to select for shifts in dispersal and migratory behaviour in numerous insect taxa. Along these lines, recent genomic analyses have revealed substantial genetic components underpinning intraspecific variation in insect dispersal and migratory behaviour (e.g. Li et al., 2019; Wang et al., 2014). In the case of monarch butterflies, for instance, genome-wide scans have revealed numerous candidate loci potentially associated with migratory differentiation (Merlin et al., 2020; Zhan et al., 2014). Ideally, temporal genomic analyses are required to test for human-driven shifts in genotypes at these dispersal loci.

Similar climate-induced elevational range shifts have been detected in a range of insect species (McCain & Garfinkel, 2021). However, in the case of many geographically restricted alpine lineages, there are few if any options for dispersal, meaning that species that cannot adapt to warming temperatures are likely to face extinction (Giersch et al., 2017; Hotaling et al., 2017; Kinzner et al., 2019). However, such climatic shifts also have potential to drive rapid adaptive change and genetic restructuring of surviving upland insect lineages (Shah et al., 2020).

Climate change may also drive dramatic shifts in insect phenology (Forrest, 2016). Phytophagous insects may be particularly impacted, as environmental shifts often alter the growing seasons of their host plants (Hamann et al., 2021). Such climate-induced phenological shifts are believed to have a strong genetic basis (Bradshaw & Holzapfel, 2001; van Asch et al., 2007, 2013), although the precise genomic mechanisms underpinning some of these changes have yet to be identified. Crucially, recent analyses of environmental clines are starting to uncover the genomic architecture underpinning climate-induced differences in diapause timing across a range of insect species (Marshall et al., 2020). In some cases, differentiation in diapause timing appears to be primarily controlled by only a few loci of large effect (Kozak et al., 2019; Paolucci et al., 2016), while in other cases, shifts in phenology appear to be polygenic, involving numerous loci with additive effects (Pruisscher et al., 2018). Future temporal genomic studies (e.g. involving insect samples collected across several decades) will allow researchers to better understand the capacity of insects to undergo rapid phenological shifts in response to global climatic change.

5 | ADAPTING TO NEW ECOSYSTEMS

Insect lineages anthropogenically introduced into new regions and ecosystems are typically exposed to novel selective regimes, and hence often show strong genomic signatures of rapid evolutionary change. Such anthropogenic processes are particularly highlighted by emerging data regarding repeated loss of song in cricket lineages following their translocation to Hawaii (Pascoal et al., 2014, 2020; Zuk et al., 2006). These 'silent' lineages have evolved in response to novel parasitic threats in the species' introduced range, with newly emerged 'flatwing' mutations reaching fixation in 20 or fewer generations (Rayner et al., 2019). Genomic analyses indicate that 'flatwing' mutations cause extensive genome-wide effects on embryonic gene expression, leading to male crickets expressing feminized chemical hormones (Pascoal et al., 2020). Intriguingly, recent analyses indicate that convergent evolutionary processes underpin these rapid phenotypic shifts across independent island populations (Zhang et al., 2021).

The recent emergence of 'Africanized' honeybees (Figure 3) across the Americas likewise emphasizes the rapid rate at which anthropogenically introduced populations can evolve. These behaviourally distinctive bee lineages emerged as a result of the accidental release of an African subspecies in Brazil in 1965, and resultant hybridization with local European-derived populations (Whitfield et al., 2006). The admixed lineages subsequently spread

rapidly across the Americas, evolving several traits apparently underpinning their success, including increased aggression, elevated reproductive rates, higher tolerances to pesticides, and lower susceptibility to *Varroa* mites (Calfee et al., 2020). Molecular analyses have linked these distinctive adaptations to multiple regions of the genome (Zayed & Whitfield, 2008), with strong selection for genes of African ancestry in some portions of the genome, and for European markers in others (Calfee et al., 2020). Notably, particularly strong selection is evident in a large, gene-rich region implicated in reproductive traits and foraging behaviours of worker bees (Nelson et al., 2017), and in the gene *AmDOP3* gene, which is implicated in hygiene behaviours (Mikheyev et al., 2015).

Intriguingly, the subsequent introduction of 'Africanized' bees to Puerto Rico in 1994 resulted in further rapid evolution. Within 12 generations, the introduced lineages had undergone drastic reversals in aggression (e.g. 'gentle Africanized' honeybees; Rivera-Marchand et al., 2012). Recent studies indicate that these rapid behavioural shifts are correlated with strong genomic signatures of selection across multiple distinct loci and regions (Avalos et al., 2017), illustrating how admixture can fuel adaptive shifts by providing diverse genetic backgrounds for selection. Behavioural shifts have also been detected in invasive ant populations in the USA, with evidence of positive selection on genes controlling neurological functions and caste determination (Privman et al., 2018). These studies illustrate the strong selective pressure on sociobiological traits in invasive social insects (Privman et al., 2018).

Evidence of local adaptation has similarly been reported for invasive populations of small hive beetles that parasitize bee nests worldwide (Liu et al., 2021), melon fly (Dupuis et al., 2018), and invasive *Drosophila* populations in Hawaii (Koch et al., 2020). In each of these cases, adaptive signatures have been found across the genome, further illustrating how responses to sudden changes in selection regimes can be polygenic. The detection of phenotypic and/or genetic clines in widespread *Drosophila* lineages also illustrate the role of natural selection across many regions, and extensive genomic data are now shedding new light on the rapid evolution of this diversity (Adrion et al., 2015). In some cases, such clines have evolved within decades of establishment of *Drosophila* taxa in new regions (e.g. Hoffmann & Weeks, 2007; Telonis-Scott et al., 2011). In many cases, this adaptation to climatic conditions is apparently underpinned by inversion polymorphisms (Rane et al., 2015; Kapun et al., 2016; Figure 3). Such inversions may be key in facilitating local adaptation, as they are resistant to recombination, and thus prevent the breakup of favourable genomically linked gene complexes (Wellenreuther & Bernatchez, 2018).

Invasive insects can also potentially drive rapid evolutionary shifts in native insects, by increasing competition, or by altering community structure (Fortuna et al., 2022). Similarly, invasive plants can lead to host-shifts, and associated adaptation (Bush, 1969; Carroll et al., 1997; see below). Introductions of new pest and weed species continue at unprecedented rates (Seebens et al., 2017), and thus it is crucial that future genomic studies examine the evolutionary responses of native taxa to such invasive lineages.

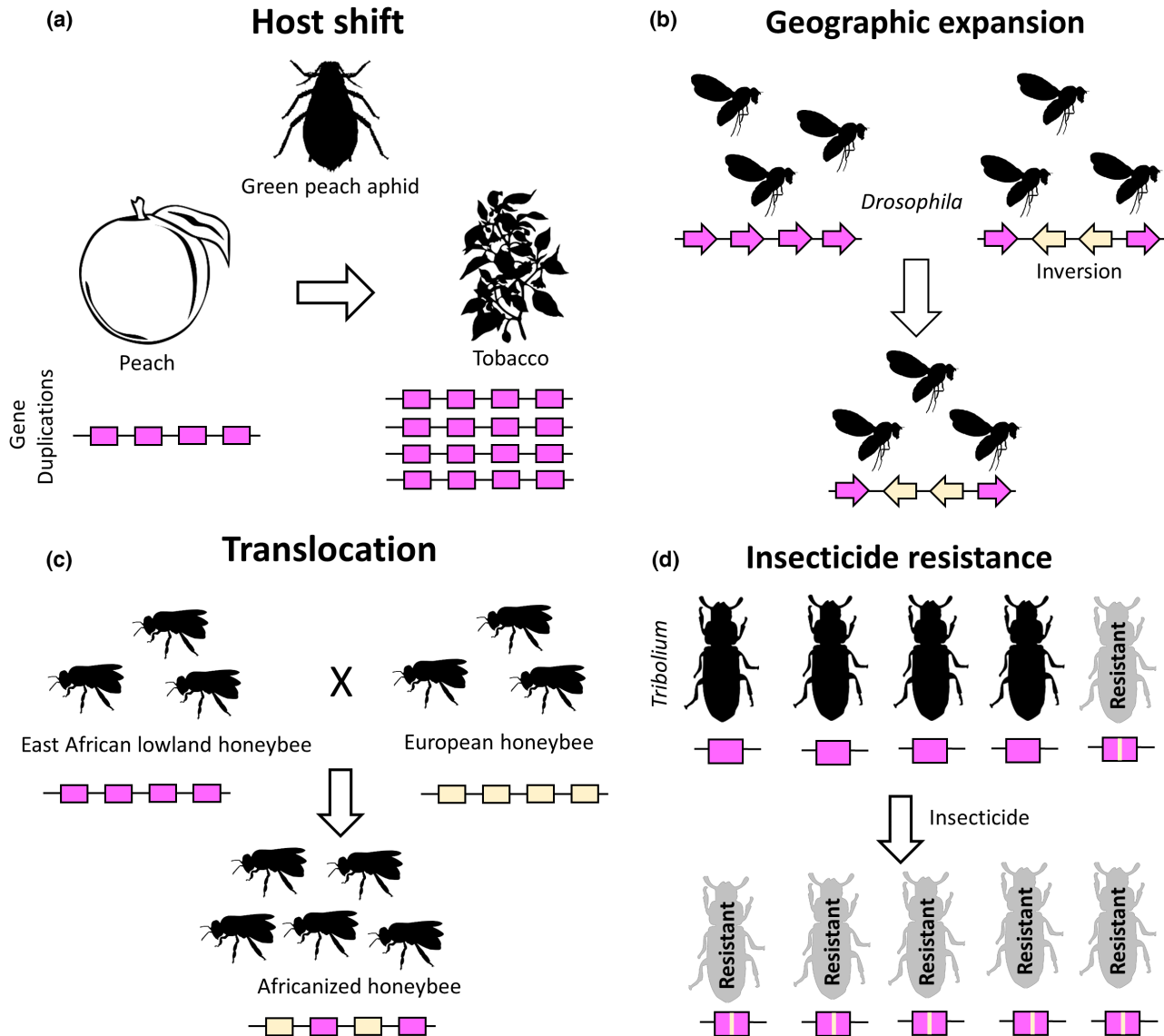


FIGURE 3 Diverse cases of human-driven evolutionary change in insect populations are underpinned by a variety of biological and genomic causes. (a) Recent evolution of tobacco-feeding aphid lineages was underpinned by gene duplications leading to overexpression of cytochrome P450 genes required for nicotine detoxification (Bass et al., 2013; Singh et al., 2020). (b) Range extension of *Drosophila* lineages has been facilitated by inversion polymorphisms that maintain coadapted loci, facilitating rapid adaptation to novel conditions (Kapun et al., 2016; Rane et al., 2015). (c) Admixed 'Africanized' bees spread rapidly across the Americas, with rapid behavioural shifts apparently facilitated by the diverse genetic backgrounds provided by hybridization between parental African and European lineages (Calfee et al., 2020). (d) Overuse of insecticides leads to the rapid development of insecticide-resistant populations, underpinned by single point mutations in key metabolic genes (e.g. Schlipalius et al., 2012).

6 | ADAPTING TO NEW HOST PLANTS

Adaptation to novel host plants has long been considered a key driver of insect diversification (Nosil, 2007; Walsh, 1861). It is becoming increasingly evident that adaptation following host shifts can occur over ecological time-scales (Forbes et al., 2017), and studies are now beginning to uncover the genomic basis of this rapid adaptation (e.g. Hood et al., 2020; Singh et al., 2020). One iconic example of rapid adaptation to new host plants is the shift of apple maggot (*Rhagoletis pomonella*) from its native hawthorn to the introduced domesticated apple fewer than 200 years ago

(Bush, 1969). This shift has resulted in significant changes in diapause timing—with apple feeding *Rhagoletis* flies eclosing about a month earlier than those feeding on hawthorn—and has led to the development of partially reproductively isolated host races (Hood et al., 2020; Inskeep et al., 2021). Recent studies indicate that the changes in diapause timing are driven by selection on standing genetic variation across the entire genome (Doellman et al., 2019; Dowle et al., 2020).

Laboratory experiments suggest that the genetic changes associated with host plant adaptation may be largely predictable, with independently derived experimental *Rhagoletis* colonies fed on

apples displaying parallel genomic shifts (Egan et al., 2015). Parallel genomic shifts have likewise been observed in Melissa Blue butterflies that have independently colonised alfalfa in different parts of North America (Chaturvedi et al., 2018). Most of the mutations associated with these shifts were on the Z chromosome, suggesting a disproportionate role of sex chromosomes in the adaptation of this species (Chaturvedi et al., 2018).

Another well studied example of rapid adaptation is the evolution a tobacco-feeding host race of the green peach aphid, which evolved during the 16th century after tobacco was introduced to the Old World (Bass et al., 2013; Figure 3). The tobacco-feeding host race overexpresses a number of cytochrome P450 genes, resulting in increased expression of the enzyme that detoxifies nicotine (Bass et al., 2013; Puinean et al., 2010). These overexpressed genes are genomically closely linked—suggesting they may be co-regulated—with recent analyses demonstrating that a large region of the genome containing these genes has been extensively duplicated in the tobacco-feeding host race (Singh et al., 2020; Figure 3).

7 | EVOLUTION OF INSECTICIDE RESISTANCE

Perhaps the best-studied example of anthropogenic evolution in insects involves the development of insecticide resistance (Ffrench-Constant, 2013; Hawkins et al., 2019; Liu, 2015). As pesticides apply extremely strong selection pressures, insecticide resistance can evolve rapidly (e.g. within a few years of initial exposure; Gassmann et al., 2014), and the frequencies of resistant lineages can increase significantly within only a few generations (Clements et al., 2017).

Pesticide resistance often stems from a single mutation of large effect (Schlipalius et al., 2012), whereas in some cases resistance can have a polygenic basis (Fournier-Level et al., 2019). Recent research suggests that a range of different genomic mechanisms can underpin insecticide resistance (Hawkins et al., 2019). Although resistance is most typically caused by single point mutations (e.g. Schlipalius et al., 2012), there is growing evidence that deletions (e.g. Baxter et al., 2011), gene duplications (e.g. Riveron et al., 2013), and inversions (e.g. Ayala et al., 2014) can all play significant roles in its evolution, with a wide variety of genomic mechanisms implicated (Bass et al., 2014; Liu, 2015).

Mutations underpinning resistance typically evolve after the introduction of the pesticide (Hawkins et al., 2019), with multiple independent de novo mutations sometimes facilitating repeated evolution of resistance within single species (Schlipalius et al., 2012). By contrast, in some cases resistance can evolve via repeated selection on ancestral standing genetic variation that predates pesticide application (Trocza et al., 2012). For instance, recent genomic scans of the Colorado Potato beetle demonstrate that pesticide resistance has evolved independently from standing variation across different agricultural regions, often involving similar genetic pathways, but distinct genes in different areas (Pélissié et al., 2022). Insecticide

resistance may also evolve through adaptive introgression (Clarkson et al., 2014; Hawkins et al., 2019). As a case in point, *Anopheles coluzzii* mosquitoes inherited a genomic island of differentiation that includes a number of insecticide resistance genes through hybridization with *Anopheles gambiae* (Norris et al., 2015).

8 | GENOMIC ARCHITECTURE OF ANTHROPOGENIC EVOLUTION: PREDICTING FUTURE ADAPTIVE POTENTIAL

What are the key genomic determinants of adaptive potential? Characterising the genomic bases of rapid adaptive shifts represents a key challenge for predicting future adaptive capacity in wild populations. Recent data increasingly highlight the role of *standing variation* as an enabler of such repeated and predictable evolutionary shifts (Pélissié et al., 2022). Indeed, genomic architecture in many cases can essentially 'pre-adapt' populations for future change by allowing for the maintenance of standing variation underpinning distinct ecotypes at co-adapted loci (e.g. 'precast bricks'; Ayala et al., 2010; Love et al., 2016; Mérot et al., 2018; Wellenreuther & Bernatchez, 2018).

A variety of genomic mechanism may potentially facilitate rapid adaptive shifts. For instance, several recent examples of rapid insect adaptation involve the insertion/deletion of mobile genetic elements (e.g. Gilbert et al., 2021; Van't Hof et al., 2016; Woronik et al., 2019). Such straightforward and fast-acting genetic mechanisms seem ideally suited for facilitating flexible and rapid evolutionary change. Intriguingly, a few recent studies of anthropogenic evolution point to the rapid accumulation of independent de novo shifts in distinct populations (Zhang et al., 2021), sometimes involving multiple parts of the genome, with diverse loci implicated (e.g. Doellman et al., 2019; Dowe et al., 2020).

While genomic data are transforming our appreciation of anthropogenic evolution, crucial questions remain regarding the potential 'reversibility' of such evolutionary shifts, and the downstream implications of anthropogenic change. While some categories of evolutionary reversal have previously been considered essentially impossible (Dollo, 1893; Trueman et al., 2004), researchers are increasingly questioning this assumption (e.g. Bank & Bradler, 2022). In this regard, the roles of genetic architecture in preserving adaptive capacity, and of gene flow in spreading adaptive alleles among lineages, may be particularly important (e.g. Waters & McCulloch, 2021). Indeed, in cases where standing variation represents a major source of adaptive potential, and gene flow among populations is high (e.g. Waters & McCulloch, 2021), there should be considerable capacity for future reversals of recent evolutionary shifts (e.g. declines in insect melanism with decreasing pollution; Clarke et al., 1985, or increased frequencies of insect melanism/flight in response to reforestation; Foster, McCulloch, Ingram, et al., 2021, Foster et al., 2022). Alternatively, when gene flow among populations is low, and selection/drift have reduced standing variation (e.g. complete loss of ancestral phenotypes/genotypes; Zhang et al., 2021), there may be

limited opportunities for such future adaptation. Indeed, in some cases anthropogenic evolution (e.g. flight loss; Foster, McCulloch, Ingram, et al., 2021) may lead to population isolation, decreased effective population size and an increase in extinction risk (Waters et al., 2020). In the case of recently silenced crickets (Zhang et al., 2021), for instance, anti-parasite adaptations for immediate fitness may potentially lead to reduced reproductive success and heightened risks of population extinction in the longer term.

9 | CONCLUSIONS

Many researchers have questioned the ability of natural populations to adapt in the face of fast-changing environmental conditions. Here, we highlight abundant new evidence for rapid adaptation in response to multiple anthropogenic pressures. These emerging data reveal diverse genomic mechanisms (single locus, polygenic, structural shifts; introgression) underpinning rapid adaptive responses to myriad human-driven selective gradients. In addition to previous studies of the evolutionary effects of pollution and pesticides, recent genomic data reveal dramatic adaptive responses to translocation, climate change and even deforestation—a globally pervasive but previously little-studied driver of insect evolution. These new emerging data thus highlight the need to better understand the evolutionary effects of broader ranges of anthropogenic pressures. Our synthesis emphasizes the key roles of genomic architecture, standing variation and gene flow in maintaining adaptive potential and pre-empting future evolutionary challenges. Knowledge of such genomic diversity is essential for understanding and predicting ongoing anthropogenic evolutionary change in a fast-changing world.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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