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Insect responses to interacting global change drivers in managed ecosystems

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Insects are facing an increasingly stressful combination of global change drivers such as habitat fragmentation, agricultural intensification, pollution, or climatic changes. While single-factor studies have yielded considerable insights, multi-factor manipulations have gained momentum recently. Nevertheless, most work to date has remained within particular domains of research, such as 'habitat destruction' or 'climate change', and linkages among subdisciplines within the ecological literature have remained scarce. Here, I provide an overview of the most recent developments in the field, with a focus on main functional groups of insects, but also their interactions with other organisms. All major global change drivers (landscape modification, climate change, agricultural management) are covered both singly and in interaction. The manuscript concludes with concepts on how to statistically and conceptually deal with interactions in experimental and observational work.

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Introduction

Human activities are increasingly altering all major components of the Earth system, affecting ecosystem flux rates, biodiversity, and community structure [1,2]. Because many different drivers of global change act simultaneously [3], the outcome for particular species or communities may be difficult to predict.

Insects are the most species-rich group of organisms on Earth [4,5], inhabiting major parts of terrestrial and aquatic ecosystems. Their responses to interacting global change drivers in a multi-factor world [6] are just beginning to be explored. In this review, I cover the key concepts necessary to understand insect responses to interacting drivers, show recent experimental progress, and provide approaches to predict the outcome of interacting drivers for insect populations and communities.

Biotic and abiotic drivers of global change

Global and anthropogenic environmental changes (GEC) affect what has been termed 'drivers' [7], most of which are directly or indirectly related to human population growth [8]. Classes of drivers important for insects can be grouped by compartments and/or biogeochemical cycles. The most important drivers currently recognized (e.g. [9]) are land-use change (including habitat loss), climatic changes, pollution, biological invasion, anthropogenic exploitation of resources, and diseases.

The concept of interacting drivers

Consider two GEC drivers, for example drought and elevated CO_2, dynamic over time. If both drought and elevated CO_2 act independently, the outcome (e.g. insect growth) will equal the sum of the impacts of both processes (e.g. negative growth [10]). However, if both drivers are correlated, the result will be a coupled time series [11]. Recent research [12] has shown that coupled nonlinear time series can appear uncorrelated, positively or negatively correlated (so-called mirage correlations). While there are methods to reconstruct cause-effect relationships from multiple interacting ecological variables [12,13], applications in the field of GEC research have so far been limited.

Another approach to multiple interacting GEC drivers is to look at temporally aggregated data, for example by calculating central tendency or working with log-response ratios [14••]. In these studies, it has become common practice to classify effects as synergistic, neutral or antagonistic. Recently, the concept of 'synergism' versus 'antagonism' among drivers was extended [15••] to include terms such as 'double positive', 'positive neutral' or similar. However, this concept falls short if there are more than two interacting drivers. Other studies [16] have differentiated additive from synergistic effects, but usually disregarded antagonistic interactions.

Overall, three main questions remain to be answered in the context of multiple interacting drivers:

(1) Which are the most important *individual* drivers for insect performance?

(2) Does the *number of drivers* per se influence insect performance?
(3) Which are the most commonly observed *combinations of drivers*, and how do they affect insect performance?

Insect responses to single global change drivers

Clearly, habitat destruction and conversion from natural to managed systems are among the most important drivers of changes in insect abundance and diversity [17], affecting agriculturally important processes such as biological control [18]. For example, in a study in 45 Swedish grassland fragments strong negative effects of habitat loss on pollinating insects were reported [19]. Resource consumption in general [20] has been shown to be negatively affected by habitat fragmentation, especially in specialist species.

Conversion from (semi-)natural to managed systems often coincides with changes in farming practices, such as organic versus conventional farming [21], or increased pesticide use [22]. A particularly recent development is the study of multiple interacting pesticides such as neonicotinoids [23,24,25•].

Biotic exchange and biological invasions may affect insects in a variety of ways, depending on the trophic level at which alien taxa enter local communities. For example, invasive alien plants may provide additional resources to herbivores or pollinators, altering the structure of interaction networks [26]. By contrast, invasive insects can dramatically alter top-down control in ecosystems [27].

In the context of climate change research, many studies have focused on altered temperature [28]. For example, Ref. [29] presented a meta-analysis of responses of insect herbivores to individual drivers and concluded that temperature (but not CO_2 or UV radiation) strongly affected key parameters of insect performance. Rapid climate warming may disrupt life-cycle regulation, leading to developmental traps (lost generation hypothesis [30•]).

Water availability, which is often closely linked to other climatic changes, can also have profound effects on insect herbivores [31–33], with particularly adverse effects on sap-sucking taxa. In dryland ecosystems, shifts in the trophic position of some insect taxa may be expected, depending on local water availability (reviewed in [34]).

Other drivers, such as nitrogen deposition or elevated CO_2 [7,35], have been shown to act indirectly via changes in primary producer abundance, diversity or physiology (but see [36]). In unfertilized systems, increased CO_2 may result in progressive nitrogen limitation [37,38], negatively affecting insect herbivores [39].

Number of drivers

In classical biodiversity experiments, the number of species present in a system is manipulated [7]. By analogy, one could imagine experiments that explicitly manipulate the number of global change drivers (e.g. [10]). As more and more drivers are combined, insect performance may be expected to decrease. This would be an example of a sampling effect, where an increasing number of drivers would increase the chance that a particularly adverse driver is present.

Interactions of drivers

Increasingly, global change experiments incorporate combinations of GEC drivers [14••,40,41] and explicitly test for interactions. In the simplest possible scenario, the interaction among several drivers can be summarized as the sum of individual effects, assuming these effects are additive [16]. However, effects of an interaction may also become stronger over time. For example, growth of insect larvae exposed to combinations of drivers may show complex dynamics over time (Figure 1). Future experiments therefore need to investigate longer-term responses to combined GEC drivers [42].

Several key ingredients are needed to understand interactions among drivers. First, full-factorial manipulations of several factors in experiments are required; that is, we need to move away from experiments manipulating only one or two drivers. Such combined experiments are best done using split-plot or nested designs [43]. Second, interaction terms of sufficient order need to be incorporated in statistical models. Third, it is notoriously difficult to interpret interactions on the basis of numerical model output alone [44], and interactions should be plotted using two-dimensional graphs, preferably showing the individual data points instead of using bar graphs (Figure 2).

Recent developments in the study of interacting drivers

Most studies so far focused on two or three interacting global change drivers. For pollinators, a recent analysis showed that global change pressures tend to interact in an additive way [45]; that is, the result of the interaction is equal to the sum of the individual effect sizes. For example, human-modified landscapes are often characterized by higher abundances of non-native plants and pollinators [46,47]. Several important interactions have remained little explored, such as those between climatic changes and landscape modification [48], or between agricultural intensification and landscape modification [49]. One of the currently most pressing research questions is the interaction between pesticides and other stressors [50•], including parasites and pathogens affecting pollinators. In addition, interacting global change drivers may unexpectedly affect attractiveness of flowers to pollinators [51] (Figure 3), reducing globally important pollination services.