Title:

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

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Abstract

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.

Highlights

1. Fire uniquely disturbs ecosystems with persistent impacts on insect communities
2. Life history, interactions, adaptive traits and habitat structure affect recovery
3. More frequent and severe fires may favor generalists and high-dispersal abilities
4. Predicting community resilience requires accounting for spatiotemporal variability
5. Experimental manipulations across habitats and fire regimes are needed

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- and long-term effects on soil nutrient availability, temperature, and moisture, and transform habitat structure (Fig. 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 (Fig. 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. 1,8,9-11](Fig. 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 re-colonization 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- 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](Fig. 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].

Fire effects vary across space and functional groups [e.g. 18,19,20], meaning that fire indirectly alters the spatial and temporal distribution of species interactions [e.g. between bees and flowers or herbivores and their hosts, 21,22] (Fig. 1F). This variation, along with the unpredictable nature of post-fire resource availability, tends to result in a higher proportion of diet generalists and fewer specialized interactions in fire affected areas [10,23]. Specialist-feeders are potentially more influenced by bottom-up effects than generalist-feeders [24], suggesting that recovery by diet specialists is likely to be slower and more closely tied to the recovery of particular plant or prey species. Thus, while the first species to colonize burned habitats are those that survive fire (e.g. some soil-dwellers) or capable dispersers from nearby unburned patches, species with generalist feeding habits are the most likely to benefit from post-fire resources and recover quickly. For instance, grasshoppers, which are good dispersers and largely generalist feeders, commonly increase in abundance post-fire as they exploit re-sprouting vegetation [e.g. 21].

Fire responses are best documented for herbivores and pollinators that depend directly on plant resources. Plant biomass and community composition are key determinants of herbivore recovery (Fig 1D), as are fire-induced changes in plant quality [e.g. 25,26,27] and plant defenses [e.g. 28]. For example, low-severity, frequent fires induce resin production that protects trees against bark beetles [29]. However, fire effects on herbivore communities have also been found to be mediated through changes in habitat structure instead of fire-related changes in host plant quality [30,31]. Fire-induced changes in both resource and habitat quality therefore select for a combination of generalist traits in post-fire herbivore communities. Despite these insights, predicting herbivore responses to changing fire regimes is still challenging and will require a better understanding of both the direct and indirect effects of fire on herbivore communities across a wider array of habitats.

Our understanding of responses of insect pollinators to fire is mainly focused on floral resources (Fig. 1D), and less on nesting habitat or mortality due to fire. Notably, many ground-nesting species do survive fires [12] and are positively associated with recent burns in some systems [32]. After fire opens space for flowering plants to thrive, pollinators are attracted to abundant floral resources [e.g. 33]. Pollinator abundance and diversity, especially of diet-generalist bees [22], show a strong time-since-fire signal, peaking soon after fire and decreasing with declining floral resources as succession proceeds [34]. These successional trajectories differ depending on fire severity [35], life history, and ecosystem. However, species with different nesting habitats (e.g. below-ground vs. above-ground) are not influenced by time-since-fire in all ecosystems [36]. Changes in fire regimes may favor large-bodied pollinators that can more rapidly colonize the center of large burns and generalists that can forage in recently burned areas despite restricted floral options.

Responses to fire by higher trophic levels (e.g. predators and parasitoids) are tied to prey recovery and are therefore sensitive to mismatches in species responses. Predators with generalized diet breadths are typically able to recover more rapidly than diet-specialists. For example, several recent studies detected no post-fire changes in the abundance and diversity of spiders and predaceous beetles, which tend to be generalist-feeders [37,38]. Relative to many predators, parasitoids tend to be more specialized on specific hosts and sensitive to fire-induced shifts in community structure. Parasitoid responses to fire may also be taxon-specific, as shown with other types of disturbances. For example, variability in precipitation and host-availability affects specialized hymenopteran parasitoids more than generalized dipteran parasitoids [39]. Taken together, diet-generalist predators are likely to be more resilient to changes in global fire regimes than diet-specialist predators and parasitoids. However, other studies have found mixed effects of fire, indicating that habitat type, taxonomic group, dispersal ability, and time-since-fire are all important components of predator recovery [e.g. 40,41,42]. Changing fire regimes may further exacerbate mismatches in species interactions post-fire, resulting in longer recovery times or altered community composition (e.g. more generalist-feeding predators). For instance, fire can cause increased soil temperatures that promote earlier hatches of soil-dwelling insects [2] or provide some organisms temporary relief from specialist natural enemies [4,43].

Habitat quantity and quality may be more important for the short-term recovery of litter- and soil-dwelling arthropod communities than other traits such as dispersal ability [44](Fig. 1E). Fire reduces or eliminates the availability of resources and habitat space for detritivores and other litter insects in the short-term [45]. In the long-term, the abundance of soil arthropods are not commonly affected [reviewed in 46], but their diversity decreases and can remain altered for decades due to persistent changes in resource quality [47]. While belowground habitat and resources for insects increase as plant communities recover in some systems [48], high-frequency fires also result in reduced soil carbon and nitrogen over decadal timescales in others (e.g. broadleaf forests and savannah grasslands)[49]. Therefore, recovery of soil arthropods [41,50] is influenced by a combination of pre- and post-fire soil quality, litter availability, and plant composition, necessitating consideration of short- and long-term legacy effects of fire to understand detritivore responses.

Adaptive Traits and Potential Evolutionary Responses to Fire

Species that are able to survive fire or recolonize fire-affected areas can benefit from post-fire conditions via increased resource availability [26,51,52], advantageous habitat alterations [33], and/or altered species interactions [e.g. reduced predation, 4,13](Fig. 1F,G). Many insects currently exhibit a variety of morphological, behavioral, and life history traits that allow them to survive fire events and recover quickly from fire disturbance [2](Fig. 1C). Some of these include morphological adaptations to detect fire, including smoke-detecting antennae in cerambycid beetles [53] and infrared radiation sensors in buprestid beetles *(Melanophila acuminata)*[54]. Such traits can allow them to escape fire, synchronize emergence, and locate resources and mates post-fire [e.g. 55]. Many insects exhibit adaptive behaviors to fire, such as climbing trees, fleeing, and burrowing into the soil [2,56-58]. Life history traits that can improve survival to fire include living some or all life stages belowground [2,59], high-dispersal capabilities [13], and diet- and habitat-generalism [23,60].

Even within habitats that have historically been exposed to fire, it is unclear how changes in the fire regime, such as increased fire frequency and severity [3], may ultimately affect insect communities. While more frequent low-severity fires could favor fire-adapted insects [13], they could also pose risks to species that thrive during later successional stages. As fires become more severe, species adapted to low-severity fires may be negatively affected and community recovery times may increase. Changing fire regimes could influence community-level succession in unpredictable ways, such as by preventing species from recolonizing from non-burned patches, or by imposing severe founder effects and genetic bottlenecks. Under certain conditions, changes in fire regimes could result in evolutionary tipping points and population collapse [61]. Insect species from more variable environments might have higher degrees of plasticity and may therefore be better adapted to cope with increasing extreme fire events [62]. However, selection and the potential for rapid evolution could be strongest on species with limited phenotypic plasticity [63].

Emerging evidence suggests that global changes have the potential to drive evolutionary trajectories of functional traits that lead to eco-evolutionary feedbacks to ecosystem processes [64]. Fire is one such global change that may serve as both an important selection pressure and driver of changes in the function of insect communities (Fig. 1). Few studies connect shifts in insect communities with ecosystem processes such as carbon and nitrogen cycling in fire-affected ecosystems, but fire does alter the functional roles of these organisms. For example, although pollination levels can be high after fire [i.e., pollen deposition, 9], pollinator visitation and seed set vary with time-since-fire [e.g. 33,65,66]. It is an open question whether post-fire insect communities alter the environment to a degree that may feedback to fire frequency and severity (Fig 1H), but this area warrants further investigation. In particular, as insects serve key functions within ecosystems as herbivores, pollinators, and detritivores, their responses to changing fire regimes could influence the susceptibility of some ecosystems to future fires (e.g. via biomass removal from herbivory).

Conclusions and Perspectives

Several fundamental challenges have limited an eco-evolutionary approach to linking insect communities and changing fire regimes. First, our current understanding of insect responses to fire is largely skewed toward observational studies in grasslands and forests where fire is common and taxa already tend to possess fire-adapted traits [1,2,13]. Second, most studies use a single fire to document insect responses, but these effects cannot be extrapolated to predict changes in community interactions, evolutionary responses, or ecosystem functions due to frequent, repeated disturbances. Third, fires do not occur in isolation of other global changes. Altered fire regimes could exacerbate effects of other selective pressures, including changes in temperature, precipitation, nutrient pollution, habitat fragmentation and degradation, invasive species, range shifts, biodiversity loss, as well as spatially and temporally mismatched biological interactions [e.g. 67,68]. How insect responses to fire are influenced by these and other drivers of global change still needs to be assessed.

Future studies can address these gaps by using manipulative experiments of fire frequency and severity to investigate effects of fire regimes (as opposed to single fires), on insect communities. These types of studies are particularly important in ecosystems where wildfire is historically rare but projected to increase (e.g. tundra)[3,69]. Experimental approaches allow for systematic manipulation of variables such as fire severity, focal taxa, burn season, and abiotic conditions, all of which play into the ecological and evolutionary responses of insect communities. While recent studies have worked towards understanding habitat and resource heterogeneity [e.g. 70], future experimental study designs should be more explicit in incorporating temporal and spatial variability when considering the resilience of insect communities to changing fire regimes. Similarly, a better understanding of post-fire feedbacks between plant recovery and insect-driven ecosystem services (e.g. herbivory, detritivory, pollination) could be achieved through experimental manipulations of these community components. Long-term experiments that manipulate other global change variables along fire frequency and severity gradients (e.g. Konza Prairie and Arctic LTERs) provide opportunities for insect ecologists to advance our understanding of the interactive effects of multiple disturbances.

As fire regimes continue to shift as a result of climate change [3], insects and the ecological communities they inhabit are also likely to change. A better understanding of the effects of these changing fire regimes on insects will require consideration of the actual traits (e.g. diet and habitat generalism, dispersal ability, belowground life stages, temperature tolerance) that enable insects to survive and/or benefit from fire, how these traits vary across sites, and how quickly they are able to change in species with different ecological and natural history backgrounds. Experimental approaches that use insects are a promising way to further develop understanding of eco-evolutionary feedbacks in response to changing fire regimes and other types of disturbances.

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Figure Caption

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.

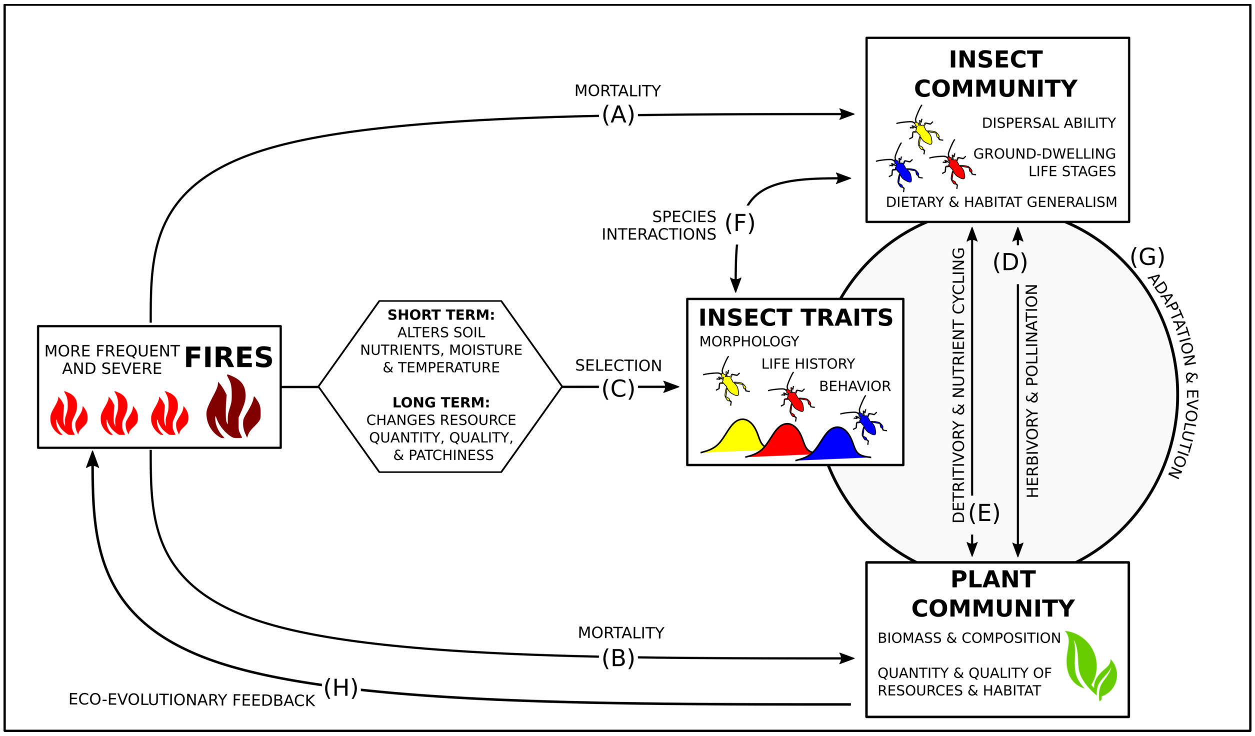
MORTALITY
(A)
INSECT COMMUNITY
DISPERSAL ABILITY
GROUND-DWELLING LIFE STAGES
DIETARY & HABITAT GENERALISM
SPECIES INTERACTIONS
(F)
(D)
(G)
ADAPTATION & EVOLUTION
DETRITIVORY & NUTRIENT CYCLING
HERBIVORY & POLLINATION
MORE FREQUENT AND SEVERE
FIRES
SHORT TERM:
ALTERS SOIL NUTRIENTS, MOISTURE & TEMPERATURE
LONG TERM:
CHANGES RESOURCE QUANTITY, QUALITY, & PATCHINESS
SELECTION
(C)
INSECT TRAITS
MORPHOLOGY
LIFE HISTORY
BEHAVIOR
(E)
PLANT COMMUNITY
BIOMASS & COMPOSITION
QUANTITY & QUALITY OF RESOURCES & HABITAT
MORTALITY
(B)
ECO-EVOLUTIONARY FEEDBACK
(H)

Figure 1.