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The complexity of global change and its effects on insects

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Abstract

Global change includes multiple overlapping and interacting drivers: 1) climate change, 2) land use change, 3) novel chemicals, and 4) the increased global transport of organisms. Recent studies have documented the complex and counterintuitive effects of these drivers on the behavior, life histories, distributions, and abundances of insects. This complexity arises from the indeterminacy of indirect, non-additive and combined effects. While there is wide consensus that global change is reorganizing communities, the available data are limited. As the pace of anthropogenic changes outstrips our ability to document its impacts, ongoing change may lead to increasingly unpredictable outcomes. This complexity and uncertainty argue for renewed efforts to address the fundamental drivers of global change.

The complexity of global change drivers

Global change in the 21st century involves multiple co-occurring and correlated anthropogenic effects on insect communities. These include 1) changes in climatic conditions, 2) changes in land use, 3) the introduction and increased use of novel compounds and chemicals, and 4) the increased transport of organisms on a continental scale (Fig. 1). Considered separately, each driver of change has multiple manifestations. Their combined effects and interactions reflect the complexity of global change.

Increases in anthropogenic greenhouse gas emissions have changed the Earth's climate. The resulting shifts in temperature and precipitation create perturbations on multiple spatial and temporal scales, altering both long-term mean trends on a global scale and the variability of short-term events at local scales. While mean global temperatures are increasing by 0.2° C per decade [1], this long-term warming trend is also associated with increases in the frequency and intensity of extreme climatic events, including heatwaves, droughts, floods, wildfires and tropical storms [2,3]. The complexity of global climate change emerges from the many ways climatic conditions are changing in different regions and habitats [4], the temporal variability of these changes [2,5], and the interactions between different kinds of changes [6,7].

Changes in land use include patterns of increasing urbanization, agricultural intensification, and habitat fragmentation. In many regions, urban warming, air pollution and illumination have created new conditions for insect ecology and evolution [8–11], while changes in the scale and practice of agriculture have effects on agroecosystems and connected non-agricultural ecosystems [12–15]. Deforestation, road-building, and other changes in natural ecosystems reduce and isolate available habitat [16–18]. These changes in urban, agricultural, and natural ecosystems are connected in heterogeneous habitats, shaping the distribution and movement of insects in complex ways.

The effects of novel compounds have become increasingly complex as well. Whereas the first-generation synthetic insecticide DDT showed a rapid mode of action, clear bioaccumulation and environmental persistence, the ecological effects of modern insecticides are more complex. Many of these compounds are now known to have sublethal and lagged negative effects on insects [19–26], synergistic effects with other novel compounds [27] and unexpected persistence in belowground and aquatic habitats [28,29] - characteristics that were detected only after their global deployment and long-term, widespread use [30]. The proliferation of novel synthetics now in wide use creates the potential for more complex combined effects on insect behavior, populations, and communities.

Global change in the 21st century also includes the dramatically increased transport of organisms outside their native ranges. This movement of species has profoundly changed the composition of ecological communities worldwide, with a range of complex outcomes. Introduced species can facilitate or hinder the establishment of subsequent introductions [31,32], increase or decrease metrics of biodiversity [33], and can have positive or negative effects on members of the native community [34]. Despite efforts to identify general patterns in the traits favored by human-mediated dispersal [35] or the kinds of ecosystems most likely to experience the negative effects of biotic reorganization [36], the increased global transport of organisms creates a particularly complex driver of global change, reflecting the unique biological context of each introduction.

In this review, we draw a distinction between the complex anthropogenic drivers (i.e., causes) of global change and the complexity of their effects on ecosystems. The multi-dimensional, multi-scale and

interactive nature of global change drivers makes establishing simple causation difficult because most observed patterns of impact will likely emerge from the combined effects of multiple drivers [37,38]. With multiple global perturbations acting simultaneously and synergistically, simple causation is not only difficult to establish but also seems unlikely to represent the real complexity of global change effects.

The complexity of global change effects

Global change drivers have direct and indirect effects on insect communities. While it may be possible to predict some of the direct abiotic effects of warming temperatures on insects based on species- and stage-specific thermal performance curves [39,40], the indirect effects of warming includes a wide range of more complex biotic pathways, including changes to host plant quality [6], natural enemy risk [6,41], and the potential for other novel or altered interactions [42–46]. Despite long-standing interest [47,48], few studies have attempted to experimentally separate direct and indirect effect pathways and these studies suggest that the balance of these two effect pathways may sometimes be counterintuitive. For example, Chen et al. [49] showed that the generally unacknowledged direct effects of rainfall events on a lepidopteran herbivore increased its development time and reduced its survival (possibly due to microclimatic cooling), while the more widely studied indirect, plant-mediated effects of rainfall were unexpectedly small.

Even relatively singular global change drivers can yield complex and counterintuitive outcomes due to the ramifications of their indirect effects [6]. For example, under ambient temperatures, wolf spiders suppressed collembola and indirectly increased the fungal decomposition of litter in the Arctic [50]. This scenario reversed under experimental warming, where higher densities of wolf spiders slowed litter decomposition, possibly driven by unanticipated effects on the composition of collembolan species or increases in intraguild predation. Similarly, while the direct effects of warming temperatures were expected to decrease development time and increase the abundance of aphids in a high elevation community, warming also advanced and increased predator populations while simultaneously decreasing the quality of the aphid's host plant, leading to an indirect decline in aphid densities under the warming [46].

When their effects are combined, multiple global change drivers can interact in more complex ways [37,38,51] and the statistical and experimental approaches necessary to disentangle these additively or non-additively combined effects are still emerging [37,38,52]. Structured observational studies have grappled with the collinearity of potential explanatory factors using large datasets, multi-model inference and partial least-squares regression [38,41,53–55], suggesting potential interactions among factors. Experimental studies aimed at understanding the ecological and physiological mechanisms of effects may be necessary to improve opportunities for generalization and prediction [52]. For example, both high [56] and low [57] temperatures can increase pesticide toxicity in insects through different physiological mechanisms, suggesting that a clearer understanding of these mechanisms [58] may be necessary to predict the interactive effects of thermal stress and pesticide exposure.

The unreplicated, historical nature of global change also contributes to the complexity of understanding its effects [59]. Relatively few datasets allow historical comparisons on a relevant scale [60–65], and their retrospective analysis is always challenging [66,67] and sometimes contentious [68–70]. These issues are likely to be especially difficult among insects, due to their taxonomic diversity, dynamic populations and limited long-term monitoring [59,71]. The paucity of historical data presents a formidable challenge for all studies of global change [59]. The problems of shifting baselines [72] and

social-ecological mismatches [73] reflect fundamental limitations of direct human experience. The spatial and temporal scales of global change are difficult to fathom and are easy to underestimate in the absence of reliable data.

Insects may also be particularly sensitive to the effects of global change. The diversity of insects includes many relatively specialized species that may be especially prone to co-extinction [71]. The vast majority of insect biodiversity is located in tropical to mid-latitudes, where the effects of global warming are expected to erode thermal buffers and increase heat stress on ectotherms [40]. Warming conditions increase the metabolic costs of ectotherms while potentially limiting their thermal activity windows and reducing the availability of resources overall, creating the potential for “metabolic meltdown” [7]. In addition, because of their shared physiology, non-target insects are especially vulnerable to the effects of new insecticides, and these novel compounds are readily capable of moving across habitat boundaries in complex, changing landscapes [74].

In order to more closely examine the complexity of global change effects on insects, we here focus on three broad and overlapping categories of effects: 1) effects on behavior, 2) effects on phenology and life histories, and 3) effects on species distributions and abundance.

Effects on behavior

Global change is affecting insect behavior in both straightforward, predictable ways, and more complex, less predictable ways (Fig. 2). For example, current rates of global warming are likely to increase insect movement rates generally, but these proximate effects often lead to more complex downstream effects on dispersal, foraging and species interactions [75]. Similarly, warming is expected to affect courtship signaling and increase mating frequency in insects, but these changes may have more complicated impacts on species recognition and hybridization [42]. While fragmented, heterogenous environments often limit insect movement and recolonization [76], behavioral avoidance of low-quality matrix habitats can also accelerate spatial spread through altered landscapes [77]. Thus, while some broad patterns of behavioral responses to global change may be predictable based on physiological first principles, the results of these changes seem likely to remain context dependent (Fig. 2).

Climate change and land use changes are increasingly affecting the structure, propagation, and perception of both insect signals and environmental cues. For example, polarized light from roads can derail the flights of aquatic insects navigating along rivers and creeks [78]. Artificial light at night affects several aspects of insect behavior, including development, movement, predation and herbivory [79,80], and may be an important overlooked contributor to insect population declines [80]. Changes in temperature can also directly affect the emission and perception of chemically mediated signals in insects [81,82], and many acoustic signals involved in insect courtship and mating are thermally sensitive as well [42]. Anthropogenic noise can drive both adaptive and maladaptive responses in acoustically signaling insects. For example, some cricket species adaptively modulate their responses to novel road noise stimuli [83], while others show maladaptive responses [84].

Novel compounds have unexpectedly complex effects on insect behavior, with ramifications for entire interaction networks. Although they were initially thought to present a low risk for non-target effects and long-term environmental toxicity [85–87], neonicotinoids have important negative effects on insect behavior, unexpected persistence in soil and water, and potentially more complex effects when combined with other stressors [27,30,88]. Recent studies suggest that the neonicotinoid imidacloprid

impairs olfactory learning and memory [21], vision [22,23], flight [24], and navigation [25,26] in a wide range of insects. These sublethal effects on insect behavior have been associated with detrimental effects on the recruitment and abundance of diverse insect populations [19,20,89,90]. Other pollutants, including heavy metals and metalloids [91], ozone and airborne free radicals [11], and respirable suspended particulates [10] are also relatively novel anthropogenic stressors that alter insect stress, foraging, predation avoidance, habitat selection and other behaviors.

Effects on phenology and life histories

Global change drives phenological shifts in many organisms (Fig. 3a), and ecologists are increasingly grappling with the complex ways in which these shifts can alter seasonal life histories [5]. These include phenological changes in the autumn and winter [92–94] and changes in voltinism [95–97]. For example, changes in the timing of diapause induction can have a strong effect on overwinter survival [98,99], while changes in voltinism can present either “demographic bonanzas” [e.g., 100] or “developmental traps” [e.g., 96] for insects responding to global change [95,96].

In some cases, phenological shifts lead to phenological mismatch: changes in the relative phenologies of interacting species (Fig. 3b). Studies aiming to understand the causes of phenological mismatch are increasingly focused on the mechanisms of phenological cueing. Phenological mismatch can result from differences in the environmental changes experienced by different organisms (*environmental mechanisms*) and differences in their sensitivity to environmental cues (*organismal mechanisms*) [101]. Thus, some observed phenological mismatches are likely to be largely explained by organisms experiencing different aspects of global change, as may be the case with habitat specialist butterflies [102]. On the other hand, other mismatches occur when global change exposes previously hidden differences in cue sensitivity and integration [103]; these differences could explain diverging phenological responses of plants and pollinators to increasing urbanization [104]. The ways in which these two mechanisms combine to generate observed variation in phenological responses remains to be determined.

Relatively few studies have been able to quantify the effects of phenological mismatches relative to appropriate historical baselines [105]. Phenological mismatches have the potential to disrupt species interactions, but their impacts on fitness and population will likely depend on the nature and specificity of the interaction (Fig. 3c). Some studies suggest that mismatches may be less likely to occur in mutualistic (e.g., plant-pollinator) [34,44,106] or highly specialized (e.g. host-parasitoid) interactions [99,107] where selection under historical environmental variability would be expected to have favored the evolution of more robust phenological cueing strategies in one or both interactors [44]. Whereas the disruption of mutualistic interactions is costly for both interactors, the disruption of antagonistic interactions is more likely to create phenological winners and losers. One possibility is that the *incidence* of mismatches might be lowest among specialist species that have the most to lose, while the *impacts* of mismatches are lowest among generalist species with more diffuse interactions. However, phenological mismatches could occur more broadly if global change continues to increase the variability of phenological shifts [108,109], or increase rapidly if the limits of adaptive plasticity are met [103,110].

When we expand phenological mismatches to a community scale (Fig. 3d-e), their consequences become harder to predict. As changes in emergence phenology, developmental rate, voltinism, and diapause induction stretch the bounds of adaptive plasticity [107], the resulting variability of phenological responses has the potential to rewire temporally explicit interaction networks [111] and

increase the complexity of phenological impacts in a community context [5,112]. Studies that have attempted to quantify how an organism's expected fitness changes throughout the year suggest that these seasonal fitness landscapes reflect multiple interactions in a community, often including both top-down and bottom-up effects. For example, the fitness landscape of cavity-nesting bees was likely influenced by a combination of floral resource availability and parasitoid phenologies [113], seasonal windows of opportunity for monarch development were likely to be influenced by both host plant traits and natural enemy activity [114], and the impacts of warming-mediated advances in aphid phenology reflected the combined effects of both host plant and predator phenologies [46]. The effects of these phenological changes likely extend to the ecosystem scale as well. For example, the timing of terrestrial insect prey inputs into an aquatic stream directly affected fish and indirectly affected aquatic insect prey, with subsequent effects on litter decomposition and nutrient cycling [115].

Effects on species distributions and abundance

Insect species ranges have both expanded and contracted in response to multiple global change drivers (Fig 4a). In a study of 58 Orthopteran species in Germany, land-use change was the primary driver of range contractions before 1990, especially in habitat specialist species, while more mobile and more thermophilic species expanded their ranges after 1990, likely reflecting the increased protection of remaining habitat patches and warming conditions [116]. Similarly, range expansions have been observed among thermophilic dragonfly species in Europe [117], and the range of the bumblebee *Bombus haematurus* increased by 20% relative to its historical range, probably due to warming winter conditions [118]. Conversely, densities of the meadow spittlebug (*Philaenus spumarius*) have declined at both the southern and northern ends of its range in California, likely reflecting drier conditions in coastal grasslands [119]. Recent studies suggest multiple factors that could have contributed to the dramatic contraction of the American burying beetle (*Nicrophorus americanus*) range, including the reduced availability of preferred resources, increased exposure to pesticides, changes in land use, and negative interactions with large grazing vertebrates [120].

Human activities have dramatically increased the global transport of insects [35], contributing to the reorganization of recipient communities [121]. In recent years, ecologists have grappled with the complexity of this reorganization and its implications. For example, it is increasingly clear that microbial associates can have complex effects in biological invasions by acting as mutualists that benefit the invading species, novel pathogens that negatively impact the native biota, or symbionts with more complex or poorly understood effects [122,123]. On a larger spatial scale, recent studies have sought to explain why established populations of introduced species seem more likely to serve as sources for subsequent invasions, creating the potential for an accelerating, positive feedback loop [35,124]. While there is continued debate about the aims of invasion biology [125], insights from the study of introduced species are also being applied more broadly to improve our understanding of climate-mediated range shifts [126].

Against this background, a growing number of studies have documented declining insect abundances at sites around the world [60–62,90,127–129], though the extent and breadth of these declines remains uncertain [59,68,121,130–135]. Key questions remain. First, are observed insect population declines representative of a broader global pattern? While there is ample evidence that some insect populations are declining, others appear to be increasing [121,130,132,136]. Second, are insects especially likely to experience population declines? It has been suggested that traits common to insects (e.g., ectothermy,

specialization) make them particularly vulnerable to global change [71,137], but this question remains largely unresolved. Third, what are the drivers of insect declines? Establishing clear causation is likely to be difficult, though the combined effects of multiple global change drivers may be a key part of the explanation [51,132]. Finally, given current uncertainty and the limitations of available data, what can be done? An emerging consensus emphasizes efforts to increase, broaden, and modernize the collection of insect population data [59], while parallel efforts contend that we already know enough to advocate more immediate policy changes to address the most likely drivers of widespread declines [138,139].

In some cases, differential changes in insect abundance could restructure the way communities and ecosystems function (Fig. 4b). For example, global change in the Arctic is generally increasing herbivore and parasitoid populations while decreasing detritivore populations, creating potential impacts on herbivory, top-down control, decomposition and nutrient cycling [140]. In particular, the Arctic has experienced dramatic declines in the abundance of flies [128] but increasing populations of butterflies and moths [141]. These changes in abundance are likely to result in broadly increased rates of herbivory and reduced insect pollination [141]. These differential changes in the abundance of Diptera and Lepidoptera have driven corresponding changes in Diptera-specific and Lepidoptera-specific parasitoid assemblages [141], illustrating how the indirect effects of global change drivers could further influence key processes that regulate communities and ecosystems. Broadly, the reorganization of biodiversity on earth seems certain to affect species interactions and ecosystem function in complex ways; predicting the nature of these changes for specific communities will likely be challenging.

Conclusions

There is wide consensus that global change is reorganizing insect communities, but the scope and implications of this reorganization remain uncertain. Are we in the midst of a widespread “insect apocalypse” [59,133,142–144]? Are there traits of insects that make them especially sensitive or robust to the effects of global change [34,62,99,141,145]? Will the limits of adaptive plasticity become more evident with mounting changes [95,103,110]? Global change is ongoing, and understanding the complex changes wrought by multiple overlapping and interacting drivers will likely require a more mechanistic, dynamic and integrated view of ecology [3,5,37,146].

It seems clear that global change will create both winners and losers, but widespread community turnover and homogenization also threaten to erode ecological intuition and understanding. Whereas ecologists often use adaptive explanations to inform null expectations, these expectations may be less justified in communities with shorter coevolutionary histories where species are responding to non-stationary conditions without historical analog. The proliferation and complexity of global change drivers raises interesting ecological questions, but also threatens to fundamentally alter our ability to accumulate ecological knowledge. The accelerating pace of change in the global ecosystem risks outstripping our ability to document those changes, and to place them into a baseline context. Over time, these changes threaten to unmoor ecology from fundamental assumptions, eroding an important source of ecological and evolutionary information, understanding and prediction.

Although the complexity of global change is widely recognized, grappling with this complexity in ecological studies remains difficult. In many respects, the clearest message to emerge from recent studies of global change is about the limitations of available data and understanding. A secondary theme concerns our limited ability to reverse the complex effects of multiple interacting drivers. In combination, these key limitations suggest that efforts to address the core drivers of global change will

provide a clearer path forward than attempts to repair their myriad effects further downstream. While the pace and complexity of global change presents a profound challenge for ecology [146], this reality does not preclude action to address the underlying drivers of global change. Even as ecologists work to understand a changing planet, we already know enough to mitigate the root causes of climate change, limit habitat loss, slow the global transport of organisms, and regulate novel compounds in ecologically meaningful ways. While the complexity of global change will limit ecological understanding, it should not limit our willingness to address the fundamental drivers of global change.

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718 are typically larger, but there is not necessarily a constraint on size for multivoltine species. Species that
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Figure 1. a) Climate change, b) land use change, c) the increased global transport of organisms and d) novel chemicals and compounds are co-occurring and overlapping drivers of global change. Much of the complexity of global change arises from this multiplicity of interacting drivers.

Figure 2. Global change drivers often have complex downstream effects on insect communities via more 'proximate' behavioral pathways. a) Polarized light signatures from roads disrupt mayfly flight navigation resulting in egg deposition on desiccation-prone surfaces. b) The biological invasion of Argentine ants resulted in reduced genetic and microbial symbiont diversity in the introduced range, which is associated with less costly interspecific conflict. c) Warming increases the chirp frequencies of male field crickets, leading to increased opportunities for hybridization. d) Exposure to pesticides can impair learning and memory in bees, contributing to population declines.

Figure 3. Curves represent the phenological distribution of a species; different hues represent different species and lighter curves of the same hue with dotted outlines represent the phenological distribution of a species at a prior time. a) Phenological shifts are changes in the seasonal timing of life history processes relative to calendar dates. b) Phenological mismatches are differences in the relative phenologies of interacting species. c) Phenological mismatches have the potential to disrupt species interactions, potentially affecting the fitness and abundance of the mis-matched species. d) The indirect effects of disrupted species interactions could impact other species in a broader community, as illustrated in the hypothetical example in panel e).

Figure 4. Representations of shifts in distribution, abundance, and community composition due to global change. a) Insect species may shift their range poleward (or up in elevation), shift their range toward the equator (or down in elevation), or have no shift in their range center. Concurrently, they may shift in their abundance: decreasing through fragmentation, decreasing through range contraction, staying stable, or increasing through range expansion. b) The composition of communities can change due to the direct and indirect effects of range shifts, global transport of insects, and declining insect abundances. In this example, the local extinction of a butterfly decreases the total number of floral visitors, while an invasive grasshopper increases the total number of herbivores in the community, changing ecosystem function.