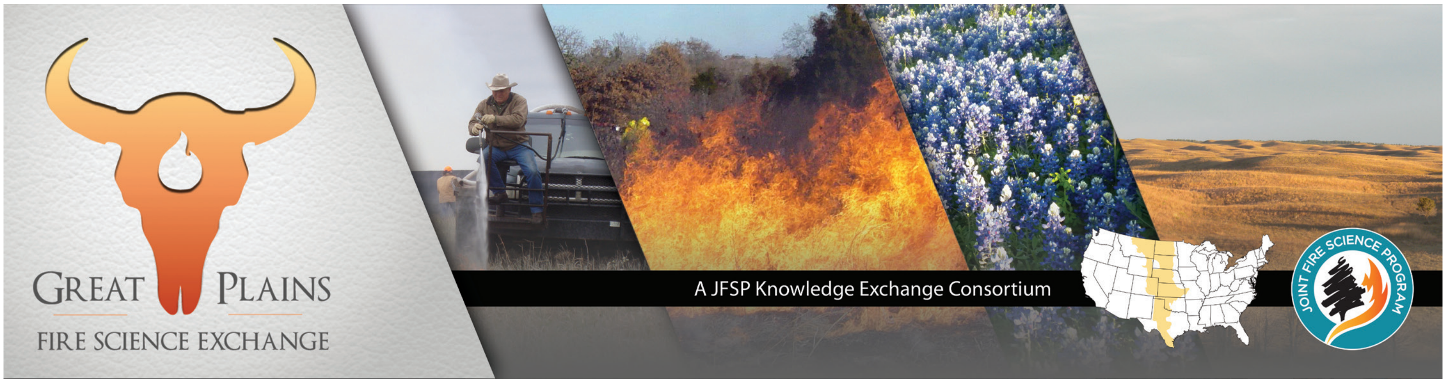

A synthesis of arthropod responses to fire in the Great Plains

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ABSTRACT

Fire is one of the natural processes in grasslands that maintains an open canopy and creates discrete disturbances. Over time, the use of fire in the Great Plains has changed from traditional use by American Indians to suppression by European settlers to reintroduction by modern landowners and managers.

Although there is a wealth of knowledge of plant and avian responses to fire in the Great Plains, responses are not as well understood for arthropods, including insects, spiders, and their close relatives.

We conducted a review of the literature to synthesize research on arthropod responses to fire in the Great Plains. Our goal was to offer more insights to managers about how arthropods typically respond to fire and highlight areas that need more research.

Overall, arthropods tend to respond positively to fire and appear to be adapted to periodic fires, but there are species that respond negatively to fire through direct and indirect effects. Certain orders (Araneae: true spiders, Hemiptera: true bugs, Homoptera: aphids, cicadas, and leaf hoppers, and Lepidoptera: butterflies and moths) appear to be more sensitive to fire, but fire effects are still species specific and contingent on species traits such as mobility, life stage, and feeding guild.

More research is needed to fully elucidate these species specific effects, but fire has the potential to be a valuable resource for land managers when applied at the correct scale. Heterogeneously-applied fire, where non-burned and burned patches create a mosaic, is a common strategy to benefit the most arthropod species while enhancing natural ecosystem processes. Although management recommendations will change for each species, available research suggests the overall arthropod community responds well to fire.

Knowledge gaps remain concerning individual species and specific mechanisms that allow them to persist after fire in the Great Plains, and future research should focus on both theoretical and applied basis for arthropod conservation using prescribed fire and other disturbances.

INTRODUCTION

Short History of Fire in the Great Plains

Fire is a natural ecosystem process in the Great Plains that has been repeatedly altered and used by humans to create disturbance (Higgins et al. 1986, Fuhlendorf and Engle 2001, Allen and Palmer 2011). Fire is imperative to the formation and continuation of grasslands (Samson and Knopf 1994), as the interaction of fire, climate, and grazing maintains a heterogeneous mixture of grasses and forbs while controlling the spread of woody species (Anderson 2006, Hartley et al. 2007).

Historically, American Indians used the interaction of fire and grazing for hunting (Diekmann et al. 2007), along with many other purposes (Levy 2005). After European colonization, fire was widely suppressed (Umbanhowar 1996), but the need for fire in grasslands remained.

Subsequently, fire suppression led to increased woody encroachment (Ratajczak et al. 2012, Twidwell et al. 2013), extreme wildfires, and decreases in biodiversity

(Coppedge et al. 2001, Fuhlendorf et al. 2012). More recently, land practitioners have reinstated fire to benefit grassland biodiversity and stability.

While research has focused on the influences of fire on plants (MacDougall et al. 2013, Koerner et al. 2014) and birds (Fuhlendorf et al. 2006, Hovick et al. 2014), organisms such as arthropods have received less attention.

Fire to Manipulate Arthopods

Studies examining the responses of arthropods to fire in the Great Plains are not as extensive as those for plants and birds, and collectively, arthropods are often researched much less than other organisms (Dunn 2015). Nonetheless, arthropod responses are both important for and interconnected with plants and animals (Meyer et al. 2002, Conway and Stapp 2015), and fire was commonly used to manipulate arthropods for some other purpose than their conservation.

Traditionally, fire was used as a means to reduce pest species that feed on grassland plants and could compete with livestock, like grasshoppers and locusts (Warren et al. 1987, Branson et al. 2006), or transmit diseases to livestock and people, such as ticks (Fischer et al. 1996, Polito et al. 2013). Conversely, fire has also been used to increase the arthropod biomass available for game birds that require arthropods for protein during brood rearing (Hess and Beck 2014).

Altogether, manipulation was not focused on benefiting arthropods for their own conservation but rather for the benefits of other organisms. Yet, these past management practices do highlight how arthropod responses to fire are often mixed (Warren et al. 1987, Swengel 2001, Doxon et al. 2011), with species responding positively, negatively, or neutrally to fire.

Variable effects of fire on certain arthropod species are likely to occur due to direct and indirect effects of fire. Fire directly causes mortality and impacts individuals through combustion and heat stress (Warren et al. 1987, Zelhart and Robertson 2009), especially to remnant-dependent species in small reserves (Panzer 2002). Nonetheless, the indirect effects of fire, particularly on the plant community, can enhance available resources, population longevity, and arthropod diversity (Engstrom 2010, Evans et al. 2013, Baum and Shaber 2012).

The decision to use fire for managing arthropods can be difficult, as fire creates both detrimental conditions and desirable outcomes. Consequently, there is a disturbance paradox for many arthropods (Swengel 2001, Tooker and Hanks 2004, Moranz et al. 2014) and more research is necessary.

Fire to Conserve Arthopods

Land managers need to be able to use disturbance to manage and conserve arthropods beyond simply decreasing or increasing total arthropod biomass. As conservation concerns for specific species continue to grow (Conrad et al. 2006, Lebuhn et al. 2013), best management practices will be vital for conserving and bolstering populations.

However, the disturbance management paradox makes it difficult for managers and conservationists to apply fire when burn effects are unknown for certain species and because fire responses are dependent on added variables such as season of burn, post-fire use, and fire frequency (Warren et al. 1987). Alternatively, if land managers have a better understanding about how arthropods respond to fire, they can effectively modify management to improve conservation of the arthropod community or particular species (Swengel 2001, Vogel et al. 2010).

Successfully using natural ecosystem processes, like fire, in grasslands are important to maintain significant ecosystem functions and services provided by arthropods (Engle et al. 2008, Ehrlich and Hart 2016), along with protecting threatened and endangered species. Therefore, our objectives are to identify short- and long-term effects of fire, outline the current understanding of arthropod responses to fire in the Great Plains, determine species traits that can predict responses to fire, define overarching management implications, and identify knowledge gaps that should be addressed by future research.

METHODS

We searched for peer-reviewed, indexed articles in Web of Science™ and Google Scholar™ between February and March of 2016 to find research published on arthropod responses to fire in the Great Plains. In these search engines, we used keywords including fire*, burn*, or wildfire* with insect orders and common names for insects and some arthropods (Table 1).

Our main objective was to determine fire effects on insects (Class Insecta), but we also included several important groups of insect relatives that are in Arthropoda, including: Araneae (true spiders), Chilopoda (centipedes), and Diplodoa (millipedes). We also used keywords to search trap types in combination with fire in case arthropods were not exclusively studied. If our search returned too many results, we narrowed the search to only include studies that included the keywords: grass*, prairie*, range*, or "Great Plain*".

Table 1. Search terms used in synthesis to find peer-reviewed, indexed journal articles concerning arthropod responses to fire in the Great Plains.

Searches always included: **fire*** or **burn*** or **wildfire*** AND an additional factor:
Arthropod classification Araneae, Blattodea, Coleoptera, Collembola, Diptera, Ephemeroptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Neuroptera, Odonata, Orthoptera, Thysanoptera, Thysanoptera, or Trichoptera
Common name Beetle, fly, flies, caddisfl*, cricket*, grasshopper*, damselfl*,dragonfl*, lacewing*, spider*, wasp*, ant*, bee*, "bumble bee*", insect*, or bug*
Sampling method "pit-fall trap*", "sweep net*", or vacuum

Over 110 papers were obtained during our initial search, but we completed a secondary evaluation of articles to make sure they met our requirements. We confirmed that research was conducted in the Great Plains, which included: Colorado, Kansas, Montana, Nebraska, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming. However, we also used research conducted in the tallgrass prairie adjacent to the Great Plains in Iowa, Illinois, Missouri, Minnesota, and Wisconsin. These states, especially Iowa and Illinois, provided more research on Lepidoptera (butterflies and moths), Coleoptera (beetles), and Araneae (true spiders). Additionally, all studies had to use the arthropod community or single species to make comparisons between fire treatments. Fire treatments could be prescribed fires or wildfires that compared burned to non-burned areas or compared different fire return intervals. In total, we found 88 papers that met our criteria.

RESPONSES TO FIRE

Total Abundance, Biomass, and Diversity Indexes

In the hours and days after fire, burning can initially reduce the total number of species and individuals (Figure 1; Swengel 2001, Larson and Work 2003, Hartley et al. 2007), but these patterns are typically undetected in subsequent years (Anderson et al. 1989, Engle et al. 2008). Moreover, species richness tends to decrease in non-burned areas and increase in burned areas in the years following fire (Andrew and Leach 2006, Parmenter et al. 2011), although diversity does not indefinitely increase after fire (Figure 1).

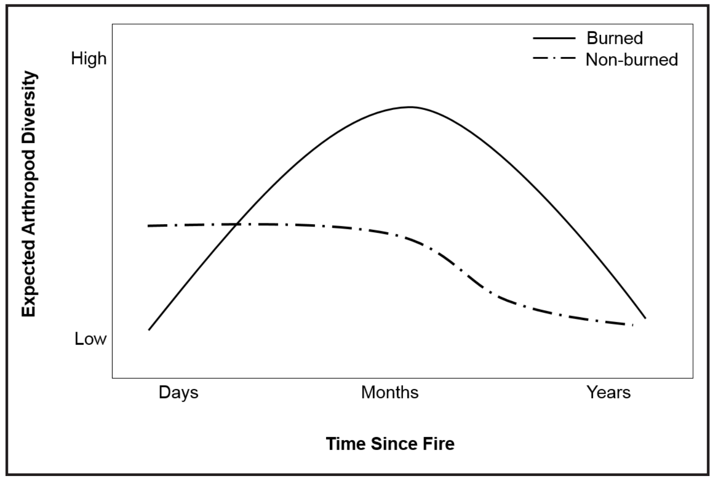

Figure 1. Expected changes in arthropod diversity with burning and no burning. Without fire, grasslands are expected to have a moderate amount of diversity but decrease when fire is not applied. Areas burned will initially have low diversity due to mortality, but diversity will increase in the following months or year after fire. Nonetheless, arthropod diversity will decrease as the times since fire increases, even on burned areas.

With the exception of two studies (Siemann et al. 1997, Callaham et al. 2003), arthropod biomass remains the same after fire (Andrew and Leach 2006, Hess and Beck 2014) or increases (Nagel 1973, Seastedt et al. 1986, Engle et al. 2008). Similarly, arthropod diversity also increases on annual fires (Hartley et al. 2007) and single fire events (Zelhart and Robertson 2009).

Most of these previous studies exclusively used spring burns, but it is possible to observe differences between arthropod abundance due to season of burn. Summer burns may lead to a higher abundance of arthropods compared to dormant season burns (Johnson et al. 2008), but season of burn does not always affect arthropod abundance (Kirkwood et al. 2000).

A large proportion of studies report neutral effects from fire in regards to overall arthropod abundance, biomass, diversity, or richness (Lussenhop 1976, Seastedt 1984b, Seastedt et al. 1986, Johnson et al. 2008, Debinski et al. 2011, Doxon et al. 2011). Primarily, neutral effects are related to variable results between years caused by changes in climatic factors (Meyer et al. 2002, Benson et al. 2007, Branson and Sword 2010, Scasta et al. 2015) or other disturbances that override responses to fire such as fertilization, mowing, and grazing (Callaham et al. 2003, Joern 2004, Vogel et al. 2010, Moranz et al. 2014).

Although some studies have reported that overall arthropod populations do not experience severe declines following fire and are neutral to fire (Anderson et al. 1989, Siemann et al. 1997), it is more likely that some groups respond positively while others respond negatively (Larsen and Work 2003), and examining diversity indices or abundance may be misleading (Johnson et al. 2008).

Individual Order Responses

Observing taxonomic groups instead of total abundance, biomass, or diversity can create a better understanding of overall arthropod responses to fire. Grassland arthropods in the Great Plains appear to be adapted to periodic fire disturbances (Anderson et al. 1989, Siemann et al. 1997, Panzer and Schwartz 2000, Larsen and Work 2003), with over 75% of common families in one study showing no changes in richness or abundance after fire (Hartley et al. 2007).

Orders which typically respond *positively* to fire are Orthoptera (grasshoppers, crickets, and locusts; Nagel 1973, Anderson et al. 1989, Reed 1997, Meyer et al. 2002, Hess and Beck 2014) and Coleoptera (beetles; Bertwell and Blocker 1975, Fellows and Newton 1999, Cook and Holt 2006, Debinski et al. 2011), while Araneae (true spiders, Rice 1932, Nagel 1973, Reed 1997, Engle et al. 2008, Doxon et al. 2011), the Suborder Homoptera (aphids, cicadas and leafhoppers, Anderson et al. 1989, Siemann et al. 1997, Radke et al. 2008), and Lepidoptera (butterflies and moths; Reed 1997, Huebschman and Bragg 2000, Powell et al. 2007, Vogel et al 2010) commonly respond *negatively* (Figure 2).

Nonetheless, each arthropod classification can have the opposite response or no response to fire (Doxon et al. 2011, Parmenter et al. 2011), even for orders with strong negative responses like Lepidoptera (King 2003, Vogel et al. 2010, Evans et al. 2013, Moranz et al. 2014). Additional arthropod orders commonly found in our literature search—Hemiptera (true bugs), Diptera (true flies), and Hymenoptera (sawflies, wasps, bees, and ants)—showed variable responses to fire with no clear positive, negative, or neutral pattern. Variable responses are expected because individual species, even within the same order, are affected differently by fire (Joern 2004, Cook and Holt 2006), depending on responses to direct and indirect effects.

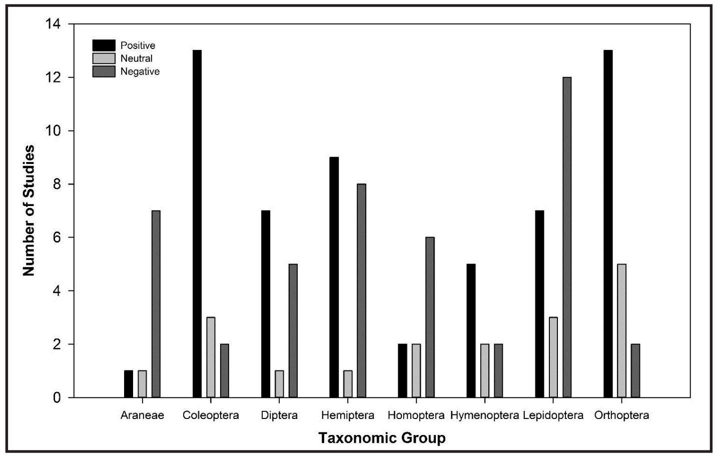

Figure 2. Common arthropod orders (Araneae: spiders, Coleoptera: beetles, Diptera: true flies, Hemiptera: true bugs, Homoptera: aphids, cicadas, and leafhoppers, Hymenoptera: sawflies, wasps, bees, and ants, Lepidoptera: butterflies and moths, and Orthoptera: grasshoppers, crickets, and locusts) and the total number of studies that report overall positive, negative, or neutral responses to fire using a variety of arthropod metrics such as abundance or biomass.

Short-term Responses to Fire

Direct Effects. Overall, available research suggests a single fire event generally has few short-term (days to a year after fire) effects on arthropods (Anderson et al. 1989, Nemee 2014), but direct effects are often severe because they can result in mortality. Most direct effects from fire are implied because few individuals are directly observed being consumed by fire (Swengel 2001, Moranz et al. 2012). More generally, researchers observe charred arthropod remains (Rice 1932) and lower abundance of certain species after fire (Zelhart and Robertson 2009, Branson and Vermeire 2016).

A majority of individuals consumed in fire are eggs and larvae with lower mobility (Powell et al. 2007), as most fires are conducted in the spring when many species are not in their adult stage (Johnson et al. 2008). Even so, heat stress after fire can still lead to the desiccation of arthropods at all life stages (Seastedt 1984a), and fires conducted in the summer may expose more adults to direct mortality, disrupting population dynamics (Branson and Vermeire 2016).

Short-term, direct effects of fire are dependent on fire characteristics, along with other species traits discussed later in this synthesis. Resident heat time and heat dosage are the principal predictors of individual direct mortality (Nagel 1973), which are influenced by wind speed, humidity, fuel loads, plant communities, and topography (Tooker and Hanks 2004). Longer heat times and higher heat dosages increase the likelihood of consumption and desiccation by fire, but the availability of insulating materials and shelter, such as litter, logs, and rocks, can reduce fire impacts (Callaham et al. 2003, Andrew and Leach 2006). Generally, direct fire effects on arthropods are short-lived, lasting one to two years, (Anderson et al. 1989, Panzer 2002, Willand et al. 2011), and less influential than short-term indirect effects.

Indirect Effects. Indirect effects are commonly considered more influential than direct effects because they involve plant biomass availability and plant community composition (Vogel et al. 2010, Nemee 2014). Where direct effects primarily involve flame and heat that last seconds to hours, indirect effects cover most of the short-term responses that last from days to a year following fire.

In the short-term, fire indirectly affects many individual arthropods simply by removing vegetation. Common among all burns, fire removes detritus and vegetative biomass to expose more bare ground (Seastedt 1984a, Benson et al. 2007). This leads to additional indirect effects because of increases in net solar radiation, causing higher soil temperatures and decreased soil moisture (Lussenhop 1976, Nemee 2014). If lower soil moisture does not kill individuals through desiccation, increased temperatures can change arthropod phenology (Riechert and Reeder 1972). Warmer soils will usually result in improved larval survival and earlier hatching and emergence dates for some arthropods (Nagel 1973, Reed 1997), including bot flies (Diptera; Conway and Stapp 2015) and grasshoppers (Orthoptera; Meyer et al. 2002).

With less plant biomass, it also makes it easier for some arthropods, especially beetles (Coleoptera), to maneuver in recently burned grasslands (Fellows and Newton 1999, Larsen and Work 2003, Parmenter et al. 2011, Conway and Stapp 2015), and some will select for areas with less surface litter (Lussenhop 1976). For example, the prairie mole cricket (Orthoptera) will select for more recently burned sites because it offers better acoustics for the mating behavior of lekking (Howard and Hill 2007). However, species that use standing dead or litter as behavioral cues are less likely to be present after fire (Callaham et al. 2003, Vogel et al. 2010).

The interaction between arthropods and vegetation is one of the most commonly discussed aspect of arthropod responses to burning. Plants affect both herbivorous and predaceous arthropods, and consequently have large influences on arthropod communities following fire. Since burning directly removes vegetation, cover and food provided by litter and plants may not be immediately available (Parmenter et al. 2011). Therefore, even if some species survive fire, they may emigrate to non-burned patches for cover and food (Riechert and Reeder 1972).

Nonetheless, many arthropods are attracted to recently burned areas (Fellows and Newton 1999, Swengel 2001, Evans et al. 2013) because fire can increase nutritious forage (Larsen and Work 2003), plant production (Anderson et al. 1989), native plant cover (Debinski et al. 2011), and available host plants (Fay and Samenus 1993). This is particularly important for species of conservation concern like the monarch butterfly that respond positively to burning when milkweed (Asclepias spp.; Baum and Shaber 2012) and Liatris spp. (Swengel 1996) become available. Plant regrowth in burned areas often occurs quickly, and arthropod recolonization happens as soon as several weeks post fire (Huebschman and Bragg 2000, Hartley et al. 2007, Moranz et al. 2012).

Arthropod interactions with other arthropods is also indirectly altered by fire. Burning disrupts successional patterns present before fire and opens up the arthropod community to other species that were outcompeted or dominated by later successional species (Zelhart and Robertson 2009, Chistiansen and Lavigne 2010, Roughley et al. 2010). However, fire can also cause some species to become dominant and prevent other species from colonizing (McCravy and Baxa 2011), especially if the dominant species is more adapted to deal with fire, as is the case with some ants (Moranz et al. 2013). Nonetheless, fire is one way to destabilize established homogenous arthropod communities, but many arthropod species interactions are predominately controlled by arthropod-plant interactions following fire.

Most indirect effects of fire concern plants and other arthropods, although there are additional factors that impact arthropod responses to burning. Fire attracts arthropods, but it also influences other animals such as small mammals and large ungulates. In some cases, the interaction of fire and grazing by large ungulates increases arthropod abundance (Fay 2003, Engle et al. 2008), but large herbivores may consume important plant species (e.g., flowering forbs) that are then unavailable for arthropods (Moranz et al. 2014). A reduction in plant material is harmful for herbivorous arthropods, but the attraction of other animals to burned areas can be advantageous for parasitic arthropods that rely on healthy, available hosts (Conway and Stapp 2015). Increased forage availability creates opportunities for parasitic arthropods, like bot flies, to find more desirable hosts. Precipitation (Benson et al. 2007) and management (Branson and Sword 2010) will also influence arthropod responses to fire, but they are typically recognized more in the long term.

Long-term Responses to Fire

Direct Effects. Although single-fire events typically do not affect the arthropod community (Anderson et al. 1989) and direct fire effects are generally short-lived for some orders like Coleoptera (beetles; Nemee 2014) and Hymenoptera (sawflies, wasps, bees, and ants; Willand et al. 2011), fire can have lasting long-term (greater than one year after fire) direct effects on arthropods.

Many species require more than a year to recover to pre-burn abundances (Engle et al. 2008, Wallner et al. 2012), but most long-term effects are related to increased fire frequency. After several years, repeated fire and increased fire frequency changes the overall arthropod community so that orders that are able to survive active flames, such as Orthoptera (grasshoppers, crickets, and locusts) and Coleoptera (beetles), increase, while Homoptera (aphids, cicadas, and leaf hoppers), an order sensitive to fire, decrease with burning frequency (Siemann et al. 1997).

There are some orders and species that are unaffected by fire frequency (Seastedt 1984b, Cook and Holt 2006, Debinski et al. 2011), but the number of species responding negatively to fire frequency is typically more than those responding positively (Siemann et al. 1997).

Periodic fire disrupts arthropod communities and allows other species to be successful (Roughley et al. 2010), but annual burning and frequent fires only allow species specifically adapted to fire-intense landscapes to persist (Siemann et al. 1997, Collins 2000, Joern 2005, Jonas and Joern 2007). In the end, it can take several years for arthropods to recover, and those populations may eventually exceed those found before fire (Panzer 2002). However, as with short-term direct effects, long-term direct effects are understudied and overshadowed by indirect effects.

Indirect Effects. As stated previously, burning has large indirect effects on arthropods because fire alters vegetation which influences the arthropod community longer than direct flames (Evans 1988b, Engle et al. 2008, Doxon et al. 2011). Still, there is often a lag between burns and arthropod responses (Seastedt et al. 1986), and indirect effects can take more than a year to occur. Arthropods, especially pollinators, recolonize recently burned areas several years after fire when more forbs are present (Reed 1997, Fay 2003, Tooker and Hanks 2004, Doxon et al. 2011, Solga et al. 2014), but there can be issues when grazing livestock after fire, as they, too, will select for forbs (Moranz et al. 2014). Although there can be some problems with grazing after fire, long-term fire and grazing interactions increase heterogeneity and result in more biodiversity (Fuhlendorf et al. 2006), including arthropod diversity (Engle et al. 2008). By providing varying microhabitats and available resources, the long-term reproductive investment of arthropods increases, even though direct mortality is a possibility (Howard and Hill 2007, Engstrom 2010).

Without fire in the Great Plains, long-term grassland productivity decreases (Lussenhop 1976), exotic herbaceous species increase, and woody cover expands (Bertwell and Blocker 1975, Hartley et al. 2007). Longer fire return intervals will favor some grassland species that select for areas with higher litter cover and thick vegetation (Van Amburg et al. 1981, Moranz et al. 2012), but eventually these communities will switch from grassland arthropods to woodland arthropods (Hartley et al. 2007). For example, the American burying beetle (Coleoptera) can use habitats with varying degrees of litter cover, but it will avoid areas with a high level of juniper encroachment (Walker and Hoback 2007), similar to other grassland species that avoid woody cover (Thompson et al. 2014). As with short-term indirect effects, long-term indirect effects are also influential to the arthropod community, although not as well studied. However, as with overall responses to fire, each arthropod species' response to short- and long-term direct and indirect effects will differ based on species traits.

SPECIES TRAITS TO DETERMINE ARTHROPOD RESPONSES TO FIRE

Fire is important for both short- and long-term arthropod persistence (Hartley et al. 2007, Evans et al. 2013), but there are still many concerns about the use of fire and its effects on individual species (Swengel 2001). As we noted earlier with total arthropod and order responses to fire, species will respond differently even within the same taxonomic group (Hartley et al. 2007, Roughley et al. 2010), and it is therefore inappropriate to group species responses with their relatives. However, for the purposes of our review, we used functional groups, rather than individual species, to examine typical arthropod responses to fire, knowing that much more research is necessary for both functional groups and individual species.

From the literature, we were able to identify three overarching species traits—mobility, life stage, and feeding guild—that may influence species responses to fire.

Mobility

Mobility is often one of the most common traits used to determine species responses to fire because it regulates a species' ability to escape moving flames (Figure 3; Engstrom 2010). Generally, species with short, limited dispersal capabilities, like some butterflies (Lepidoptera) and true bugs (Hemiptera), are not expected to survive fire due to combustion or heat stress (Panzer 2002, Andrew and Leach 2006, Swengel and Swengel 2007, Wallner et al. 2012). Consequently, poor fliers with short dispersal are negatively associated with increased fire frequency, and strong fliers with longer dispersal are positively associated with fire frequency (Panzer 2002, Jonas and Joern 2007).

Moreover, species that are mobile at different times of the year also change responses to fire. Individuals that fly mid- to late-summer are often unaffected by fire because they are inactive or otherwise protected when most fires are conducted in the spring (McCravy and Baxa 2011). Nonetheless, flying is not the only way to escape fire, and high mobility, in any form, is important to survive fire (Seastedt et al. 1986, Swengel 1996). Carabid beetles, flightless ground beetles (Coleoptera), are able to move quickly on the ground in a short time to escape fire by going underground and often survive grassland fires (Cook and Holt 2006). Additionally, species with high mobility are able to recolonize burns and take advantage of improved resources. While mobility can solely affect species' responses to fire, it is frequently coupled with life stage to determine burning influences.

Life Stage

Life stage is an important factor for arthropod fire responses, as most life stages are associated with a certain amount of vulnerability (Figure 3; Swengel 2001). Eggs and larvae are considered the most vulnerable to fire because they lack mobility to avoid or escape fire (Anderson et al. 1989, Huebschman and Bragg 2000). This relationship is more apparent when eggs and larvae are at the surface or in the plant canopy (Nagel 1973, Anderson et al. 1989, Bomar 2001) because eggs below the surface experience less heat stress (Vermeire et al. 2004, Branson and Vermeire 2013).

For grasshoppers (Orthoptera), eggs laid deeper in the soil—a consequence of oviposition differences between species—are more likely to survive fire (Branson and Vermeire 2013), but survivability decreases as heat application increases and soil moisture decreases (Branson and Vermeire 2007, Branson and Vermeire 2013). Unlike eggs and larvae, adults with sufficient mobility are more likely to survive fire since they can escape direct mortality and recolonize burned areas.

Nonetheless, species that are inactive during fire, regardless of life stage, can be vulnerable to fire if they are not protected from heat. Conversely, inactivity may be beneficial if food resources are low immediately following fire, and individuals emerge after plant regrowth (Menke et al. 2015). Consequently, feeding guild is an additional mechanism that determines species' response to fire.

Feeding Guilds

Guilds corresponding to different feeding locations (belowground, soil surface, and aboveground) also affect arthropod responses to fire by controlling potential flame and heat exposure (Figure 3; Benson et al. 2007). Species that live or feed belowground escape combustion (Nagel 1973, Howard and Hill 2007, Moranz et al. 2013, Menke et al. 2015), but there is the possibility that

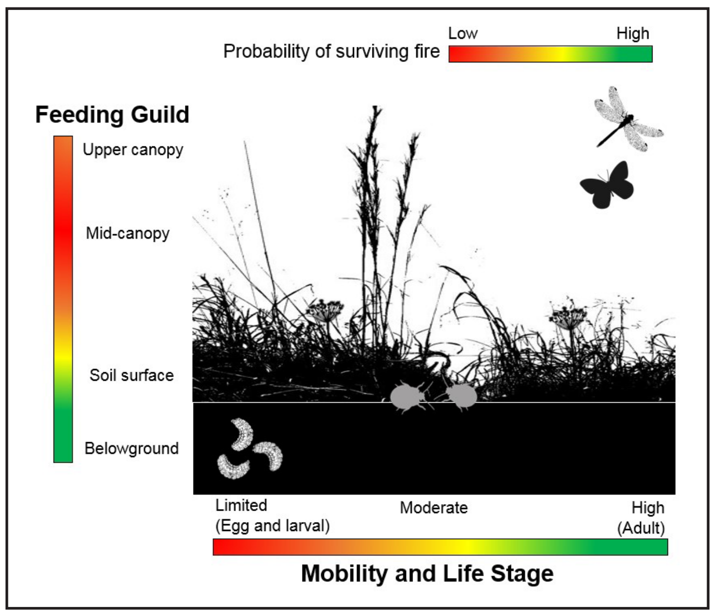

Figure 3. The probability of surviving fire at various feeding guilds in combination with different levels of mobility and life stage (in parentheses). Arthropods with higher mobility are able to escape direct effects of fire, while feeding guilds belowground are the most protected from fire. Some arthropods may escape flame fronts in the upper canopy or under rocks and insulating litter at the soil surface, and adult arthropods typically have more mobility to escape fire and recolonize recently burned areas.

species close to the surface—within 1 and 5 cm from the surface—may be at higher risk of mortality due to heat stress (Seastedt 1984b, Branson and Vermeire 2013). Individuals at the soil surface, similar to belowground individuals, can escape direct mortality under insulating materials like dense clumps of vegetation or rocks (Anderson et al. 1989), but there are risks associated with using vegetative cover for refuge because insulating properties of litter change depending on moisture and litter amounts (Riechert and Reeder 1972, Anderson et al. 1989, Huebschman and Bragg 2000, Panzer 2002). Some material will help to insulate from heat, but at some point, the litter material will ignite (Andrew and Leach 2006), although this may only be problematic in areas where litter is completely consumed during fire (Panzer 2002). Even though individuals at the soil surface may appear to be the most vulnerable to direct mortality, survivability is quite variable depending on life stage, mobility, and the ability to retreat underground.

Aboveground individuals that do not reside in the litter layer or the soil surface are potentially more at risk of direct mortality because there are fewer refuge areas (Benson et al. 2007). Spiders (Araneae) are particularly exposed because they spin webs in the plant canopy (Doxon et al. 2011), but endophytic arthropods that reside inside vegetation are also unlikely to survive fire (Rice 1932, Tooker and Hanks 2004, Nemee 2014). However, some wasps (Hymenoptera) that form galls above the height of flames may survive fire (Fay and Samenus 1993). Although feeding location determines direct effects of burning, additional feeding guild characteristics can affect arthropod responses to indirect effects.

Feeding guilds based on diet breadth also help predict indirect arthropod fire responses associated with vegetative changes. Several months after fire, surface detritivores will decrease because there is less organic matter to consume (Seastedt 1984b, Seastedt et al. 1986), but grass root feeders increase, as fire increases biomass allocation to roots (Seastedt et al. 1986, Seastedt and Reddy 1991). Reduced vegetative cover also increases the success of predators that use visual cues to capture prey (Riechert and Reeder 1972, Anderson et al. 1989, Parmenter et al. 2011, Willand 2011), but prey availability may be reduced after burns if prey are consumed in the fire or emigrate to find forage at a different location (Zelhart and Robertson 2009).

Therefore, generalists that consume a variety of species will do better compared to specialists that rely on specific host plants and prey (Swengel 2001, Cook and Holt 2006, Vogel et al. 2010, Wallner et al. 2012). Moreover, phytophagous species, especially those that consume grasses (Meyer et al. 2002), and generalists predators are favored by fire and often attracted to recently burned areas with adequate regrowth (Nagel 1973, Cook and Holt 2006, Evans et al. 2013).

Most grassland plants are adapted to fire, quickly recover with adequate precipitation, and are able to provide food and cover for arthropods (Nadeau et al. 2006, Menke et al. 2015). Grasses typically increase in cover more than forbs the first year after fire (Evans 1988b), so forb-feeding arthropods, including grasshoppers (Orthoptera), may be less abundant on recently burned patches compared to grass-feeding arthropods. However, forb feeders still require some disturbance, such as burning, to create disturbance and floral flushes (Evans 1984, Evans 1988a, Jonas and Joern 2007). Collectively, previous fire patterns hold true when examining certain species traits; fire will benefit some species while harming others. Grasslands in the Great Plains evolved with fire, so it is reasonable to assume that grassland arthropods are also evolved with fire (Panzer and Schwartz 2000, Larsen and Work 2003), despite some controversy (Swengel et al. 2011).

MANAGEMENT RECOMMENDATIONS

From our synthesis, there are emerging management recommendations that encompass the entire arthropod community, but we are unable to make management recommendations for individual species. Currently, there is insufficient research for all species to make pertinent recommendations, and species management recommendations would be contingent on site specific characteristics like current arthropod and plant communities, previous land use, and desired outcomes.

Additionally, direct and indirect effects can change the positive or negative impacts of fire on arthropods, as direct mortality can reduce vulnerable arthropods but enhance resource availability. Nonetheless, the current available literature indicates burning may be an appropriate conservation strategy when considering all arthropods collectively in the Great Plains (Anderson et al. 1989, Engle et al. 2008), and it cannot be entirely replaced with other management strategies (Andrew and Leach 2006). Here, we focus on recommendations for fire, one of the disturbances used to maintain grasslands, acknowledging that additional disturbances like grazing are also necessary to maintain grassland arthropod communities (Joern 2005).

Fire must be applied heterogeneously to the landscape to produce anticipated, positive outcomes for arthropods (Panzer and Schwartz 2000). Heterogeneous fire allows managers to optimize short- and long-term direct and indirect effects to promote the highest number of species (Larsen and Work 2003, Roughley et al. 2010, Moranz et al. 2014) because it provides a mosaic of non-burned (refuges) and burned areas. Refuge areas provide protection for certain life stages, feeding guilds, and species with lower mobility that are more vulnerable to short-term direct effects from flame and heat (Swengel and Swengel 2007, Moranz et al. 2012). After fire, refuge areas provide cover which can be important for regulating body temperatures, maintaining water balances (Joern 2004, Doxon et al. 2011), and providing food resources.

Conversely, fire resets successional patterns in burned grasslands and can promote native plant cover and diversity necessary for diverse arthropod communities (Engle et al. 2008), especially for species attracted to recently burned areas. In the long-term, rotating burn patches decreases the likelihood of refuge areas becoming homogenized or invaded by woody species while promoting a patchwork of necessary resources for the arthropod community. Additionally, applying heterogeneous fire temporally by alternating the burn season can reduce repeated impacts to certain life stages that are vulnerable, like eggs (Johnson et al. 2008).

Heterogeneously applying fire in patches creates a structural matrix composed of different plant species, which allows more arthropods to coexist (Joern 2005). Patches can be formed with man-made (mow or plow lines, roads) or natural (bare ground and low fuel loads) fire breaks to stop fire from burning entire management units (Robinson et al. 2013, Swengel and Swengel 2014). Reducing fuel loads is also important to decrease the likelihood of complete burns (Robinson et al. 2013) and can be done by increasing fire frequency to reduce litter accumulations (Andrew and Leach 2006). Patches that are not burned then become source areas that provide individuals for recolonization (Benson et al. 2007), and species typically recover two to four years following fire (Huebschman and Bragg 2000, Panzer 2002, Joern 2004, Engle et al. 2008, Wallner et al. 2012).

There are some species, particularly butterflies (Lepidoptera), that will take longer than two to four years to reach pre-burn abundance (Swengel and Swengel 2007, Vogel et al. 2010). Therefore, intermediate burn frequencies ranging between recovery periods is recommended (Johnson 1995). Prescribed fire is an excellent management tool for arthropods in the Great Plains, especially when the conservation of one species is not the main focus (Hartley et al. 2007), but our understanding is fairly rudimentary with many aspects that require more research to fully understand arthropod responses to burning.

KNOWLEDGE GAPS

More research needs to be conducted on arthropod responses to fire, particularly long-term studies. There are numerous studies that look at common species and orders, but we found several taxonomic groups that were not as well represented in our literature search, including Collembola (springtails; Van Amburg et al. 1981, Reed 1997), Chilopoda (centipedes) and Diplopoda (millipedes; Seastedt 1984a, Seastedt et al. 1986, Reed 1997, Parmenter et al. 2011), Acari (mites; Johnson 1995, Hartley et al. 2007, Polito et al. 2013), Trichoptera (caddisflies; Benson et al. 2007), and Blattodea (cockroaches; Parmenter et al. 2011), although research should increase for all taxonomic groups.

Additionally, another large area of research interest should be placed on the season of burn, since many studies focus on spring burning (Swengel 2001). This may lead to more knowledge on optimal fire timing and frequency that will benefit the most species, another large knowledge gap (Evans 1984, Doxon et al. 2011).

Generally, there is a need to understand more in-depth questions about species responses to fire. How do eggs survive fire (Andrew and Leach 2006)? What size refuge areas do different species require (Robinson et al. 2013)? How do plant-arthropod interactions change after fire (Swengel 2001)? Potentially even more important is replicating studies to see how results differ in time and space. There are cases, even within this synthesis, where different studies observed dissimilar results (Panzer 2002). By expanding research beyond species abundance or diversity changes after fire, we can gain more insight into both theoretical and applied arthropod responses to fire (Enstrom 2010).

CONCLUSIONS

Many groups of grassland arthropods, including true spiders (Araneae), grasshoppers (Orthoptera), and beetles (Coleoptera), are adapted to periodic fire disturbances (Riechert and Reeder 1972, Nadeau et al. 2006, Hartley et al. 2007, Johnson et al. 2008). Although this may seem counterintuitive because fire causes direct mortality, fire also maintains necessary host plants and microclimate conditions necessary for different arthropods found in the Great Plains (Siemann et al. 1997). Even researchers that found some negative effects on arthropods in their studies still supported the use of fire (Tooker and Hanks 2004, Moranz et al. 2014), as positive indirect effects often outweigh negative direct effects (Hartley et al. 2007).

Based on the current literature, heterogeneously applied fire is the best strategy to optimize direct and indirect effects of fire on arthropods. However, discretion must be used when considering specific species management, such as threatened and endangered species, that may not be able to withstand negative direct effects (Andrew and Leach 2006).

Individual arthropod species will respond differently—positively, negatively, or neutrally—to fire based on species traits which can help predict their vulnerability to fire (Panzer 2002). Yet, it is important to note that there are other factors that may be more significant than fire to determine arthropod responses, such as grazing (Moranz et al. 2014), mowing (Callaham et al. 2003), and land-use legacies (Nadeau 2006, Debinski et al. 2011, Moranz et al. 2012).

Although this review focused on fire as a disturbance, other disturbances are also commonly used for arthropod conservation, such as haying for butterfly habitat specialists (Schlicht et al. 2009, Smith and Cherry 2014, Swengel and Swengel 2015). Haying and grazing disturbances can mimic some aspects of fire, such as creating forb flushes (Pickens and Roots 2009), but these disturbances cannot fully replace all characteristics associated with fire, especially chemical reactions (Chiwocha et al. 2009, Light et al. 2009). In some situations, other disturbances may logistically be more practical for arthropod conservation, but a thorough discussion is beyond the scope of our synthesis and has initially been presented in other reviews (e.g. Swengel 2001). While different disturbances are applicable, they, like fire, still need to be applied heterogeneously and at the appropriate scale across the landscape (Swengel 1996).

Future research exploring past results and delving further into fire responses will be vital to parse out explicit details on overall and specific arthropod responses to fire, since we have only just begun to understand arthropod responses to fire in the Great Plains.

ACKNOWLEDGEMENTS

We would like to extend our thanks to John Delaney for previous work on this synthesis, two reviewers for their helpful comments, and to the Great Plains Fire Exchange for funding.

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