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1 **The complexity of global change and its effects on insects**

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11

12 **Abstract**

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

22

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

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

68 **The complexity of global change effects**

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

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

90 When their effects are combined, multiple global change drivers can interact in more complex ways
91 [37,38,51] and the statistical and experimental approaches necessary to disentangle these additively or
92 non-additively combined effects are still emerging [37,38,52]. Structured observational studies have
93 grappled with the collinearity of potential explanatory factors using large datasets, multi-model
94 inference and partial least-squares regression [38,41,53–55], suggesting potential interactions among
95 factors. Experimental studies aimed at understanding the ecological and physiological mechanisms of
96 effects may be necessary to improve opportunities for generalization and prediction [52]. For example,
97 both high [56] and low [57] temperatures can increase pesticide toxicity in insects through different
98 physiological mechanisms, suggesting that a clearer understanding of these mechanisms [58] may be
99 necessary to predict the interactive effects of thermal stress and pesticide exposure.

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

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

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

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

121 *Effects on behavior*

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

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

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

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

153 *Effects on phenology and life histories*

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

160 In some cases, phenological shifts lead to phenological mismatch: changes in the relative phenologies of
161 interacting species (Fig. 3b). Studies aiming to understand the causes of phenological mismatch are
162 increasingly focused on the mechanisms of phenological cueing. Phenological mismatch can result from
163 differences in the environmental changes experienced by different organisms (*environmental*
164 *mechanisms*) and differences in their sensitivity to environmental cues (*organismal mechanisms*) [101].
165 Thus, some observed phenological mismatches are likely to be largely explained by organisms
166 experiencing different aspects of global change, as may be the case with habitat specialist butterflies
167 [102]. On the other hand, other mismatches occur when global change exposes previously hidden
168 differences in cue sensitivity and integration [103]; these differences could explain diverging
169 phenological responses of plants and pollinators to increasing urbanization [104]. The ways in which
170 these two mechanisms combine to generate observed variation in phenological responses remains to be
171 determined.

172 Relatively few studies have been able to quantify the effects of phenological mismatches relative to
173 appropriate historical baselines [105]. Phenological mismatches have the potential to disrupt species
174 interactions, but their impacts on fitness and population will likely depend on the nature and specificity
175 of the interaction (Fig. 3c). Some studies suggest that mismatches may be less likely to occur in
176 mutualistic (e.g., plant-pollinator) [34,44,106] or highly specialized (e.g. host-parasitoid) interactions
177 [99,107] where selection under historical environmental variability would be expected to have favored
178 the evolution of more robust phenological cueing strategies in one or both interactors [44]. Whereas the
179 disruption of mutualistic interactions is costly for both interactors, the disruption of antagonistic
180 interactions is more likely to create phenological winners and losers. One possibility is that the *incidence*
181 of mismatches might be lowest among specialist species that have the most to lose, while the *impacts* of
182 mismatches are lowest among generalist species with more diffuse interactions. However, phenological
183 mismatches could occur more broadly if global change continues to increase the variability of
184 phenological shifts [108,109], or increase rapidly if the limits of adaptive plasticity are met [103,110].

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

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

200   *Effects on species distributions and abundance*

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

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

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

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

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

250 **Conclusions**

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

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

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

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