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Global change and the importance of fire for the ecology and evolution of insects

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Climate change is drastically altering global fire regimes, which may affect the structure and function of insect communities. Insect responses to fire are strongly tied to fire history, plant responses, and changes in species interactions. Many insects already possess adaptive traits to survive fire or benefit from post-fire resources, which may result in community composition shifting toward habitat and dietary generalists as well as species with high dispersal abilities. However, predicting community-level resilience of insects is inherently challenging due to the high degree of spatiotemporal and historical heterogeneity of fires, diversity of insect life histories, and potential interactions with other global change drivers. Future work should incorporate experimental approaches that specifically consider spatiotemporal variability and regional fire history in order to integrate eco-evolutionary processes in understanding insect responses to fire.

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Introduction

Natural wildfire is an important form of periodic disturbance that disrupts ecological processes at a landscape scale [1,2•] and places unique selective pressures on fire-affected communities. In particular, fire alone can alter the abundance and quality of basal resources, cause short-term and long-term effects on soil nutrient availability, temperature, and moisture, and transform habitat structure (Figure 1). Recent changes in the intensity and frequency of droughts are leading to higher incidences of fire [3]; ecosystems are also experiencing changes in fire frequency, seasonality, extent, duration, and severity as a result of global climate change [3]. Such changes in fire regimes will likely affect insect community composition via ecological and evolutionary mechanisms with consequences for the strength of biological interactions and the provision of ecosystem services (Figure 1) [3].

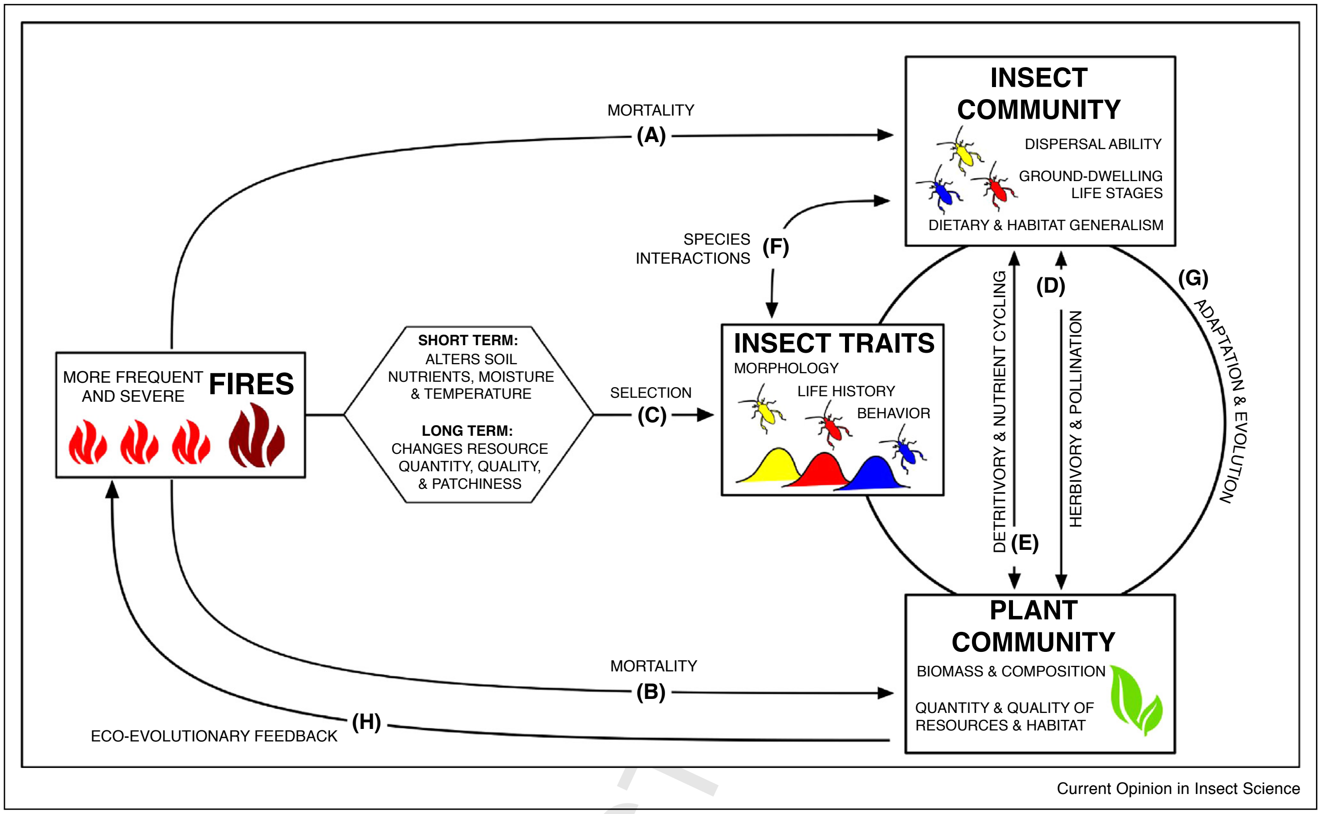
Many insects are adapted to survive fire and some even benefit from ecosystem changes associated with fire [4••]. For example, immediately after grassland fires, prairie mole crickets (*Gryllotalpa major)* profit from enhanced acoustics within their burrows for improved signaling to potential mates [5]. Similarly, some forest beetles (e.g. Buprestidae and Cerambycidae), respond to heat and smoke generated by fires to colonize newly available, high-quality habitat [6]. It is nevertheless unclear, even in fire-prone habitats, whether existing morphological, life history, and behavioral adaptive traits will be sufficient for maintaining species and functional insect diversity as fire regimes continue to change. Moreover, many insect species that rarely experience fire (e.g. high latitude biota) are beginning to do so on a more regular basis. Despite the importance of fire as a natural disturbance in many ecosystems, the role of evolutionary processes in shaping insect responses to fire is an underdeveloped research area. Yet the potential for adaptation is especially important in this context, because many insect species have short generation times and large population sizes, which facilitate rapid evolution [7].

Here we provide a brief review of recent advances in our understanding of insect responses to fire from an ecological perspective that considers how responses to fire alter species interactions and functional roles of insects within ecological communities. We also discuss specific traits that allow insects to survive fire and how these traits may contribute to certain groups having the capacity to cope with or adapt to rapidly changing fire regimes.

Ecological responses to fire

Various aspects of fire, including severity, extent, frequency, and seasonality, impact the abundance and diversity of insects across all trophic levels [e.g. 1,8,9,10••,11]

Figure 1



Conceptual diagram depicting the ecological and evolutionary effects of fire on insect and plant communities. Fire directly affects insect (A) and plant (B**)** mortality and also has a number of indirect effects that act as selection pressures on insect traits (C). Indirect effects of fire (C) can include long-term changes to plant and detrital resource availability, quality, and heterogeneity, as well as habitat structure. Short-term indirect effects include immediate changes to soil nutrients, moisture, and temperature. Plant community responses and recovery to fire are influenced by insect herbivory and pollination (D) and by insect effects on detritivory and nutrient cycling (E). Likewise, recovery of the insect community is tightly tied to the resources and habitat provided by the plant community (D,E). The strength and timing of species interactions within the insect community (F), such as predation, parasitism, competition, and mutualism, vary with time since fire and can also affect insect community recovery. Insect and plant communities are adapting and evolving in response to fire-induced selection pressures on insect traits (G). On a longer timescale, post-fire changes to plant community biomass and composition due to interactions with insects (e.g. biomass removal due to herbivory) may result in eco-evolutionary feedbacks to fire regimes that either promote or inhibit future fires (H). Changes in fire severity, extent, frequency, and duration may amplify and/or attenuate the strength of these fire effects on insect and plant communities.

(Figure 1A,C,F). For instance, high soil temperatures during severe fires kill ground-nesting insects, such as Megachilidae bees [12] that typically survive lower intensity fires. Most community-level recovery depends on recolonization from nearby undisturbed areas [13], so increased fire extent will delay recovery in central portions of burned areas. Effects of fire on some insects are short-lived, with certain groups recovering quickly post-fire. However, increased fire frequency may not allow enough time for many arthropods to recover. Further, changes in soil moisture and temperature due to fire can alter soil arthropod community composition for decades [14]. Some soil-dwelling arthropods may recover more quickly [13], but this response is linked to seasonality, demonstrating that fire timing also influences recovery. Even ephemeral responses to disturbance can have cascading effects on communities [e.g. 15]. Given that insects are key herbivores, pollinators, and detritivores, their short-term and long-term responses to changing fire regimes could have important consequences for ecosystem functioning.

Our understanding of insect responses to fire has historically come from a bottom-up perspective that primarily considers insect recovery in relation to recovery of the plant community [13] (Figure 1B,D). This narrow focus is understandable as recovery of the plant community defines habitat structure and availability of resources for the entire insect community [16,17]. Thus, fire return intervals that maximize plant diversity, such as mosaic burns that increase spatial heterogeneity of resources, should maximize post-burn insect functional diversity even though this is rarely measured explicitly [13].

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