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Rapid evolution of insects to global environmental change: conceptual issues and empirical gaps

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Understanding how insects will respond both ecologically and evolutionarily to complex and interacting factors linked to global change is an important challenge that underpins our ability to produce better predictive models and to anticipate and manage ecosystem-scale disruption in the Anthropocene. Insects have the capacity to rapidly adapt to changing conditions via a variety of mechanisms which include both phenotypically plastic and evolutionary responses that interact in important ways. This short review comments on the current state of knowledge surrounding rapid evolution in insects and highlights conceptual and empirical gaps. Emphasis is placed on the need to consider direct and indirect community-level feedbacks via both ecological and evolutionary mechanisms when examining the consequences of global change, with particular focus on insects and their facultative and obligate symbionts.

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Introduction

As with many of the once sharply perceived distinctions in science, the lines between ecological and evolutionary time have now thoroughly blurred. While observable signs of evolution had historically been relegated to the deep past and near-geologic time scales, careful observation of phenotypic change together with DNA sequence variation has enabled the reconstruction of signatures of evolutionary patterns at time scales of years to decades [1,2••,3••] or even shorter [4]. Among insects with the propensity to cause ecological or economic damage, evolutionary responses to strong selective forces (i.e. synthetic or biopesticides or resistant genes or cultivars) have brought contemporary or 'rapid evolution' into sharp relief for farmers, land managers, and scientists. Likewise, there are a growing number of studies demonstrating shifts in traits under changing climatic conditions or in response to environmental or community change. Many of these changes appear to involve adaptive evolution [5••], though plastic and/or epigenetically controlled phenotypic responses are also common and deserving of explicit consideration [6].

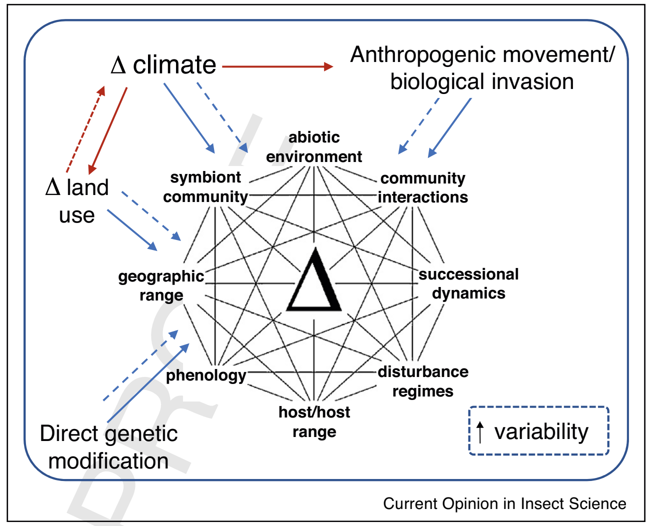
Insects are clearly capable of rapid adaptation to a variety of environmental changes, as evidenced by a growing body of field and laboratory research summarized in recent reviews [5••,7]. Examples to date can be roughly classified as first, changes in tolerance to climate or environmental stressors (e.g. heat shock proteins or cryoprotectants in response to thermal or other stressors) [8]; second, phenology [9•]; third, interactions with novel host plants and associated plant chemistry [2••]; fourth, life history parameters (e.g. voltinism, maximum growth rates, dispersal) [4]; fifth, morphology or coloration, including melanism [10•]; and finally, traits that mediate interactions with other species (i.e. with prey, natural enemies, competitors or mutualists [including endosymbionts and ecto-symbionts [11••,12,13]). Changes in community composition also occur regularly in the context of biological invasion and geographic range expansion (or local extinction and recolonization in a meta-community context), and there is growing evidence that climate change may select for or otherwise promote invasiveness [14]. Community change carries with it the additional and considerable complexity of indirect effects [11••,15•]. In fact, many of the drivers and responses to global change interact in complex ways, making the quest for generality or predictive science challenging. The goal of this short review is to synthesize and contextualize the current state of knowledge surrounding rapid evolution in insects, focusing primarily on conceptual concerns and particularly on responses to global change. A comprehensive review of empirical examples in insects would be impossible in the limited space available, and focus is instead on broad patterns that may be generalizable across insect taxa, life histories and ecological contexts.

Setting the scene

Evolution in response to environmental change is a hallmark of life on Earth and has shaped the current diversity in form and function among extant insects globally. Insects have evolved and diversified under vastly different ecological conditions, both within and among lineages and across time. Across their >410 million years on the planet, the magnitude of these changes is scarcely imaginable and have included multiple glaciations, major geologic upheavals (volcanos, earthquakes, asteroid impacts, etc.), and dramatic fluctuations in climate and atmospheric gas concentrations. With these changes have come massive reorganizations of the Earth's biomes and biota, to say nothing of individual communities. Still, change is anticipated to be particularly rapid and multifaceted in the coming decades and the important question remains of how and whether many species will respond, both ecologically and evolutionarily. Recent reports of significant regional declines across unrelated insect taxa with diverse life histories and habitat affinities represent cause for concern [16], as are declines in important groups that have received more focused attention and that are putatively linked to climate and land use change (i.e. moths and butterflies [17]) or to a suite of complex interacting factors (e.g. pollinators [18]). Alternatively, some species are responding positively to climate change and other factors and have increased in abundance and geographic range to staggering degrees, in part due to (or at least accompanied by) adaptive evolution. In one dramatic example, climate change-facilitated range expansion in the mountain pine beetle (*Dendroctonus ponderosae*) has resulted in catastrophic ecosystem disruption and associated community declines, along with a suite of single nucleotide polymorphisms (SNPs) with putative functions in cold adaptation and dispersal [19•]. While evidence for adaptive evolution to specific stressors in insects is overwhelming, plastic or evolutionary responses to complex, interacting factors represents a significant challenge that is sure to produce both winners and losers. Insects as a group have weathered (and perhaps benefitted from) four of the five recognized mass extinction events on the planet's history, though past history and current trends suggest the increased dominance by a relatively small number of widespread, broadly adapted taxa is likely as a consequence [20].

Figure 1 summarizes the major drivers of global change in the Anthropocene. Climate change, land use change (including habitat loss), and biological invasion are perhaps the most dominant, though resource over-exploitation, pollution, pesticide/herbicide inputs and nutrient deposition are also clearly important. Many of these factors interact to varying degrees and in complex ways. Cascading effects of environmental forcing are considerably more complex, however, where they drive large-scale and largely unpredictable restructuring of ecological communities and evolutionary landscapes [11••]. It is important to keep this complexity in mind when envisaging selective landscapes which are highly likely to be shaped by a multiplicity of interacting factors that vary spatiotemporally.

Figure 1



Conceptual diagram highlighting the interactive nature of multiple domains in rapid flux in the Anthropocene. Central triangle is the Greek Δ, signifying change. Red arrows correspond to interactions among the major drivers of change (shown around the outside of the central interaction network); blue arrows depict impacts on proximate drivers (or outcomes) of rapid evolutionary change on point generally to the network given the high likelihood of impacts on multiple factors simultaneously, or on interactions among them. Solid and dashed lines signify direct and indirect effects. Proximate factors have the strong potential to interact in complex ways and are thus depicted as a maximally interconnected network. Genetic modification refers to the increasing deployment of genetically modified organisms, predominantly in agriculture but increasingly likely to be deployed in natural systems given recent advances in gene editing techniques (e.g. CRISPR-Cas9) coupled with gene drive mechanisms (that facilitate the rapid spread of human-designed or assembled genotypes throughout populations). Elevated variability (Box 1, lower right) is an explicit prediction of most climate models and further complicates prediction of the directionality and outcomes of rapid evolutionary change in species, populations, and communities.

What is (and is not) rapid evolution

As with many concepts in biology, precise definitions of rapid evolution are elusive [21]. The 'rapid' part of the term has been variously delineated by time frame [i.e. <100 years; 2] but is perhaps more generally accepted as referring to cases where measurable (or at least plausible) feedbacks can occur between changes in genetically based phenotypes and ecological dynamics [22]. This latter phenomenon together with enhanced tools for the detection of genetic change has spawned the growing field of 'eco-evolutionary dynamics' [23]. Examples of evolutionary changes in insects driving community-level ecological feedbacks are likewise accruing, particularly as mediated through co-evolution of insect herbivores and plant defenses [24]. One particularly well studied case is that of reciprocal though geographically variable co-evolution between *Pastinaca sativa* and the introduced parsnip webworm (*Depressaria pastinacella*) in North America [25]. Evolutionary dynamics between insects

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