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Is fire exclusion in mountain big sagebrush communities prudent? Soil nutrient, plant diversity and arthropod response to burning

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Abstract. Fire has largely been excluded from many mountain big sagebrush communities. Managers are reluctant to reintroduce fire, especially in communities without significant conifer encroachment, because of the decline in sagebrush-associated wildlife. Given this management direction, a better understanding of fire exclusion and burning effects is needed. We compared burned to unburned plots at six sites in Oregon. Soil nutrient availability generally increased with burning. Plant diversity increased with burning in the first post-burn year, but decreased by the third post-burn year. Burning altered the arthropod community, which included doubling the density of arthropods in the first post-burn year. Some arthropod Orders increased and others decreased with burning. For example, Araneae were 1.7- and 1.8-fold less and Hemiptera were 6.6- and 2.1-fold greater in the burn compared with the control in 2008 and 2009. Our results provide evidence that burning can create spatial and temporal heterogeneity in sagebrush communities and thus, it is an important component of the ecosystem. We suggest that management plans for many mountain big sagebrush communities may need to include infrequent burning. At the very least managers should be aware that fire exclusion has some potentially negative effects other than the encroachment of conifers in these communities.

Additional keywords: *Artemisia tridentata*, biodiversity, disturbance, fire management, spatial heterogeneity.

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Introduction

Disturbances are an important component of ecosystems and are key drivers of spatial and temporal heterogeneity (Turner 2010). Fire, in many arid and semiarid wildland ecosystems, is a common disturbance that alters plant community composition and dominance. For example, infrequent fires in sagebrush communities historically shifted dominance from woody shrubs to perennial herbaceous vegetation (Wright and Bailey 1982; Miller and Rose 1999). In mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) plant communities, infrequent fire also removed encroaching conifers that, in time, exclude sagebrush from the community, decrease herbaceous vegetation and increase erosion and runoff risk (Miller and Rose 1999; Miller *et al.* 2005; Pierson *et al.* 2007). However, in mountain big sagebrush plant communities without significant encroachment of conifers, fire is generally viewed as a negative disturbance because present-day managers are almost exclusively focussed on greater sage-grouse (*Centrocercus urophasianus*) habitat. Wide-spread loss of sage-grouse habitat has resulted in a mentality that fire should be excluded from sagebrush-dominated communities, largely because sagebrush is temporarily removed from the community with fire. The following directive from the 'Greater Sage-grouse Conservation Objectives: Final Report' provides a representative example of

this mentality: 'Immediately suppress fire in all sagebrush habitats' (USFWS 2013).

Despite the concerns for sage-grouse habitat, other organisms may benefit from fire in sagebrush communities. For example, burning big sagebrush plant communities can increase soil resources (Davies *et al.* 2007; Rau *et al.* 2007), which is probably one of the main reasons burning often results in a 2- to 3-fold increase in herbaceous production (Harniss and Murray 1973; Wambolt and Payne 1986; Davies *et al.* 2012). The removal of the dominant plant species may increase plant diversity (McCain *et al.* 2010); however, burning Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) plant communities did not increase plant diversity (Davies *et al.* 2007). Information on the influence of burning on plant diversity in mountain big sagebrush communities is lacking. However, there are reasons to expect that burning mountain big sagebrush communities may increase plant diversity. For example, burning big sagebrush plant communities creates two distinct microsites (under shrub canopy *v.* interspace) that may influence plant community diversity (Davies *et al.* 2009) because recruitment from seed varies considerably between these post-fire microsites (Boyd and Davies 2010). Plant diversity influences community stability and other trophic levels (Tilman *et al.* 1997; Knops *et al.* 1999; Tilman 1999;

Haddad *et al.* 2001); thus, it is important to understand how fire influences plant diversity in mountain big sagebrush communities.

Increases in herbaceous vegetation and the change in plant community structure with the loss of sagebrush with burning may influence higher trophic levels, such as arthropods. Changes in plant community structure can significantly influence arthropod communities (Engle *et al.* 2008; Pearson 2009). Many arthropod taxa may also decline with burning depending on the exposure to lethal temperatures, the post-burn environment and the mobility of the arthropod group; however, post-burn flora may be appealing to recolonising arthropods (Swengel 2001). In contrast, Fischer *et al.* (1996) found that burning had little effect on arthropods, other than a decrease in ants, when burning Wyoming big sagebrush plant communities. However, Rhodes *et al.* (2010) found that most arthropod Orders differed between burned and unburned Wyoming big sagebrush communities, but they questioned, other than a decrease in ants with burning, if the differences were biologically significant. Wyoming big sagebrush plant communities are less productive and occur on drier sites than mountain big sagebrush plant communities (Davies and Bates 2010). Therefore, it may not be appropriate to extrapolate results from Wyoming big sagebrush plant communities to mountain big sagebrush communities as arthropod response to fire may vary considerably between these two different plant community types. Pyle and Crawford (1996) found no difference in arthropod abundance between burned and unburned mountain big sagebrush plant communities, but arthropods were only trapped for a 10-day period each year. A better understanding of the response of arthropods to fire in mountain big sagebrush plant communities is needed, because arthropods are an important component of ecosystems and influence other trophic levels (Loosey and Vaughan 2006).

Considering the current efforts to limit fire in mountain big sagebrush plant communities, it is critical to develop a better understanding of the influence of fire in these communities. This information is needed to better assess the potential benefits and risks of fire and fire exclusion. The purpose of this research project was to determine the influence of fire on soil nutrient availability, plant diversity and arthropods in mountain big sagebrush plant communities. We speculated that burning mountain big sagebrush plant communities will increase soil nutrients and this would increase plant diversity and richness. We also expected that burning mountain big sagebrush plant communities would alter the arthropod community, probably because of direct mortality as well as indirectly by altering the plant community structure by removing sagebrush and causing changes in herbaceous vegetation.

Methods

Study area

We evaluated the responses of soil nutrients, plant diversity and arthropods to burning in mountain big sagebrush plant communities on the Hart Mountain National Antelope Refuge (42°21'16"N, 119°22'54"W). The study sites were on fairly flat to 7° slopes with aspects ranging from north to south between 2013- to 2166-m above sea level. Climate is typical of the Intermountain West with cool, wet winters and hot, dry

summers. Most precipitation occurs in the winter and spring. Average annual precipitation was between 400 to 510 mm at the study sites (NRCS 1998). Precipitation was 80% of the long-term average in 2007 when burning occurred (Eastern Oregon Agricultural Research Center, unpubl. data, 2010). In 2008, 2009 and 2010, annual precipitation was 66, 87 and 101% of the long-term average. Prior to prescribed burning, plant communities were dominated by mountain big sagebrush with few other shrubs present. The understory consisted of perennial grasses and perennial forbs. The study sites would be considered intact mountain big sagebrush steppe (Davies and Bates 2010). Mountain big sagebrush, perennial grass (excluding Sandberg bluegrass, *Poa secunda* J. Presl) and perennial forb cover averaged 30, 20 and 12% before treatment. Perennial grass density averaged 23 individuals m⁻² before treatment. Common perennial grasses included Columbia needlegrass (*Achnatherum nelsonii* (Scribn.) Barkworth), Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), mountain brome (*Bromus marginatus* Nees ex Steud.) and bluegrasses (*Poa* L.). Common perennial forbs included biscuitroots (*Lomatium* Raf.), milkvetches (*Astragalus* L.), hawksbeard (*Crepis* L.), yarrow (*Achillea millefolium* L.), fleabanes (*Erigeron* L.), paintbrushes (*Castilleja* Mutis ex L. f.), ragwort (*Senecio integerrimus* Nutt.) and lupines (*Lupinus* L.). Domestic livestock have been excluded from the Hart Mountain National Antelope Refuge since the mid-1990s, although a few cattle and wild horses infrequently trespass on the Refuge. We saw no evidence (sightings, faeces or tracks) that would indicate that cattle or horses utilised our study sites during the study. Wildlife were not excluded from the study sites, but a general lack of observations of wildlife (other than sage-grouse) and low ungulate numbers in the area suggest that utilisation was low.

Experimental design

A randomised complete block design was used to determine the response of soil nutrients, plant diversity and arthropods to prescribed burning in mountain big sagebrush plant communities. Six blocks (sites) with varying topography, elevation, soil and vegetation characteristics were selected for this experiment. Plots within a block had similar vegetation and site characteristics. Treatments were randomly assigned to two 60 × 90-m plots within each block. Treatments were a fall prescribed burn and an untreated control. Burned treatments were applied between mid-October and early November of 2007 as strip-head fires ignited with drip-torches. Fine fuel loads varied between 327 and 977 kg ha⁻¹ and sagebrush cover averaged 30%. Air temperatures were between 6 and 11°C with relative humidity ranging from 33 to 43%, and wind speed varied from 2 to 10 km h⁻¹ during the prescribed burns.

Measurements

Soil nutrient concentrations of nitrate, ammonium, calcium, magnesium, potassium, phosphorus, iron, manganese, zinc, boron and sulfur were estimated using four cation and anion ion exchange probes (PRS-probes Western Ag Innovations,

Saskatoon, Saskatchewan, Canada) randomly placed in each treatment plot in each block. PRS-probes are buried in the soil to estimate the availability of soil nutrients to plants (Jowkin and Schoenau 1998). PRS-probes attract and adsorb ions using electrostatic attraction on an ion-exchange membrane. The PRS-probes were buried vertically in the upper 20 cm of the soil profile to estimate nutrient concentrations from 15 May until 15 July in 2008, 2009 and 2010. PRS-probes were returned to Western Ag Innovations where probes were extracted with 0.5 N HCl and analysed colourimetrically with an autoanalyser to determine nutrient concentrations.

Plant species diversity and richness were determined using plant density data collected in July of 2008, 2009 and 2010. Plant density by species was measured using sixty 0.2-m² quadrats. The 0.2-m² quadrats were placed at 3-m intervals on four 50-m transects in each plot (15 quadrat per transect). The four 50-m transects were placed parallel to each other at 20-m intervals. Plant density was determined by counting every plant rooted inside the 0.2-m² quadrats. Rhizomatous species were considered individual plants if separated by greater than 15 cm. Plant diversity was calculated as the Shannon Diversity Index (Krebs 1998). Richness was determined by counting the number of species present in each plot.

Pitfall traps were used to evaluate the response of arthropods to burning. Pitfall traps were 114-mm diameter by 76 mm-deep plastic containers that were 1/2 filled with a 1 : 1 mixture of propylene glycol (low toxicity antifreeze) and water. A few drops of denatonium benzoate were added to the 1 : 1 mixture to deter animals from drinking it. The top of the pitfall traps were flush with the soil surface. Plastic plates were placed over the pitfall traps to reduce evaporation and to prevent soil and rainfall from filling traps. Three traps were placed near the centre of each treatment plot. Traps were active from May through August and were sampled monthly in 2008 and 2009. The 1 : 1 mixture was replaced at each sampling date. Captured arthropods were identified to Order and density was determined by counting all captured arthropods. Arthropod Order diversity was calculated as the Shannon Diversity Index (Krebs 1998) based on density data. Order richness was determined by counting the arthropod Orders present in each plot. The density of the six most common arthropod Orders was compared between treatments.

Statistical analyses

We used repeated-measures analysis of variance (ANOVA) using the mixed models procedure (Proc Mix) in SAS ver. 9.1 (SAS Institute Inc., Cary, NC) to determine the influence of burning on response variables. Fixed variables were time since treatment (year) and treatment and their interactions. Blocks and block by treatment interactions were treated as random variables. Akaike's Information Criterion (Littell et al. 1996) was used to select covariance structures used in the repeated-measures ANOVAs. Treatment effects were also analysed in each year of the study using ANOVAs, because the response of sagebrush communities often varies significantly by time since disturbance (Harniss and Murray 1973; Davies et al. 2007). Data were evaluated for normality using the univariate procedure in SAS ver. 9.1 (Littell et al. 1996). Data that violated assumptions of normality were log-transformed. All graphic

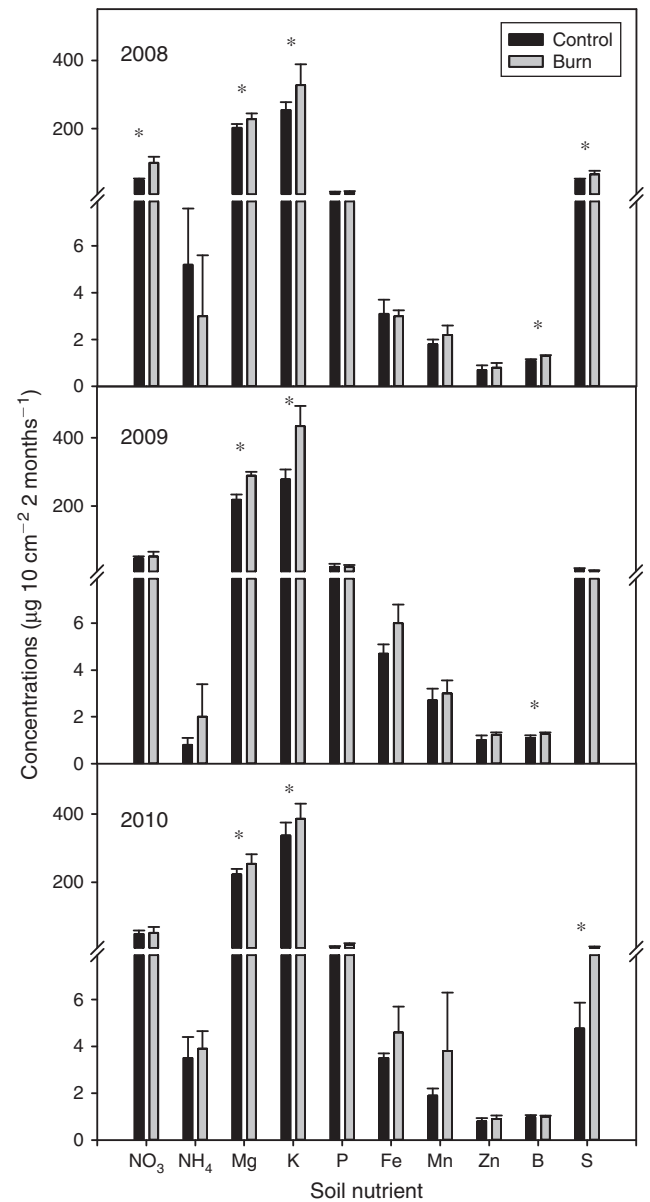


Fig. 1. Soil nutrient concentrations (mean + s.e.) in burned and unburned (control) mountain big sagebrush plant communities measured from 15 May to 15 July in 2008, 2009 and 2010. Asterisks indicate significant difference ($P \leq 0.05$) between treatments in that year.

presentations display original data (i.e. non-transformed). Differences between treatment means were considered significant at $P \leq 0.05$ and means were reported with standard errors.

Results

Soil nutrients

Nitrate concentrations varied by the interaction between treatment and year (Fig. 1; $P = 0.02$). In 2008, nitrate concentrations were 2-fold greater in the burn compared with the control treatment ($P = 0.04$). In 2009 and 2010, nitrate concentrations did not differ between the burn and control treatment ($P = 0.76$ and 0.82). Ammonium concentrations did not differ between

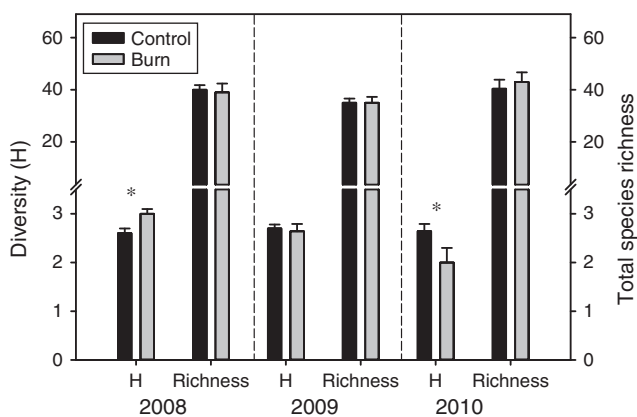


Fig. 2. Plant diversity (H) and species richness (mean + s.e.) in burned and unburned (control) mountain big sagebrush plant communities in 2008, 2009 and 2010. Plant diversity and species richness were determined from density measurements. Diversity was calculated as Shannon Diversity Index (Krebs 1998). Richness was determined by counting the number of species in each plot. Asterisks indicate significant difference ($P \leq 0.05$) between treatments in that year.

treatments ($P = 0.59$). Calcium and magnesium concentrations were on average 1.2-fold greater in the burn than control treatment ($P < 0.01$ and 0.01). Calcium concentrations respectively averaged $1510 \pm 37 \mu\text{g}$ per 10 cm^2 per 2 months and $1264 \pm 37 \mu\text{g}$ per 10 cm^2 per 2 months in the burn and control. Potassium concentrations were 1.3-fold greater in the burn than the control when averaged across all years ($P = 0.01$). Phosphorus concentrations did not differ between treatments ($P = 0.60$). Iron, manganese and zinc concentrations did not differ between the burn and control treatment ($P = 0.23$, 0.42 and 0.41). Boron concentrations were 1.1-fold greater in the burn compared with the control ($P = 0.02$). Sulfur concentrations were 1.3-fold greater in the burn than the control treatment ($P = 0.04$).

Plants and arthropods

Plant diversity (H) varied by the interaction between treatment and year (Fig. 2; $P < 0.01$). In 2008, plant diversity was 1.1-fold greater in the burn than control treatment ($P = 0.03$). In 2009, no difference in plant diversity was detected between the treatments ($P = 0.61$) and in 2010 plant diversity was 1.3-fold greater in the control compared with the burn treatment ($P = 0.03$). Plant species richness did not differ between the burn and control treatments ($P = 0.55$).

Arthropod diversity (at the order level) was greater in the control (1.38 ± 0.06) than the burn (1.16 ± 0.08) in 2008 ($P = 0.05$). In contrast, arthropod order richness was greater in the burn (10.4 ± 0.4) than the control (9.6 ± 0.3) treatment ($P = 0.01$). In 2009, arthropod diversity and richness were not different between the control and burn treatments ($P = 0.95$ and 0.26). Total density of arthropods was greater in the burn (219 ± 21 individual month^{-1}) than control (164 ± 18 individual month^{-1}) in 2008 ($P = 0.05$). In 2009, we did not find evidence that the density of arthropods differed between the burn (193 ± 23 individual month^{-1}) and control (179 ± 18 individual month^{-1}) treatments ($P = 0.66$).

Hymenoptera (ants) density was 1.9-fold greater in burn compared with the control treatment in 2008 (Fig. 3a; $P = 0.02$). In 2009, Hymenoptera density did not vary between treatments ($P = 0.86$). In 2008, Orthoptera (crickets and grasshoppers) density was 1.5-fold greater in the burn than the control treatment (Fig. 3b; $P = 0.05$). In 2009, Orthoptera density did not differ between treatments ($P = 0.74$). Coleoptera (beetles) density did not vary by treatment in 2008 or 2009 (Fig. 3c; $P = 0.28$ and 0.18). Araneae (spiders) density was 1.7- and 1.8-fold greater in the control compared with the burn treatment in 2008 and 2009 (Fig. 3d; $P < 0.01$ and 0.02). In 2008 and 2009, *Zygentoma* (silverfish) density was more than 2-fold greater in the control compared with the burn treatment (Fig. 3e; $P = 0.05$ and < 0.01). Hemiptera (true bugs) density was 6.6- and 2.1-fold greater in the burn compared with the control treatment in 2008 and 2009 (Fig. 3f; $P < 0.01$).

Discussion

Our first hypothesis that burning would increase soil nutrient concentrations was supported by our data. Approximately half of the measured soil nutrients were greater in the burn than the untreated control. Similarly, Davies *et al.* (2007) measured an increase in soil nitrate with burning Wyoming big sagebrush plant communities. However, dissimilar to our results, Davies *et al.* (2007) reported that nitrate was still higher in the burn 2 years after burning and that ammonium was greater in the burn than the untreated control. Rapid increases in perennial grass production in the burn (Davies *et al.* 2012) may have reduced excess nitrate after the first year in our study plots. Rau *et al.* (2008) also measured an increase in nitrate and ammonium when burning a conifer encroached mountain big sagebrush community. Similar to our results, Rau *et al.* (2008) also measured an increase in calcium in response to burning and speculated that burning increased manganese. Rau *et al.* (2008) also reported that zinc appeared to increase with burning because before treatment it was less in the burn compared with the control plots, but after burning it was not different between the burn and control plots. In contrast, we did not find any evidence that zinc differed between burned and unburned plots in our study. General patterns of soil nutrient responses to burning reported in Rau *et al.* (2008) were similar to our results. The few differences between Rau *et al.* (2008) and our study are not surprising considering that their study area was encroached by conifers (ours was not) and that burn conditions probably varied between the studies.

Our second hypothesis that plant diversity would increase with burning was partially supported in the first year post-burning, but subsequent years did not support it. The more than 2-fold increase in nitrate and other soil nutrients after fire was associated with increased diversity in the first post-burn year. Increases in soil resources can increase plant diversity by decreasing competition effects (Newman 1973). When dominant species are removed, diversity often increases because more resources are available to other species (Kunte 2008; McCain *et al.* 2010). In the burn, plant diversity (H) decreased from 3.02 in 2008 to 2.01 in 2010, but remained approximately the same in the untreated control (Fig. 2). As perennial grasses doubled their production (Davies *et al.* 2012), there were

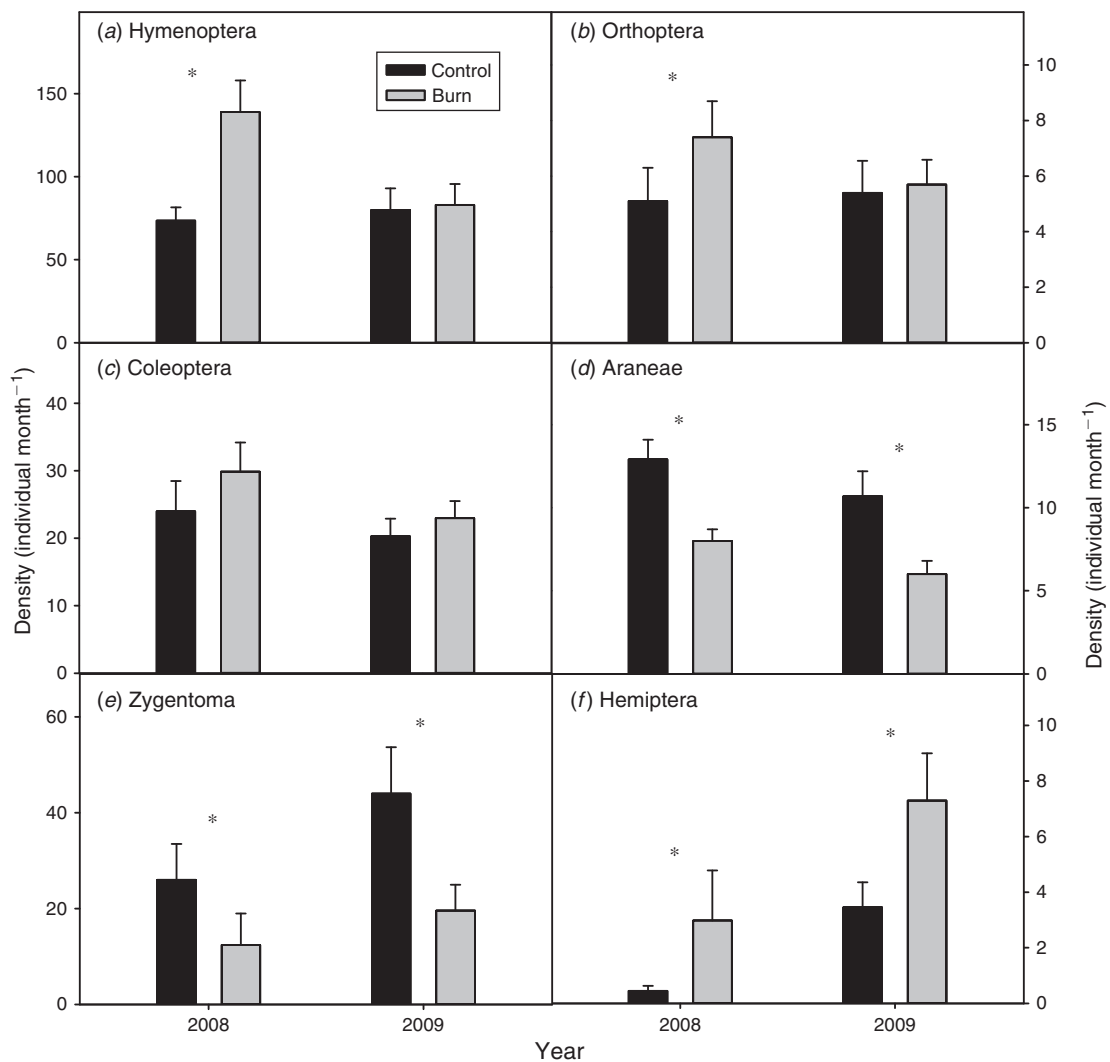


Fig. 3. Densities of arthropod Orders captured in pitfall traps in burned and unburned (control) mountain big sagebrush plant communities in 2008 and 2009. (a) Hymenoptera (ants); (b) Orthoptera (crickets and grasshoppers); (c) Coleoptera (beetles); (d) Araneae (spiders); (e) Zygentoma (silverfish) and (f) Hemiptera (true bugs). Asterisks indicate significant difference ($P \leq 0.05$) between treatments in that year.

probably less resources available and thus diversity decreased. Similarly, McCain *et al.* (2010) found that the dominant perennial grass limited resource availability to other species and its removal increased diversity. Increases in resources (fertilisation) have been shown to increase vegetation production leading to a decrease in diversity (DiTommaso and Aarssen 1989). Nitrogen is often the most limiting soil resource after water in semiarid and arid rangelands (Ettershank *et al.* 1978), thus increased soil nitrate likely was one of the major factors contributing to the measured increase in herbaceous productivity. Therefore, burning probably initially increased plant diversity by increasing resources, but as perennial grass production increased (Davies *et al.* 2012) in response to increased resources, diversity decreased because of added competition and shading (DiTommaso and Aarssen 1989; Hautier *et al.* 2009). The lack of differences in nitrate between the burn and control treatment by the second year post-burn further suggests

that competition for resources may have increased after the first year post-burn.

Arthropod response to burning supported our third hypothesis that burning would influence the arthropod community. In 2008, arthropod diversity was less in the burn than the control, but that was probably largely due to the large increase in ants decreasing evenness as richness was higher in the burn than the control. In contrast to Fischer *et al.* (1996) and Pyle and Crawford (1996), we found many arthropod groups varied between the burn and unburned control treatments. The mountain big sagebrush plant communities treated in our study were probably much more productive than the burned Wyoming big sagebrush communities sampled by Fischer *et al.* (1996) and thereby, probably explains at least some of the differences in measured responses. Our sampling period was longer than Pyle and Crawford (1996) used in their study and may explain why they found no evidence of an arthropod response to burning.

In our study, density of some arthropod Orders were greater in the burn, whereas other Orders were lower in the burn. Some differences were only evident the first year after burning suggesting that some effects are ephemeral. Cumulatively, our results demonstrate that the burning in mountain big sagebrush communities can create temporal and spatial heterogeneity in arthropod communities. Similarly, [Rutigliano *et al.* \(2013\)](#) reported that a mosaic of burned and unburned patches could promote biodiversity in Mediterranean maquis soil.

Burning probably altered arthropod communities by several different mechanisms. Fire-induced mortality during the burns was probably one of the main factors decreasing some arthropod Orders. Fire-induced mortality of arthropods has been repeatedly reported in the literature (e.g. [Daubenmire 1968](#); [Fay and Samenus 1993](#)). Changes in habitat with the loss of sagebrush with burning may also have negatively affected some arthropods. Changes in habitat from fire can cause arthropod declines due to starvation and exposure ([Rice 1932](#); [Warren *et al.* 1987](#)). Increases in some arthropod Orders may have been caused by changes in the plant community with burning. Post-burn flora may be quite appealing to some arthropods ([Swengel 2001](#)). Increases in nitrogen in sagebrush plant communities have increased the nitrogen concentration in leaf tissues of perennial grasses ([Witwicki *et al.* 2013](#)). Therefore, the increases in soil resources with burning in our study plots could have increased the nutritional value of herbaceous vegetation and this may have attracted some arthropods. Alterations to predator–prey relationships with burning may have also influenced arthropod responses. Burning can alter wildlife predator–prey relationships ([Fisher and Wilkinson 2005](#); [Milakovic *et al.* 2012](#)) and, logically, it may influence interactions at other trophic levels. These multiple factors associated with burning are probably also interacting amongst themselves to influence the arthropod community.

More than double the number of ants in the burn in the first post-treatment year was not expected as [Rhodes *et al.* \(2010\)](#) and [Fischer *et al.* \(1996\)](#) reported a decrease in ants after burning Wyoming big sagebrush communities. Similar to our results, [Nelle *et al.* \(2000\)](#), in a post-hoc study, found that 1-year-old burns contained more ants than unburned areas. Dissimilar to our results, [Nelle *et al.* \(2000\)](#) found a short-term increase in Coleoptera with burning mountain big sagebrush plant communities. Similar to [Rhodes *et al.* \(2010\)](#), we measured a 1.5-fold increase in Orthoptera in the first year after fire. However, by the second post-burn year the burn and control treatments did not differ. Variation in results among these studies and our study suggests that further analyses of fire effects on arthropods are needed to determine mechanisms underlying responses. In addition, it would be valuable to sample the complete array of arthropods not just the ones that can be sampled with pitfall traps to get a more complete understanding of the response of the arthropod community to burning.

Increases in ants and Orthoptera may be beneficial to sage-grouse, a species of conservation concern, and other arthropod-consuming wildlife (e.g. sagebrush lizard, northern horned lizard, sage thrasher). Arthropods are an important component of young sage-grouse diets and can comprise 75–100% of their diet the first several weeks post-hatching ([Patterson 1952](#); [Johnson and Boyce 1990](#); [Gregg and Crawford 2009](#)).

Arthropods are so important that young sage-grouse suffer high mortality if deprived of arthropods ([Johnson and Boyce 1990](#)). Though, to be beneficial to sage-grouse, burns must be fairly small in size as sage-grouse will not venture far from the protective cover of sagebrush ([Boyd *et al.* 2011](#)). Furthermore, the increase in some arthropods may be short-lived as the increases in ants and Orthoptera lasted only 1 year.

Our results suggest that fire is an important ecosystem process in mountain big sagebrush communities. The differences in arthropod communities between burned and unburned plots in our study suggest that even without conifer encroachment, excluding fire from mountain big sagebrush plant communities alters natural spatio-temporal variability of organisms that depend on the variable vegetative states that infrequent fires create. Thus, more fire-adapted species are likely being negatively affected by fire exclusion policies. In agreement with our results, [Ellsworth and Kauffman \(2013\)](#) reported that fire-adapted mountain big sagebrush communities can benefit from re-introduction of the natural fire regime. Thus, fire in mountain big sagebrush plant communities is a driver of spatial and temporal heterogeneity and an important component of the ecosystem.

Conclusions

The decline of sage-grouse tacitly has resulted in a mentality that we must strive to maintain sagebrush dominance on lands currently occupied by sagebrush, and that maintaining this dominance is associated with preventing disturbances such as fire that result in removal of most sagebrush taxa ([USFWS 2010, 2013](#)). The short-term benefit of such a policy is clear (i.e. maintenance of sage-grouse habitat), but the longer-term implications for mountain big sagebrush communities that include species favoured by fire have not received adequate consideration. Our results suggest that fire is important to creating heterogeneity in the arthropod community, which probably influences other trophic levels. The doubling of arthropod density the first year after fire is essentially creating a ‘hotspot’ of arthropods that may be beneficial to arthropod-consuming wildlife. Undoubtedly we have to balance the needs of sage-grouse and other species of conservation concern, but should also be cognitive that excluding fire from mountain big sagebrush communities may be negatively affecting other species. Similar to our results, [Holmes and Robinson \(2013\)](#) found that though six species of birds showed a negative response to fire in mountain big sagebrush communities, two species showed a positive response. Considering our research and [Holmes and Robinson \(2013\)](#), burned and unburned mountain big sagebrush communities provide a heterogeneity of habitats that meet the needs of multiple organisms. Fire in mountain big sagebrush plant communities also has the benefit of removing encroaching conifers ([Miller *et al.* 2005](#)). We are not advocating for immediately burning large swaths of mountain big sagebrush habitat, as the consequences would be dire for sage-grouse and other sagebrush-associated wildlife, but we are suggesting that long-term maintenance of diversity in mountain big sagebrush habitat may need to include applying fire at spatial and temporal scales that complement the diversity of habitat needs of sage-grouse and other species.

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References

- Boyd CS, Davies KW (2010) Shrub microsite influences post-fire perennial grass establishment. *Rangeland Ecology and Management* **63**, 248–252. doi:10.2111/REM-D-09-00025.1
- Boyd C, Petersen S, Gillert W, Rodgers R, Fuhlendorf S, Larsen R, Wolfe D, Jensen KC, Gonzales P, Nenneman M, Danvir R, Dahlgren D, Messmer T (2011) Looking toward a brighter future for lekking grouse. *Rangelands* **33**, 2–11. doi:10.2111/1551-501X-33.6.2
- Daubenmire R (1968) Ecology of fire in grasslands. *Advances in Ecological Research* **5**, 209–266. doi:10.1016/S0065-2504(08)60226-3
- Davies KW, Bates JD (2010) Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the northern Great Basin. *Rangeland Ecology and Management* **63**, 461–466. doi:10.2111/REM-D-09-00055.1
- Davies KW, Bates JD, Miller RF (2007) Short-term effects of burning Wyoming big sagebrush steppe in southeastern Oregon. *Rangeland Ecology and Management* **60**, 515–522. doi:10.2111/1551-5028(2007)60[515:SEOBWB]2.0.CO;2
- Davies KW, Bates JD, James JJ (2009) Microsite and herbaceous vegetation heterogeneity after burning *Artemisia tridentata* steppe. *Oecologia* **159**, 597–606. doi:10.1007/S00442-008-1231-7
- Davies KW, Bates JD, Nafus AM (2012) Comparing burned and mowed treatments in mountain big sagebrush steppe. *Environmental Management* **50**, 451–461. doi:10.1007/S00267-012-9898-2
- DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetation: a review. *Vegetatio* **84**, 9–29. doi:10.1007/BF00054662
- Ellsworth LM, Kauffman JB (2013) Seedbank responses to spring and fall prescribed fire in mountain big sagebrush ecosystems of differing ecological condition at Lava Beds National Monument, California. *Journal of Arid Environments* **96**, 1–8. doi:10.1016/J.JARIDENV.2013.04.001
- Engle DM, Fuhlendorf SD, Roper A, Leslie DM Jr (2008) Invertebrate community response to a shifting mosaic of habitat. *Rangeland Ecology and Management* **61**, 55–62. doi:10.2111/06-149R2.1
- Ettershank G, Ettershank J, Bryant M, Whitford W (1978) Effects of nitrogen fertilization on primary production in a Chihuahuan desert ecosystem. *Arid Environments* **1**, 135–139.
- Fay PA, Samenus RJ Jr (1993) Gall wasp (Hymenoptera: Cynipidae) mortality in a spring tallgrass prairie fire. *Environmental Entomology* **22**, 1333–1337.
- Fischer RA, Reese KP, Connelly JW (1996) An investigation on fire effects within xeric sage grouse brood habitat. *Journal of Range Management* **49**, 194–198. doi:10.2307/4002877
- Fisher JT, Wilkinson L (2005) The response of mammals to forest fires and timber harvest in the North American boreal forest. *Mammal Review* **35**, 51–81. doi:10.1111/J.1365-2907.2005.00053.X
- Gregg MA, Crawford JA (2009) Survival of greater sage-grouse chicks and broods in the northern Great Basin. *Journal of Wildlife Management* **73**, 904–913. doi:10.2193/2007-410
- Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist* **158**, 17–35. doi:10.1086/320866
- Harniss RO, Murray RB (1973) 30 years of vegetal change following burning of sagebrush-grass range. *Journal of Range Management* **26**, 322–325. doi:10.2307/3896846
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* **324**, 636–638. doi:10.1126/SCIENCE.1169640
- Holmes AL, Robinson WD (2013) Fire mediated patterns of population densities in mountain big sagebrush bird communities. *Journal of Wildlife Management* **77**, 737–748. doi:10.1002/JWWMG.540
- Johnson GD, Boyce MA (1990) Feeding trails with insects in the diet of sage grouse chicks. *Journal of Wildlife Management* **54**, 89–91. doi:10.2307/3808906
- Jowkin V, Schoenau JJ (1998) Impact of tillage and landscape position on nitrogen availability and yield of spring wheat in the Brown soil zone in southwestern Saskatchewan. *Canadian Journal of Soil Science* **78**, 563–572. doi:10.4141/S97-065
- Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant richness on invasion dynamics, disease outbreaks, insects abundances, and diversity. *Ecology Letters* **2**, 286–293. doi:10.1046/J.1461-0248.1999.00083.X
- Krebs CJ (1998) 'Ecological methodology', 2nd edn. (Benjamin Cummings: Menlo Park, CA)
- Kunte K (2008) Competition and species diversity: removal of dominant species increases diversity in Costa Rican butterfly communities. *Oikos* **117**, 69–76. doi:10.1111/J.2007.0030-1299.16125.X
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) 'SAS System for mixed models.' (SAS Institute Inc.: Cary, NC)
- Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. *Bioscience* **56**, 311–323. doi:10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2
- McCain KNS, Baer SG, Blair JM, Wilson GWT (2010) Dominant grasses suppress local diversity in restored tallgrass prairie. *Restoration Ecology* **18**, 40–49. doi:10.1111/J.1526-100X.2010.00669.X
- Milakovic B, Parker KL, Gustine DG, Lay RJ, Waler ABD, Gillingham MP (2012) Seasonal habitat use and selection by grizzly bears in northern British Columbia. *Journal of Wildlife Management* **76**, 170–180. doi:10.1002/JWWMG.235
- Miller RF, Rose JA (1999) Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management* **52**, 550–559. doi:10.2307/4003623
- Miller RF, Bates JD, Svejcar TJ, Pierson FB, Eddleman LE (2005) Biology, Ecology, and Management of Western Juniper. Oregon State University Agricultural Experiment Station, Technical Bulletin 152. (Corvallis, OR)
- Nelle PJ, Reese KP, Connelly JW (2000) Long-term effects of fire on sage grouse habitat. *Journal of Range Management* **53**, 586–591. doi:10.2307/4003151
- Newman EI (1973) Competition and diversity in herbaceous vegetation. *Nature* **244**, 310. doi:10.1038/244310A0
- NRCS (1998) Climate dataset. National Cartography and Geospatial Center. (National Cartography and Geospatial Center: Fort Worth, TX)
- Patterson RL (1952) 'The Sage Grouse in Wyoming.' (Sage Books, Denver, CO)
- Pearson DE (2009) Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. *Oecologia* **159**, 549–558. doi:10.1007/S00442-008-1241-5
- Pierson FB, Bates JD, Svejcar TJ, Hardegree SP (2007) Runoff and erosion after cutting western juniper. *Rangeland Ecology and Management* **60**, 285–292. doi:10.2111/1551-5028(2007)60[285:RAEACW]2.0.CO;2

- Pyle WH, Crawford JA (1996) Availability of foods of sage grouse chicks following prescribed fire in sagebrush-bitterbrush. *Journal of Range Management* **49**, 320–324. doi:10.2307/4002590
- Rau BM, Blank RR, Chambers JC, Johnson DW (2007) Prescribed fire in a Great Basin sagebrush ecosystem: dynamics of soil extractable nitrogen and phosphorus. *Journal of Arid Environments* **71**, 362–375. doi:10.1016/J.JARIDENV.2007.05.006
- Rau BM, Chambers JC, Blank RR, Johnson DW (2008) Prescribed fire, soil, and plants: burn effects and interactions in the central Great Basin. *Rangeland Ecology and Management* **61**, 169–181. doi:10.2111/07-037.1
- Rhodes EC, Bates JD, Sharp RN, Davies KW (2010) Fire effects on cover and dietary resources of sage-grouse habitat. *Journal of Wildlife Management* **74**, 755–764. doi:10.2193/2009-143
- Rice LA (1932) Effect of fire on animal communities. *Ecology* **13**, 392–401. doi:10.2307/1932316
- Rutigliano FA, Migliorini M, Maggi O, D'Ascoli R, Fanciulli PP, Persiani AM (2013) Dynamics of fungi and fungivorous microarthropods in a Mediterranean maquis soil affected by experimental fire. *European Journal of Soil Biology* **56**, 33–43. doi:10.1016/J.EJSOBI.2013.02.006
- Swengel AB (2001) A literature review of insect response to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation* **10**, 1141–1169. doi:10.1023/A:1016683807033
- Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474.
- Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 1857–1861. doi:10.1073/PNAS.94.5.1857
- Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* **91**, 2833–2849. doi:10.1890/10-0097.1
- USFWS (2010) Twelve-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. *Federal Register* **75**, 13 910–14 014.
- USFWS (2013) Sage-grouse (*Centrocercus urophasianus*) conservation objectives: final report. US Fish and Wildlife Service. (Denver, CO)
- Wambolt CL, Payne GF (1986) An 18-year comparison of control methods for Wyoming big sagebrush in southwestern Montana. *Journal of Range Management* **39**, 314–319. doi:10.2307/3899770
- Warren SD, Scifres CJ, Teel TD (1987) Response of grassland arthropods to burning: a review. *Agriculture, Ecosystems & Environment* **19**, 105–130. doi:10.1016/0167-8809(87)90012-0
- Witwicki DL, Doescher PS, Pyke DA, DeCrappeo NM, Perakis SS (2013) Nitrogen limitation, ¹⁵N tracer retention, and growth response in intact and *Bromus tectorum*-invaded *Artemisia tridentata* ssp *wyomingensis* communities. *Oecologia* **171**, 1013–1023. doi:10.1007/S00442-012-2442-5
- Wright HA, Bailey AW (1982) 'Fire Ecology: United States and Southern Canada.' (Wiley: New York)