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

Short title: Rapid evolution of insects to global environmental change

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Abstract:

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.

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 [1-3] 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 1) changes in tolerance to climate or environmental stressors (e.g., heat shock proteins or cryoprotectants in response to thermal or other stressors) [8]; 2) phenology [9]; 3) interactions with novel host plants and associated plant chemistry [2]; 4) life history parameters (e.g., voltinism, maximum growth rates, dispersal) [4]; 5) morphology or coloration, including melanism [10]; and 6) traits that mediate interactions with other species, (i.e., with prey, natural enemies, competitors or mutualists [including endo- and ecto-symbionts [11-13]]). 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.

What is (and isn't) 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 and parasitoids or predators are also important [23]. For example, natural selection on stick insect coloration imposed by bird predation strongly influences overall arthropod abundance on host plants [26].

Phenotypic change must be heritable to constitute adaptive evolution, rapid or otherwise [2]. Phenotypic plasticity (where single genotypes can give rise to divergent phenotypes across different environmental conditions) is sometimes thought of as antithetical or inhibitory to adaptive evolution [27]. The relationship between phenotypic plasticity and evolution is complex, however. Acclimatization, a form of phenotypic plasticity whereby individual reaction norms reversibly shift in response to exposure to environmental conditions, is extremely common in insects and other forms of life [28]. The impacts of environmental exposure on subsequent phenotypes can also span generations via maternal or epigenetic effects [29]. Both acclimatization and cross-generational effects produce similar phenotypic landscapes across environments that could easily be misconstrued as evolutionary responses in the absence of careful controls and can thus confound the detection of genetic adaptation. Still, plasticity itself is a trait that can be under genetic control and that can thus be selected for under variable conditions [27]. Trait plasticity can also promote individual and/or population persistence under stressful conditions when adaptive genetic variation is insufficient [30]. In other cases, plasticity may buffer populations from strong selection such that they retain suboptimal or even maladaptive alleles [6]. Such buffering can afford time for adaptive evolution to occur and maintain additive genetic

variance that might be purged by a purely evolutionary response to strong selective pressures. Plastic traits can also evolve genetic bases via a process called genetic assimilation [6].

Rapid adaptation to environmental stressors

Figure 2 lists some of the major drivers and constraints of adaptive evolution and highlights some of the traits that are particularly relevant to insect rapid adaptation to changing conditions. There is abundant literature on the factors that either facilitate or inhibit adaptive evolutionary change in populations, mostly from a theoretical perspective. Empirical data are difficult to come by except for some well-studied taxa. Insects have relatively short generation times which should drive higher rates of adaptive evolution. Also, effective population size is probably large for at least some insects, and some estimates suggest that the ratio of N_e to census population size is high relative to other taxa [31]. Additive genetic variance (V_A) is highly trait-specific and estimates can also vary among environments making it difficult to generalize, particularly for low-heritability traits [32]. One study of phenotypic clines in heat and cold resistance in Australian populations of *Drosophila melanogaster* did detect a contribution of heritable genetic change, though plastic responses were comparatively more important [33].

Despite the importance of abiotic controls on distributional range, on population dynamics, and on species interactions [34], the literature on rapid evolution to environmental stressors is relatively scant [5]. By far the most studied climate parameter to be considered as a selective agent is temperature. As poikilotherms, key life history traits (i.e., development rate, generation time/voltinism) respond directly to changes in temperature, often with important consequences for population dynamics. Temperature extremes are significant mortality factors and strong selective forces for many insects at parts of their range. One recent study demonstrated genome-wide responses in warm climate-associated chromosomal inversions in *Drosophila subobscura* in response to a spring heat wave

in Europe [35]. Interestingly, inversion frequencies regularly vary seasonally in ways that are likely to influence population dynamics, constituting an eco-evolutionary feedback. Range boundaries are likewise strongly driven by temperature, especially on the poleward edge. Northern range boundaries of the southern pine beetle (SPB), for example, as for many temperate insects, are largely determined by winter cold, which kill approximately 80% of overwintering beetles if air temperatures dip below -20 C [36]. This appears to be a hard constraint that may represent a trade-off between the beetle's lack of a cold-tolerant diapause stage and rapid population growth rates under more optimal conditions. Thus, the northward range expansion of SPB likely does not reflect adaptive evolution but simply changing climate conditions. The ecological and evolutionary consequences of the arrival of this keystone species into naïve pine communities outside of its historical range is an area of active research, though community-wide evolutionary responses seem likely given other examples documented to date.

In other cases, rapid evolutionary responses do occur, especially where invasive species that have encountered novel climate conditions or in some cases have expanded their range across considerable environmental gradients. For example, a strong latitudinal cline in chromosomal inversion frequency and in wing size *Drosophila subobscura* arose in both North and South American introduced populations, recapitulating a pattern (though with slightly reduced magnitude) present in its native Europe, despite the likelihood of founder effects or genetic bottleneck associated with the small number of initial colonists [reviewed in 37]. Other examples where there are reasonably strong cases for adaptive evolution include phenological matching in winter moth (*Operophtera brumata*) populations to the timing of bud break in oak and of the apple maggot fly (*Rhagoletis pomonella*) to fruiting in apple and hawthorn, as well as the loss of diapause behavior and timing of burrowing in the Colorado potato beetle (*Leptinotarsa decimlineata*) in Europe [reviewed in 5,38].

Role of microbial symbionts

Microbial symbionts are ubiquitous among insects and impact myriad aspects of host physiology, metabolism, growth and reproduction. Endo- and ectosymbionts also influence behavior and environmental tolerances and mediate ecological interactions with host plants, competitors, and natural enemies (including parasitoids and other microbes). Increasingly, symbiont communities are recognized as important sources of evolutionary novelty [39]. Such novelty can be a property of the “hologenome” (genetic material contained within a focal organism together with that of all symbiotic associates). Parts of the hologenome that are not part of the focal organism’s genetic code are effectively heritable via vertical symbiont transmission, though the concept of heritability above the level of the individual and outside the focal organism’s genome is still controversial, and it’s not clear how well traditional evolutionary and population genetic theory would apply [40]. Additionally, genetic elements can be shared laterally via horizontal gene transfer between host and symbiont with apparent ease and can even be shuffled among insect species or across trophic levels with symbiotic microbes acting as intermediaries [41]. In fact, the merging of genomes and/or loss of redundant function in hosts and/or microbial partners appears to be a pervasive if not universal property of co-evolution in the case of obligate endosymbiosis [42].

Only recently have researchers begun to explore important aspects of function, spatial variability, or interactions in complex symbiont communities (both within and among hosts). As such, the consequences of this variation for host or community evolution are still largely unknown. Association with symbionts may provide a certain buffering capacity to tolerate changing conditions by increasing the range of suitable temperatures or environmental conditions or by facilitating host plant switching via the detoxification of novel host plant compounds or by facilitating digestion and/or nutrient acquisition from recalcitrant or low-quality host tissues. Symbiont communities also appear to respond particularly strongly to temperature. For example, high temperatures can lead to a breakdown in transmission frequency of bacterial endosymbionts associated with the gastric cecae in the

cosmopolitan green stink bug (*Nezara viridula*); similar patterns are seen in cockroaches as well as aphids, which have been shown to consistently lose obligate endosymbionts at elevated rearing temperatures, at least under experimental rearing conditions [43,44]. Loss and gain of “obligate” symbioses is also possible over evolutionary time [42].

Both laboratory and field data on facultative symbionts support the idea that environmental temperatures strongly predict symbiont performance and identity (e.g., among facultative fungal symbionts of the bark beetles in the Ophiostomales) [45]. Of course, rapid evolution in symbionts to variable climate regimes is also highly likely. Large-scale correlations between SNP variation within three fungal associates of the Mountain pine beetle and environmental factors such as cold, drought, precipitation, and temperature provide one such example that supports adaptive evolution in symbionts to diverse environmental conditions, and the ability of the beetles to switch among symbionts with divergent optima appears important to their current ecological success [46].

In addition to climate or environmentally driven changes, symbiont communities can also change dramatically as a consequence of biological invasion and range expansion. Loss of antagonistic microbes (together with predators and parasitoids) is strongly linked with enhanced performance and success of invasive species, and underpins the “Enemy Release Hypothesis.” Novel associations with microbes can directly or indirectly facilitate invasion and/or population growth, sometimes leading to major disruptions at the ecosystem scale [12]. In other cases, impacts may be more subtle. For example, swapping of obligate fungal symbionts among siricid woodwasps was recently shown to be common in both invaded [47,48] and uninvaded [49] pine forests or plantations by the globally distributed *Sirex noctilio*. The arrival of a putatively non-native *Amylostereum areolatum* fungus associated with *S. noctilio* into North America has potential consequences not only for virulence of native wasps (e.g., if association with a non-co-evolved fungus increases aggressiveness, for example), but also for the

potential transmission of a sterilizing nematode that obligately feeds on the wasp's fungus during the mycetophagous part of its life cycle [50].

Microbially-provided services often come at an evolutionary cost, however. First, association with *Wolbachia* and other reproductive parasites is linked to sex ratio bias and reduced outcrossing via male killing or cytoplasmic incompatibility [51], with consequences for additive genetic variance and effective population size. Additionally, the immune function of some symbionts may shield the host from selection pressures which could lead to adaptive evolution. For example, one recent study showed that *Wolbachia* infection was highly protective against Drosophila C virus but inhibited selection for host virus-resistance alleles in *D. melanogaster* [52]. While the suppression of a genetic response to artificial infection was moderate, the authors refer to this phenomenon as “evolutionary addiction” which could constrain adaptive evolution. Whether such constraints are widespread enough to have long-term consequences on insect evolvability if host-symbiont communities risk decoupling under changing environmental conditions is unknown.

The way forward

Global change in the Anthropocene is already manifesting as a complex, interconnected and evolutionarily unprecedented suite of selective pressures on insects with major consequences for the communities and ecosystems they inhabit. Understanding how species and communities will respond is of critical importance if we are to minimize negative consequences for biodiversity and ecosystem function. Insects are key components of many ecosystems and are tractable and useful study organisms both in terms of their abundance, diversity (functional, taxonomic and life history), and amenability to experimentation, particularly those that can be reared in the lab or in common garden mesocosms or field experiments. Common garden experiments, where multiple families, genotypes, and/or source populations – preferably originating from a range of relevant environments (often from across

latitudinal or elevational gradients that correlate strongly with climate) – are reared in a common environment, are particularly powerful in climate adaptation studies as they allow for the characterization of local adaptation within populations and for the partitioning of phenotypic variance into genetic (G) and environmental (E) components. There are ample studies that demonstrate that rapid evolution to environmental change is occurring and is likely common, though there is a relative dearth of carefully controlled studies that can truly separate adaptive evolution from acclimatization and other forms of plasticity [5,32]. When replicated across a climate gradient in a reciprocal transplant framework (or across a similar suite of artificial rearing conditions, as appropriate), common garden trials also facilitate studies of trait plasticity (= gene-by-environment [G×E] interactions [53]), including in some cases cascading effects on communities and ecosystem services [13]. Care should be taken, however, when moving genotypes and source populations experimentally as unintended consequences of human-aided dispersal are possible, even with native organisms or widely-distributed invasives [37].

In conjunction with carefully designed experiments or field trials, the growing availability of insect genomes and ‘-omics’ tools has a major role to play in global change adaptation research. CRISPR-Cas9 and related technologies stand poised to facilitate a new generation of knockout and direct genetic manipulation studies which have great power for both basic research and to management, especially when coupled to gene drive mechanisms which rapidly propagate desired sequences through populations via the germ line [54]. Gene drive itself and genetic manipulation of host plants and other organisms also represent important selection pressures for insects (Fig. 1), and in some cases also a non-trivial threat to associated species and communities. Molecular tools and analysis including whole genome/transcriptome sequencing offer the ability to uncover patterns of selection and/or gene expression across populations and environments as well as to examine function of key genes shown to differ systematically in response to climate, for example. Finally, techniques such as bisulfite sequencing

or chromatin immunoprecipitation (ChIP) now offer the ability to study epigenetic controls on gene expression and phenotype in non-model systems [55].

Perhaps the biggest challenge is that of understanding the role and importance of community evolution and indirect effects. There are only a handful of studies that have begun to consider this complexity at the interface between community and evolutionary ecology [11]. This is no doubt a reflection of the exponential accrual of plausible interactions which increase at a rate of $S \cdot (S-1)/2$ (where S is the number of species in a community of interest; Fig. 3). In light of accumulating evidence that facultative and obligate symbionts of co-occurring organisms can interact in complex and indirect ways including through host plant-mediated feedbacks, the number of possible permutations can become truly staggering. Evaluating the relative importance of indirect and complex community feedbacks and under what conditions they are likely to emerge is a worthwhile first step, especially where common gardens, manipulative experiments, and/or spatially replicated observational studies can be coupled with community-level analysis. Efforts to date have been incredibly fruitful, having spawned fascinating sub-disciplines and novel theory [13,56]. Analytical tools or approaches to identify and evaluate multi-way interactions at the community scale are still insufficient, though increasing computational power together with traditional and developing methods for handling such complexity – i.e., by examining community properties globally (e.g., network analysis), evaluating among specific direct and indirect effects (e.g., path analysis), or by reducing parameter space (e.g., using Morris sensitivity or random forest algorithms) offer some options. However, explicit consideration of evolutionary feedbacks where trait changes in one species alter selective landscapes or the nature and strength of interactions among species in communities in direct or indirect ways is a monumental undertaking [11,57] but is nonetheless a goal that warrants attention.

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Figure captions

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, 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.

Figure 2. Non-exhaustive list of the potential drivers and constraints on adaptive evolution and key traits on which selection is likely to act in a global change context. See text for discussion and examples.

Figure 3. Conceptual diagram depicting some of the diversity and complexity of direct and indirect eco-evolutionary feedbacks in communities. Blue arrows represent ecological feedbacks (e.g., mediated through changes in abundance); red arrows represent evolutionary (trait) changes. Solid and dashed arrows refer to direct and indirect effects, respectively. Lines that terminate in a 'T' indicate changes that influence the nature or strength of interactions. Here, species A and B can influence one another directly via ecological (e.g., via competition, facilitation, etc.) or evolutionary feedbacks (i.e., changes in

the selective landscape for each species of the presence or abundance of each), or both. Species B can also influence species A via indirect eco-evolutionary feedbacks either mediated by a third species (Sp. C, a shared host plant perhaps) or more diffusely via changes in the community). Finally, communities themselves interact via migration and gene flow (i.e., in a meta-community framework) which, since eco-evolutionary dynamics are highly likely to vary spatiotemporally in response to distinct communities and environmental conditions, can influence ultimate trajectories.

Fig. 1

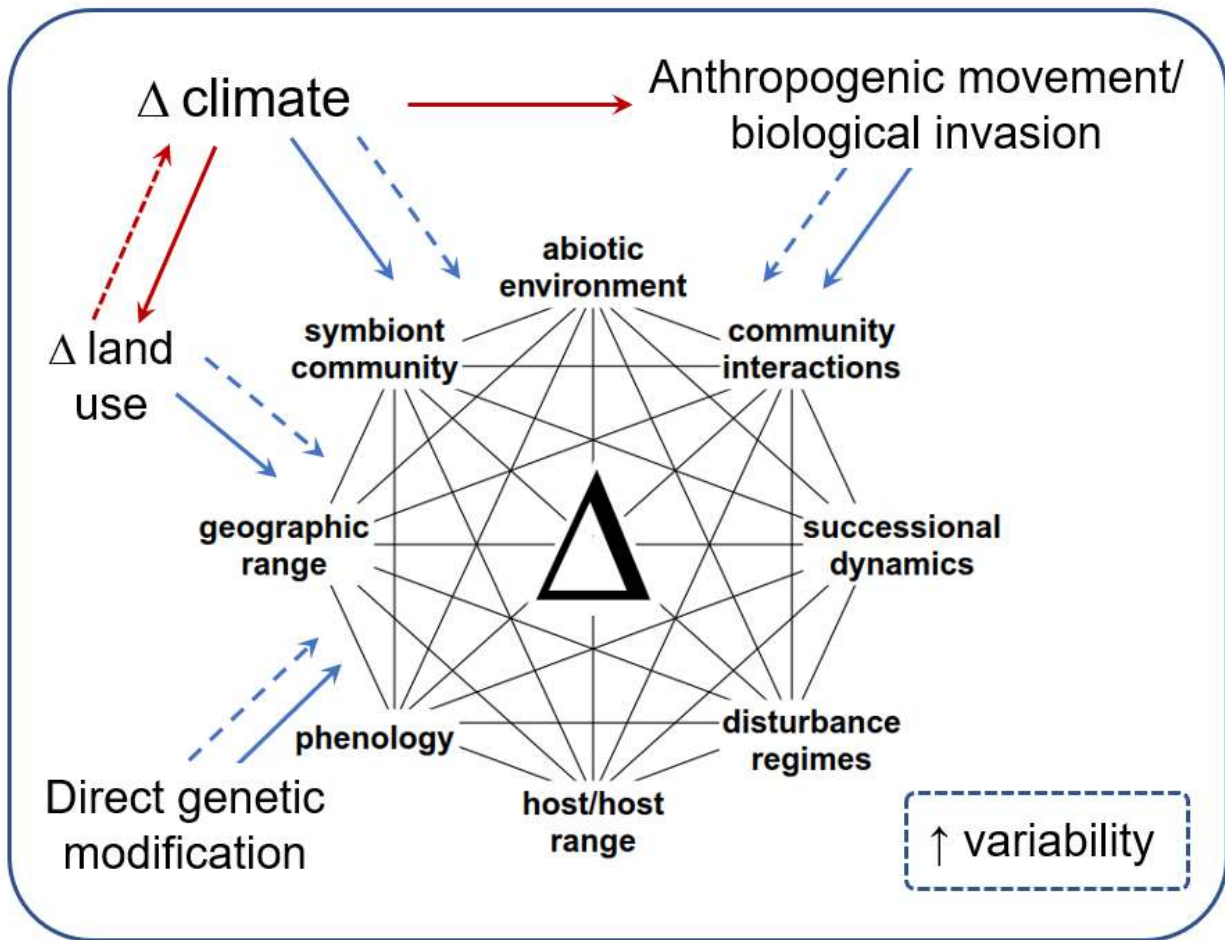


Fig. 2

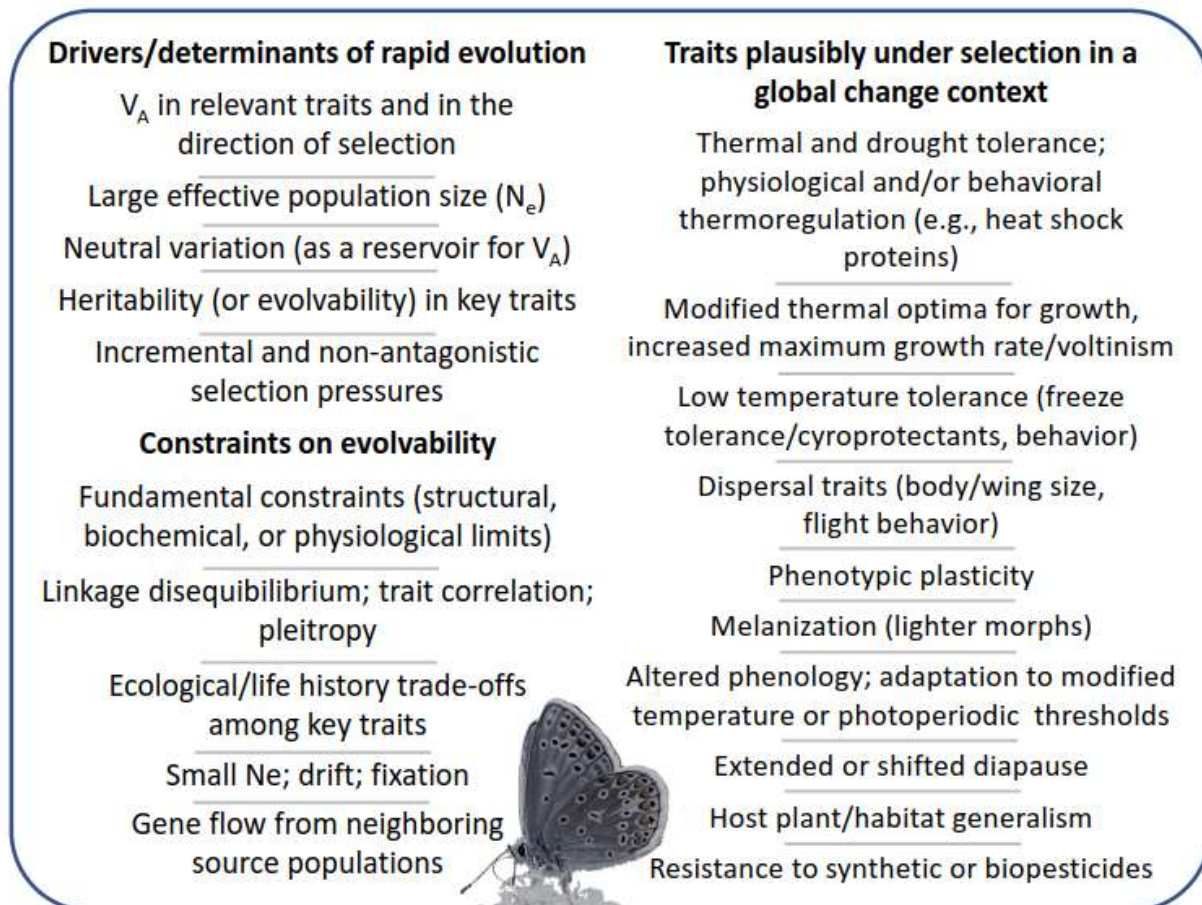
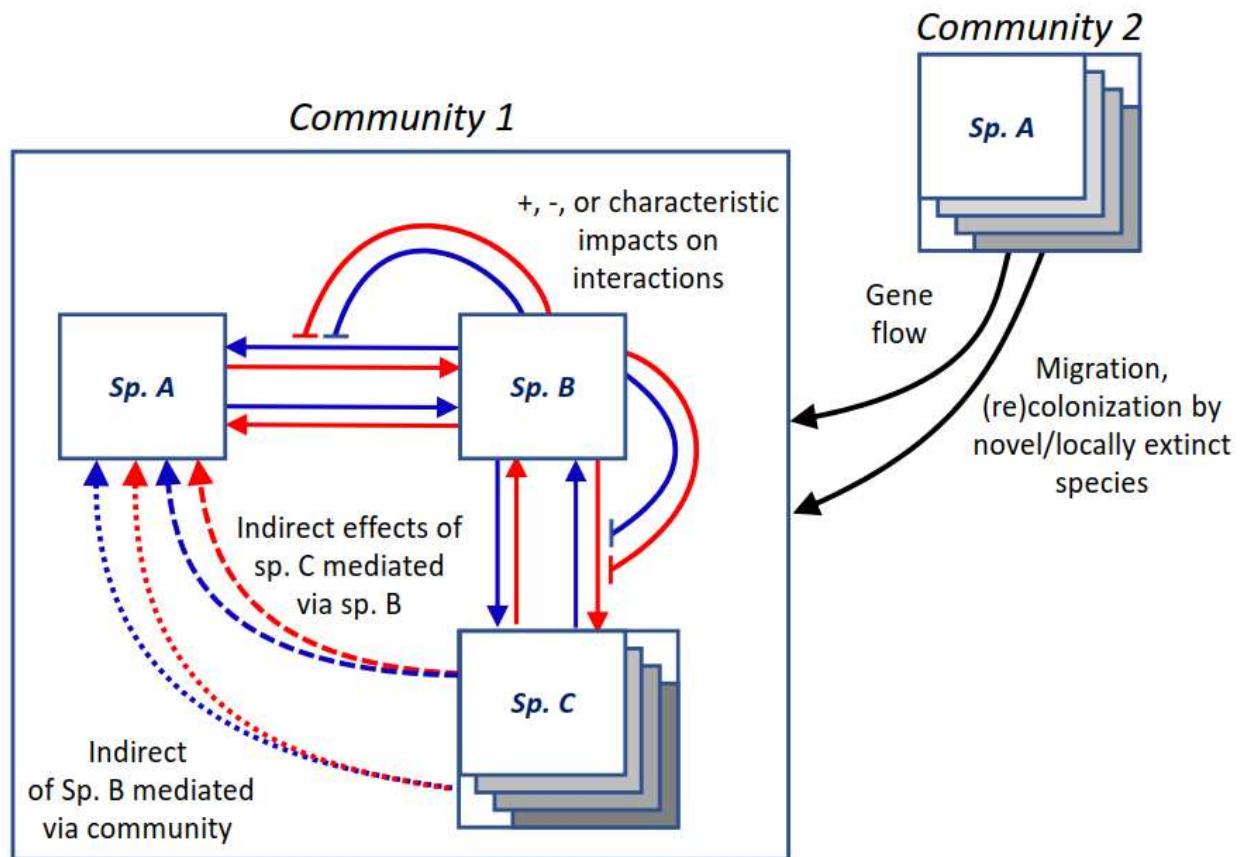


Fig. 3



Box 1. Glossary of terms

Additive genetic variance (V_A): Genetic contribution to the total variance (V_G) in a phenotypic trait conferred by the summed effects of contributing alleles but exclusive of variation due to dominance (V_D) and epistatic (gene-gene interaction; V_I) effects. The ratio of V_A to V_G , referred to as *narrow sense heritability* ($h^2_N = V_A/V_G$), is a measure of average similarity between parents and offspring in a population and of the adaptive capacity within that population to respond to selection [32].

CRISPR (or CRISPR-Cas9): Clustered Regularly Interspaced Short Palindromic Repeats, or CRISPR, is a new and rapidly changing technology that co-opts an ancient bacterial mechanism of acquired immunity against attacking plasmids or phage to allow researchers to effectively “search and replace” specific sequences within an individual’s genome, thus facilitating precise genome editing. Cas9 is a specific (within the class of Cas or CRISPR-associated) RNA-guided protein that binds to specific matching sequence across the genome and produces a double-stranded break in the DNA where novel DNA can then be inserted.

Cryoprotectants: cold-protective metabolites, often low molecular weight sugar alcohols, sugars such as glucose or trehalose, or amino acids such as proline, etc., synthesized by insects during cold acclimation that lower the crystallization (= freezing) temperature (T_c) and reduce tissue damage or death due to freezing [58].

Eco-evolutionary dynamics: Emerging subdiscipline at the interface between ecology and evolutionary biology that reflects growing recognition that evolutionary changes can produce important feedbacks with ecological impacts (e.g., on population growth rates) and that ecological changes can also lead to rapid evolutionary changes [23].

Effective population size (N_e): the # of individuals in a population contributing genes or offspring to the next generation, often considerably lower than the census population abundance (N). In population genetics, N_e can be calculated in various ways that reflect different aspects and impacts on genetic drift, on genetic diversity and the rate of spread (or loss) of alleles within a population [59].

Epigenetic effects: Phenotypic changes arising from alterations in gene expression rather than the genetic code itself. Though recognized for decades, renewed focus on epigenetic effects, including trans-generational (heritable) responses to environmental change, has highlighted their role in rapid evolution [29].

Founder effect: Characteristic reduction of genetic variation in introduced population due to both the reduced variability carried within a small number of founders (a genetic bottleneck) followed by genetic drift in an originally small population. Founder effects can have positive effects on populations by purging deleterious (rare, often recessive) alleles from population, and has the capacity to convert epistatic or dominance variation into additive genetic variation, though the importance of this phenomenon is unclear [37].

Gene drive: Method for promoting the rapid spread of alleles preferred by researchers throughout natural populations by coupling them to an appropriate CRISPR-Cas9 motif inserted into an organism’s genome. The CRISPR system can be specifically designed to cut out the homologous allele contributed by the non-engineered parent in a mating pair such that all offspring will be homozygous for the desired allele, ultimately driving it toward fixation in the population. This technology makes it possible to effectively engineer whole populations rather than individuals and has profound management implications, together with seriously non-trivial risks [54].

Genetic assimilation: Process by which natural selection on an adaptive, environmentally-induced phenotype results in a trait becoming constitutively expressed, no longer requiring the environmental signal or stimulus to manifest. By this process, novel phenotypic variation only revealed in a new environment can become fully genetically determined (no longer plastic) or expressed in association with an altered reaction norm [6].

Heat shock proteins (HSPs): A family of proteins produced in response to diverse environmental stresses (i.e., heat, cold, anoxia, crowding) that function in maintaining cell homeostasis by regulating protein-protein interactions, including acting as molecular chaperones and as facilitators of protein folding, translocation, and degradation [8].

Linkage disequilibrium (LD): Nonrandom association of alleles from distinct loci within a population. LD can emerge via co-inheritance due to physical proximity on the chromosome (limiting the density of recombination sites between two loci) or from drift in small populations, from natural selection favoring particular allele combinations, or from assortative mating [59].

Phenotypic plasticity: Capacity of a single genotype to express distinct phenotypes under different environmental conditions. The degree to which plasticity is itself a heritable trait, and whether it predominately aids or impedes adaptive evolution is an important area of active research [28,30].

Pleiotropy: Phenomenon whereby single genes influence the expression of multiple, apparently unrelated traits [38].

Reaction norm: A description (often a graphical or mathematical representation) of the relationship between the expression of a single genotype and an expressed phenotype across a range of environments, typically those that vary continuously (i.e., temperature) [30]

Thermal acclimation/acclimatization: Plastic response to stressful temperatures (i.e., winter cold) that increases performance or tolerance in the presence of that stimulus. Plastic responses that take place during development (i.e., developmental acclimation) are often irreversible, whereas seasonal acclimatization (e.g., cold hardening) typically reverts in the absence of the stimulus [28]. Though the terms are sometimes used interchangeably, acclimation technically refers to responses to one or a few controlled conditions in the field or lab while acclimatization refers to responses to changes in natural systems [60].

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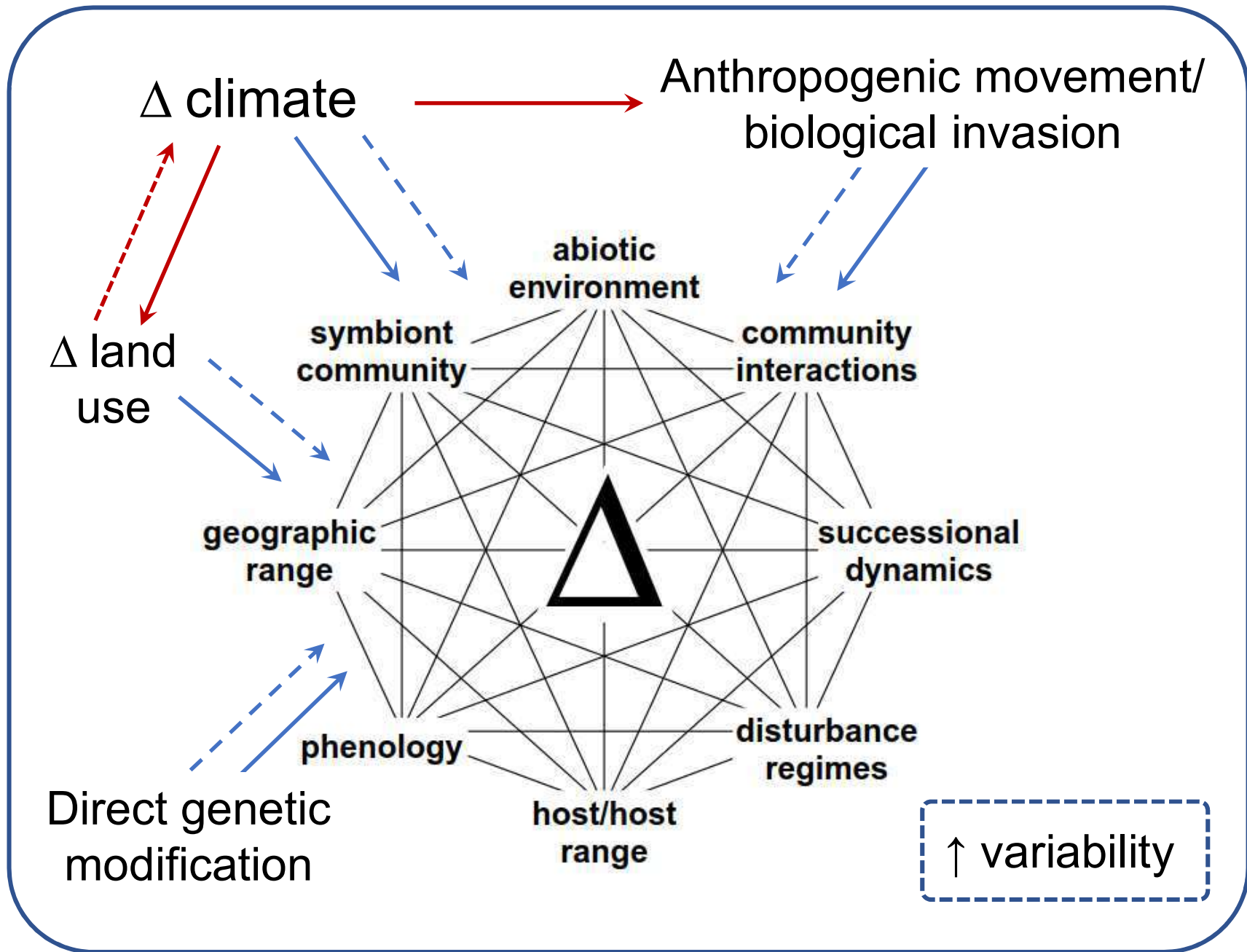
 ** Show the rapid spread (from near absence to near "fixation" in 6 years) of a bacterial symbiont (*Rickettsia* sp. nr. *bellii*) through southwestern populations of the invasive whitefly, *Bemisia tabaci*. Infected individuals had enhanced reproduction, survival and development rates. They also showed significant female-bias, consistent with the bacterium's role as a reproductive parasite.

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Drivers/determinants of rapid evolution

V_A in relevant traits and in the
direction of selection

Large effective population size (N_e)

Neutral variation (as a reservoir for V_A)

Heritability (or evolvability) in key traits

Incremental and non-antagonistic
selection pressures

Constraints on evolvability

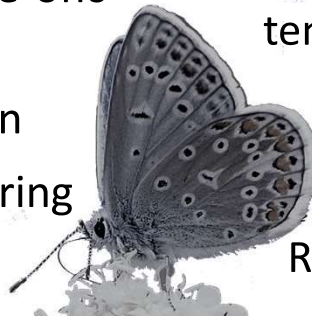
Fundamental constraints (structural,
biochemical, or physiological limits)

Linkage disequilibrium; trait correlation;
pleiotropy

Ecological/life history trade-offs
among key traits

Small N_e ; drift; fixation

Gene flow from neighboring
source populations



Traits plausibly under selection in a global change context

Thermal and drought tolerance;
physiological and/or behavioral
thermoregulation (e.g., heat shock
proteins)

Modified thermal optima for growth,
increased maximum growth rate/voltinism

Low temperature tolerance (freeze
tolerance/cytoprotectants, behavior)

Dispersal traits (body/wing size,
flight behavior)

Phenotypic plasticity

Melanization (lighter morphs)

Altered phenology; adaptation to modified
temperature or photoperiodic thresholds

Extended or shifted diapause

Host plant/habitat generalism

Resistance to synthetic or biopesticides

