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Prescribed Burning Alters Insects and Wood Decay in a Sagebrush-Steppe Rangeland in Southwestern Idaho, United States ☆

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ABSTRACT

Prescribed fall burning is commonly used worldwide on rangeland sites to enhance vegetation resources and restore disturbed ecosystems, but little is known about how it may alter microbial communities and insect activities. We used two site treatments (low- to moderate-burn severity plots and unburned control plots) at a high-elevation (2 100 m above sea level) shrub-steppe rangeland site. Four yr after the prescribed burn, captured insects primarily consisted of Coleoptera (beetles), Hymenoptera (ants, bees, and wasps), and Orthoptera (grasshoppers and crickets) species with similar or greater numbers captured on burned plots as compared with unburned plots. We used wood stakes to assess microbial population changes. Aspen (*Populus tremuloides* Michx.) and pine (*Pinus taeda* L.) wood stakes were placed horizontally on the soil surface and vertically into the mineral to determine microbially altered wood decay rates. In mineral soil, mass loss (wood decay) of both aspen and pine increased significantly in the burned plots after 5 yr. Surface aspen also had increased decay in the burned plots, but pine surface stakes were unaffected. Surprisingly, at this high-elevation site we also found subterranean termites (*Reticulitermes tibialis* Banks) feeding on both stake species, with greater numbers on aspen stakes in burned plots leading to greater wood mass loss and organic matter turnover rates. Our results suggest that that fall prescribed burning can enhance insect numbers and microbial decay in sagebrush-steppe ecosystems. Understanding these changes can help land managers predict the influence of fall prescribed burning operations on soil biological properties and insect communities.

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Introduction

Rangelands encompass approximately 31% of the land area in the United States with the federal government managing 62 million ha mostly in the West (Lubowski et al. 2006). They support a diverse invertebrate community of more than 40 families of protein-rich invertebrates, especially ants (Hymenoptera), beetles (Coleoptera), grasshoppers (Orthoptera), and moth and butterfly larvae (Lepidoptera), which are a critical food source for many birds and mammals, including greater sage-grouse *(Centrocercus urophasianus),* throughout their life history (Gregg and Crawford 2009; Hess and Beck 2014). The abundance and structure of insect communities in rangeland habitats are a function of the composition and quality of the plant community (Southwood et al. 1979; Strong et al. 1984) and underlying soil biological, physical, and chemical properties (Pyke et al. 2002).

Rangeland soils provide essential services of carbon (C) sequestration, nutrient cycling, water retention and release, and soils connect pollinator plants and insects (Gilger and Vaughan 2011). Soils are often high in organic matter (OM), thereby favoring microbial decomposition and N mineralization (Gustine et al. 2021; Pyke et al. 2003), but burning can change the amount of surface and min-

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eral soil OM and carbon (C) and nitrogen (N) cycling (DeBano and Klopatek 1988; DeBano et al. 1998; Gustine et al. 2021). Changes in soil OM can affect decomposer fungi and wood-feeding insects such as subterranean termites in the genus *Reticulitermes* (Hanula et al. 2012).

In the Great Basin, there are numerous ecological pressures from population growth, past and present land uses, climate change, and altered fire regimes (Chambers et al. 2007). In addition, livestock grazing has exerted pressure on the ecosystem since the area was settled (Torregrosa et al. 2007). To combat these pressures and restore vegetation and soil properties, many rangelands are being treated with prescribed fire (Pilliod et al. 2016).

Fire is a historic part of these ecosystems, but postsettlement alterations in fire frequency have altered ecosystem processes (Pyke et al. 2002). Specifically, fall prescribed burning is used on rangelands for fuel reduction and ecosystem restoration, mimicking the beneficial properties of wildfire (Fuhlendorf et al. 2011; Brooks et al. 2015). However, prescribed burning may alter the structure and function of these ecosystems; influence plant species diversity, pollinator habitat, and the quantity of invertebrates used as food resources (Pyle and Crawford 1996; Beck et al. 2009; Dahlgren et al. 2016); and reduce invasive plant species (Rau et al. 2008). For example, ant, beetle, and grasshopper abundance can increase in burned rangelands the year following a fire (Chambers and Samways 1998; Nelle et al. 2000), but frequent prescribed burning may decrease the community richness for forb-feeding grasshoppers (Vermeire et al. 2004).

Overall, fall prescribed burning is an effective tool for removing sagebrush cover on rangeland sites to promote grasses and forbs (Beck et al. 2009) and it can restore degraded ecosystems, including aboveground and belowground pollinator insects (Black et al. 2011), termites (Kard et al. 2022), and soil properties (Limb et al. 2016). However, relatively few studies on rangeland sites have explored both surface and mineral soil decomposition, the contribution to wood decay by termites, and surface and flying insect populations. Therefore, the objectives of our study were to quantify the impacts of a fall prescribed burn on insects moving in and on the burned and unburned soil and on OM decomposition rates to assess microbial impacts. Specifically, we hypothesized that fall prescribed burning would increase 1) insect diversity and numbers, 2) OM decomposition, and 3) the activity of termites in the mineral soil.

Materials and Methods

Study area

Our study was located within the Red Mountain Prescribed Burn activity unit on the Caribou-Targhee National Forest (42.42°N and 111.09°W), approximately 27 km northeast of Montpelier, Idaho (Fig. 1). The entire Red Mountain prescribed burn operation consisted of 19 burn units covering 642 ha, was fall burned, and was designed to increase the diversity of mountain big sagebrush (*Artemisia tridentata* Nutt.) to improve bird and mammal habitat. The study site aspect averaged 215°, slope steepness was 8%, and elevation ranged from 2 100 to 2 200 m. A weather station was installed in Unit 11 (see Fig. 1). Average annual precipitation for this area was 509 mm and mean annual temperature was approximately 1.5°C. Average annual low temperature was –3°C, and average annual high temperature was 12°C. The general climate has cold, wet winters and hot, dry summers, with most of the precipitation occurring as snow from October through April. Before burning, the site was dominated by little sagebrush (*Artemisia arbuscula* Nutt.; 35% cover) and mountain big sagebrush (30% cover). Major grass species were Idaho fescue (*Festuca idahoensis* Elmer; 25% cover) and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve; 5% cover), and the greatest forb coverage was from Jones' fleabane (*Erigeron jonesii* Cronquist; 10% cover).

The soil series is in the Squawval-Bischoff family complex (Soil Survey Staff 2014) and is classified as fine loamy, smectitic, Xeric Argicryoll over a colluvium derived from red conglomerate parent material (Kara Green, Soil Scientist, Caribou-Targhee National Forest, pers. comm.) with 15–20% rock-fragment content. The parent material consists of conglomerate and sandstone sedimentary rocks.

Experimental design

The prescribed burn was carried out on October 3, 2003, when soil water content in the surface 10 cm was near field capacity, which resulted in low- to moderate-severity burns as measured by mapping postfire burn severity (Parsons et al. 2010). Because of the mosaic pattern of the burn, we were able to locate burned and unburned control plots adjacent to each other in units 6 (Rep 3), 11 (Rep 2), and 16 (Rep 1). Each burned and unburned pairs were approximately 2–5 acres in size. Unit locations and boundaries are noted in Figure 1. Units (replicates) ranged from 4 to 10 ha in size, and within this area we randomly placed two 10×10 m subplots, as shown in Figure 1, in the burned and unburned portions of each unit (3 replicates x 2 site treatments (burned and unburned) x 2 subplots per treatment). For subplot placement, we were able to locate areas within the burned units that had similar low-to-moderate burn severities (Parsons et al. 2010) and had adjacent unburned controls of similar size, soil, and aspect. We used precipitation and temperature data from a weather station installed in Unit 11 and from the SNOTEL site Giveout, which are applicable only to unburned plots (see Fig. 1). All data from the site weather station are archived at: https://www.fs.usda.gov/rds/archive/Catalog/RDS-2020-0005 and data from the SNOTEL site can be found at: https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=493.

Ground cover

In the spring of 2004, canopy cover of grass, forb, and shrub lifeforms was measured with three random transects in the vicinity of each of the burned and unburned wood stake subplot 6 mo after the burn. Each transect was 30.5 m long. Canopy cover life forms of shrubs, forbs, and grasses were determined by the length of each respective canopy type intersecting the transect (Canfield 1941). Overlapping canopies were measured separately if they were from different life forms.

Soil sampling

In the spring of 2004, we randomly selected three points in units 6, 11, and 16 in each burned and control plot and collected soil from the 0- to 30-cm depth in 10-cm or 15-cm increments using a slide hammer corer 4.8-cm diameter. All samples were taken to the Soil Analytical Laboratory at the US Department of Agriculture, Forest Service, Moscow, Idaho, where they were composited into the 0-30 cm depth, dried at 105°C for 24 h, weighed, and sieved through a 2-mm mesh screen to remove coarse material to calculate soil fine fraction bulk density (Page-Dumroese et al. 1999). Sieved samples were analyzed for C and N (LECO CN analyzer, St. Joseph, MI), OM by weight loss on ignition at 375°C for 8 h, and pH on a 2:1 water:soil slurry (vol/vol). Mineral soil samples were dry-ashed at 475°C for 5 h and extracted with 2M nitric acid for estimating exchangeable cations of calcium (Ca), magnesium (Mg), and potassium (K) (Thomas 1996). Soil chemical concentrations were corrected for fine fraction bulk density and expressed on a per-hectare basis. Biologically active C was determined using

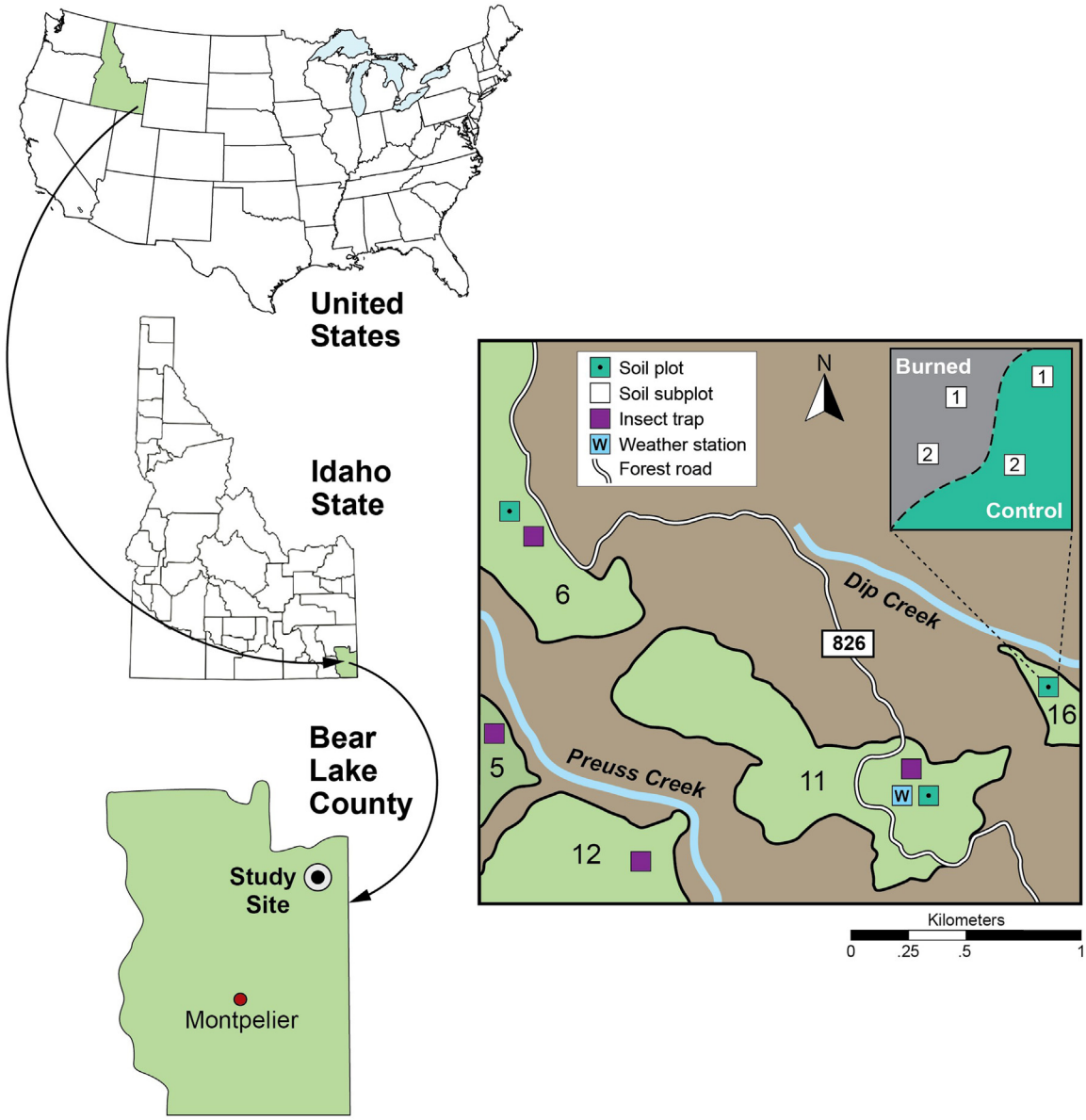

Figure 1. Study site map. Study location in Bear Lake County near Montpelier, Idaho, indicating the three soil and wood stake units (6, 11, and 16) and four insect trap units (5, 6, 11, 16) with a mosaic of prescribed burned and unburned areas. The map also shows the weather station location.

the modified permanganate oxidizable C method and can be a sensitive indicator to land management (Weil et al. 2003).

Insect communities and diversity

On May 16–20, June 16–20, and July 13–17 2007, we sampled insect communities on four burn units (Units 5, 6, 11, and 12, see Fig. 1) and four adjacent unburned sites. Because different traps are more effective for sampling various insect taxa in sagebrush steppe habitats (Caselton-Lowe et al. 2010), multiple types of traps were placed on each plot. A linear 50-m transect of five pitfall traps 10 m apart was installed, and each trap was 25% filled with a low-toxicity antifreeze. Four aerial traps were also placed 10 m apart at the end of one randomly selected pitfall trap transect, with the middle trap directly in line with the pitfall traps. These traps were 1) one standard yellow cross-vane beetle trap suspended approximately 1 m above the ground on a metal shepherd's hook, 2) one long (1.13-m) Lindgren funnel trap (Lindgren 1983) suspended approximately 2 m above the ground, and 3) two short (0.57 m) Lindgren funnel traps suspended approximately 1 m above the ground. Aerial traps were randomly assigned to their positions, were not baited with any olfactory baits, and had an insecticide strip (Hercon Vaportape II) placed in them. All collected insects were sorted and identified to order (Triplehorn and Johnson 2005) at the Natural Resource Entomology Laboratory at the University of Idaho, Moscow, Idaho. Three orders were identified to family (Orthoptera; Hymenoptera; Coleoptera). The total number of individuals per trap and trap location were recorded for each order and family of insects captured.

Wood stakes

We used standard loblolly pine (*Pinus taeda* L.) and trembling aspen (*Populus tremuloides* Michx.) wood stakes as an index of the prescribed burn impact on OM decomposition (mass loss). Wood stakes have been used in numerous studies to measure the effects of timber harvesting, fire, and climate gradient on the decomposition process (e.g., Finér et al. 2016; Page-Dumroese et al. 2019;

Figure 2. Subterranean termites in an aspen stake.

Risch et al. 2022). Two surface ($2.5 \times 2.5 \times 15$ cm) and two mineral ($2.5 \times 2.5 \times 20$ cm) stakes of both species were cut from longer kiln-dried, knot-free sapwood stakes. The center portion of each stake was kept as a laboratory control (time = 0) to determine mass loss of the surface and mineral stakes after placement in the study site. The top of each mineral stake was treated with a wood sealer to reduce moisture loss after installation. For additional details see Jurgensen et al. (2006).

Stakes were installed following the protocol outlined in Page-Dumroese et al. (2019). Briefly, in each subplot in units 6, 11, and 16, 25 surface stakes of each species were placed horizontally on the soil surface and secured with a landscape staple. In addition, 25 stakes of each wood species were inserted vertically into the mineral soil so that the stake tops were flush with the soil surface. To minimize soil compaction at the wood stake−mineral soil interface, stakes were placed into a square hole, 2.5 cm on a side, formed with a square coring tool. This resulted in a total of 1 200 stakes used in the study: 2 stake species x 3 replicates x 2 site treatments (burned, unburned) x 2 subplots x 2 soil locations (surface and mineral) x 25 stakes.

Each June for the next 5 yr (2005–2009), five stakes of each species were randomly selected and removed from each subplot and soil location in the three replicates. Stakes were gently scraped to remove adhering soil and weighed in the field to calculate wood stake moisture content at extraction. If stakes had termite damage, as much soil as possible was removed from the stake and termites collected before weighing. All stakes were sent to the College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan for processing. In one unburned replicate, the mineral soil stakes were missing for unknown reasons, and so we could only use two replicates of the burn and unburned plots in our analysis.

During the first stake sampling in June 2005, we found live subterranean termites and termite damage on several stakes (Fig. 2). It became apparent that subterranean termites had an important role in wood decomposition on this site, which was not expected due to the high elevation and low winter soil temperatures. Therefore, the objectives and protocols were changed to assess the effect of prescribed burning on OM decomposition by both microorganisms and termites. This entailed separating wood stakes into two groups for subsequent laboratory and statistical analyses based on the presence or absence of termite attack.

In the laboratory, all stakes were dried at 105°C for 48 h, weighed, and separated into two groups: 1) microbial decay with no evidence of termite activity—mass loss was due to microbial activity and 2) termite-damaged stakes (e.g., feeding on wood surface; holes in wood) —mass loss from termite activity and from microbial decay that may have occurred before, during, or after termite attack. Termite-damaged stakes were checked for soil moved into the wood by termites, and if present, soil was removed with small scrapers. Wood blocks (2.5-cm long) were cut from all microbial-decayed mineral soil stakes at the 5- and 15-cm stake length to assess the effect of soil depth on decomposition. Stake moisture content was calculated as the ratio of the stake water content to the stake dry mass.

Decomposition (mass loss) of both microbial-decayed and termite-damaged stakes was determined by comparing the dry mass of individual field stakes to the dry mass of the corresponding laboratory control stakes. Mass loss averages for each subplot were used as treatment observations in the statistical analyses. The impact of termites on stake decomposition was assessed by comparing mass loss of termite-damaged stakes to mass loss of microbial-decayed stakes taken from the same treatment plot and sample date.

Termite collection, morphology, and molecular analysis

Termites found on aspen and pine stakes on the soil surface or in the mineral soil in burned and unburned plots were collected, placed in labeled vials containing 90% EtOH, and sent to the Oklahoma State University Plant, Disease and Insect Diagnostic Laboratory, Stillwater, for processing and identification using morphometric and genetic analyses. Termite soldiers were identified morphologically using standard keys (Banks 1946; Gleason and Koehler 1980; Scheffrahn and Su 1994; Brown et al. 2005). Measurements of body components were obtained using an Olympus SZ61 stereo microscope using SPOT software version 4.6.4 (Diagnostic Instruments, Center Valley, PA). Termites were analyzed using polymerase chain reaction (PCR) protocols. The 428-bp region of the mtDNA 16S rRNA gene was amplified using universal primers: forward primer LR-J-13017 [5′-TTACGCTGTTAT CCCTAA-3′] (Kambhampati and Smith 1995); reverse primer LR-N-13398 [5′-CGCCTGTT TATCAA AAACAT-3′; Austin et al. 2005]. BLASTn searches using GENBANK accession numbers were used to validate species identification. For a complete description of analytical procedures see Smith et al. (2010).

Statistical Analyses

Insects, soil properties, and vegetation coverage

Effects of prescribed burning on insect orders and families, soil properties in the 0- to 30-cm depth, and vegetation cover in burned versus unburned treatments were evaluated using paired *t*-tests (Steel and Torrie 1980). Because of large variabilities in insect numbers among the plots, insect analyses were conducted at $\alpha = 0.10$ and soil and vegetation analyses were conducted at $\alpha = 0.05$ significance levels.

Wood stakes

The weight loss of the five stakes of each species sampled from each subplot was averaged and used as an observation for

Table 1
Yearly total precipitation (mm) and average soil temperature (°C) at the 2 cm and 8 cm soil depths at the Giveout SNOTEL installation near the Red Mountain study site near Montpelier, Idaho.

Water yr	Rainfall	Soil temperature 2-cm depth	Soil temperature 8-cm depth
	– mm –	–°C –	–°C –
2004	502.9	5.9[1]	—
2005	563.9	4.4	4.1[2]
2006	581.7	4.8	7.3
2007	424.2	2.8	7.2
2008	459.7	3.2	5.4
2009	581.7	3.7	5.9

[1] Data only available for June–December.
[2] Data only available for July–December.

each treatment in the statistical analyses. An analysis of variance (ANOVA) was conducted in SAS (ver. 9.2) using a factorial design, and the factors in the analysis were extraction date (2005, 2006, 2007, 2008, and 2009); treatment (prescribed burned and unburned); stake location (surface or mineral); stake depth in the mineral soil (5 cm and 15 cm); and subplot (3 replicates with 2 subplots each for surface stakes and only 2 replicates with 2 subplots each for mineral stakes for each sampling date-treatment combination). One replicate of mineral stakes could not be relocated for sampling. Within this model subplots were treated as nested effects within the burned and unburned treatments. The nested effects were estimated by their own means instead of the mean across all subplots. The initial model employed was the standard "effects model" with factors and their interactions included. When significant interactions were detected, the "means model" was used to clarify relationships. All wood stake analyses were conducted at $\alpha = 0.05$ significance level.

Stake mass loss was averaged by replicate and used for each treatment x sampling date combination. Two wood stake datasets were created to assess the effect of termites on decomposition: 1) mass loss from only microbial decay and 2) mass loss from microbial decay plus termite damage. Next, a third dataset was created with all data by combining dataset 1 and 2. The frequency of termite attack between treatments, between wood species, and among plot replicates were compared with Fisher's Exact test using SAS PROC FREQ.

Results

Climate

The average annual precipitation (rain plus snow) for water yr 2004 through 2007 was 622 mm, and the precipitation distribution and average daily air temperature were typical for the climate, with summer highs between 20°C and 25°C and winter lows around –20°C (Elliot et al. 2020). Maximum daily precipitation was 70 to 80 mm during 2006 and 2009. The hottest months were June through August with daytime highs averaging 12°C. Average yearly precipitation from the nearby SNOTEL weather station (Giveout) indicates variable total precipitation amounts during our study (Table 1). Soil temperature at the 2- and 8-cm soil depths declined at the SNOTEL site over the course of our study.

Soil properties

The spring after conducting the fall burn, soil OM, C, N, and bulk density were all significantly lower as compared with the unburned control treatment soil (Table 2). Active C was lower, but the difference between burned and unburned plots was not significant. Furthermore, soil pH increased slightly after burning, but the difference was also not significant. Exchangeable cations were relatively unaffected in the 0- to 30-cm soil depth.

Table 2
Average (± standard error) soil chemical and physical properties for the 0- to 30-cm mineral soil and vegetation cover for the unburned and burned plots 6 mo postburning on the Red Mountain study site near Montpelier, Idaho.

Soil and vegetation characteristics	Unburned	Burned	*P* value
Soil			
Organic matter (Mg · ha^{-1})	26.1 (7)	24.0 (6)	**0.031**
Carbon (Mg · ha^{-1})	15 (5)	11 (4)	**0.020**
Active carbon (kg · ha^{-1})	10.7 (1)	9.2 (1)	0.130
Nitrogen (kg · ha^{-1})	1100 (21)	840 (20)	**0.048**
C:N	13 (0.2)	13 (1)	0.415
Bulk density (Mg · m^{-3})	1.05 (0.3)	0.99 (0.4)	**0.043**
pH	5.5 (0.1)	5.8 (0.1)	0.121
Calcium (kg · ha^{-1})	65.4 (11)	65.6 (12)	0.525
Magnesium (kg · ha^{-1})	3.7 (0.5)	3.3 (0.4)	0.332
Potassium (kg · ha^{-1})	8.9 (1.0)	9.0 (0.8)	0.135
Soil cover %			
Grass cover	30 (0.5)	35 (1.0)	0.053
Forb cover	10 (0.5)	5 (0.4)	**0.025**
Shrub cover	40 (3.2)	32 (4.0)	**0.042**

Bold *P* values are significantly different ($P \leq 0.05$).

Vegetation and ground cover

Vegetation regeneration measurements were carried out 6 mo post burn on burned and unburned plots adjacent to the soil and wood stake plots. Grass cover was slightly, but not significantly, greater on burned plots compared with unburned plots. Forb and shrub cover were significantly less on burned plots (see Table 2). Postburn, we found three main perennial forb species in the burn treatment: common yarrow (*Achillea millefolium* L), Jones' fleabane, and helianthella (*Helianthella* Torr. & A. Gray) in similar amounts as preburn. In addition, we found small numbers (< 5% cover post burn) of lupine (*Lupinus* spp.) and penstemon (*Penstemon* spp.) beginning to colonize the burned plots.

Insect communities

There were 15 668 individual insects captured and identified to order. Total abundance of insects captured was not significantly different between burned and unburned plots. Three insect orders captured in the greatest numbers in both burned and unburned plots were Hymenoptera (ants, bees, wasps); Orthoptera (grasshoppers, crickets); and Coleoptera (beetles). At the ordinal level, only Orthoptera were captured in significantly different numbers between treatments, with more individuals captured in burned plots compared with unburned plots ($P = 0.0287$; Table 3).

The most commonly captured family of Hymenoptera during the study was Formicidae (ants; 4 233 captured). The number of ants captured was similar between burned and unburned plots, with individuals belonging to two different genera and species (*Pogonomyrmex salinus* and *Formica obscuripes*) making up > 95% of the total number of ants captured. Both species tend to live in large colonies and are commonly found in sagebrush-steppe ecosystems. Because of trail-marking pheromones used by these ants, the trapping method used in our study is only appropriate for determining their presence, not for comparing population densities.

Because of the ecological importance of forbs and their associated insects to greater sage-grouse and other birds and mammals, we also compared families of bee pollinators between burned and unburned plots (see Table 3). Individuals of four families of bees were captured in both burned and unburned plots. Sweat bees (Halictidae) were the most common family and had greater num-

Table 3
Average number (± standard error) of individuals in select insect families captured on paired burned and unburned plots for three 5-d sampling periods in 2007 at the Red Mountain study site near Montpelier, Idaho. Within each row, significantly different means are bold ($P \leq 0.10$).

Order	Family	Burned	Unburned
Hymenoptera	Andrenidae	1.8 (0.8)	2.0 (0.4)
	Apidae	39.8 (1.6)	35.3 (0.8)
	Halictidae	**64.5 (0.2)**	**42.3 (3.7)**
	Megachilidae	24.5 (4.4)	22.9 (3.3)
Orthoptera	Acrididae	**25.0 (4.0)**	**3.5 (1.9)**
	Gryllidae	1.0 (0.4)	2.8 (1.4)
	Rhaphidophoridae	**4.5 (1.5)**	**1.3 (0.8)**
	Tettigoniidae	3.0 (0.7)	2.5 (0.6)
Coleoptera	Anthicidae	**32.0 (10.0))**	**3.3 (1.5)**
	Carabidae	**40.0 (4.0)**	**11.8 (3.8)**
	Meloidae	**11.5 (4.7)**	**5.8 (2.8)**
	Staphylinidae	**18.0 (2.4)**	**6.3 (1.3)**
	Tenebrionidae	**51.0 (0.8)**	**37.8 (7.6)**

bers on burned compared with unburned plots and had statistically greater numbers ($P = 0.0705$). Similar numbers of three other families were also obtained on both burned and unburned plots: mining bees (Andrenidae), bumble bees (Apidae), and leafcutter bees (Megachilidae). No European honeybees (*Apis mellifera*) were captured during this study.

Four families of Orthoptera were captured (Acrididae, Gryllidae, Rhaphidophoridae, Tettigoniidae), all found in both burned and unburned plots (see Table 3). The most abundant of the four families was short-horned grasshoppers (Acrididae), one of the insect groups commonly listed as prey items for Greater Sage-Grouse (Wallestad and Eng, 1975). Of the four families, grasshoppers ($P = 0.0051$) and camel crickets (Rhaphidophoridae; $P = 0.0899$) had significantly greater numbers in the burned plots. Crickets (Gryllidae) and katydids (Tettigoniidae) had similar numbers in burned and unburned plots.

Overall, 29 families of beetles were collected during the study, in both burned and unburned plots. Beetles included both families commonly listed as food sources for greater sage-grouse and other birds and small mammals (Scarabaeidae: June and dung beetles; Tenebrionidae: darkling beetles) (Wallstead and Eng 1975). Darkling beetles and four other beetle families had significantly greater numbers of individuals in burned compared with unburned plots ($P = 0.0766$; see Table 3). Ground beetles (Carabidae) were the most common family in both burned and unburned plots, but greater numbers of individuals were in burned plots ($P = 0.0227$). Antlike flower beetles (Anthicidae; $P = 0.0510$), blister beetles (Meloidae; $P = 0.0805$), and rove beetles (Staphylinidae; $P = 0.0335$) had significantly greater numbers in burned plots. No beetle families were captured in significantly greater numbers in unburned plots.

Wood stakes

Table 4 presents the significant ANOVA main effects. There were no significant main effects of soil depth, subplot, or block and no significant interactions for stakes on the soil surface or in the mineral soil. The explanatory powers of stake species and stake location in the ANOVA (F value) were large, which may have confounded the separation of burn effect (treatment) from other study variables in the model. Therefore, separate analyses for stake location and tree species on wood mass loss were used. Separate analyses, while still statisticially valid, reduced the overall power of the test, but it made the effects of the treatment terms more apparent. The variability of termite presence or absence among the three treatment replicates also impacted our statistical results

Table 4
Wood stake full model analysis of variance main effects in the Red Mountain study site with microbe-only wood stake mass loss as the dependent variable and treatment (burned or unburned), incubation time (1–5 yr), wood species (pine or aspen), stake location (surface or subsurface), treatment (burned or unburned), and incubation time (1–5 yr) and as independent factors. Most interactions were not significant ($P \geq 0.05$), and those are found in Table S1, available online at ….

Factor	Df	F	P
Species	1	366.45	< 0.0001
Location	1	90.91	< 0.0001
Treatment	1	106.53	< 0.0001
Sample date	4	57.47	< 0.0001
Replicate (treatment)	2	6.07	0.0031

and will be addressed in greater detail in the following sections (Table 5).

Surface stakes

Decomposition of wood stakes placed on the soil surface was significantly less as compared with stakes inserted into the mineral soil ($P \leq 0.0001$). Aspen surface stakes had greater mass loss in the burned plots starting in 2006, but significant differences in mass loss between the burned and unburned plots were not measured until 2008 (Fig. 3A). Termites had relatively little impact on surface mass loss on either burned or unburned plots ($P = 0.3530$). Only 9 of the 150 surface stakes across the three replicates on burned soil, and six surface stakes on unburned soil had termite damage, but once found, these stakes were severely attacked (see Table 4). All termite-damaged stakes sustained mass losses of > 35%, and nine stakes had > 50% mass loss. By the end of the third yr, aspen stake mass losses from only microbial decay and microbial + termite damage were significantly greater on burned soil than on unburned soil but averaged < 30% loss at the end of the study. However, increased variability in the incidence of termite attack among treatment replicates increased the variance of stake mass loss in the fourth and fifth yr, which decreased the ability to detect a prescribed burning effect on surface aspen stake decomposition.

Compared with aspen, pine surface stake decomposition was slower (see Fig. 3B). Significant surface pine stake mass loss was not found ($P = 0.101$) for the entire study. Similar to aspen, termites attacked a low number of the 150 pine stakes on the soil surface of each treatment (6—burned; 7—unburned), and mass loss from all termite-damaged surface stakes was < 15%. At the end of the study, surface pine stake mass loss was greater on burned soil compared with unburned soil, but only for microbial decay plus termite-damaged stakes, which averaged < 10%.

Mineral soil stakes

As mentioned earlier, most of the aspen and pine mineral soil stakes in one burned and unburned replicate could not be found, so only two replicates were used to examine the effects of fall burning for stakes in the mineral soil. There were no significant differences in mineral aspen mass loss during the first yr, but starting in yr 2 (2006) aspen stakes in the unburned plots had significantly greater mass loss due to termite activity (see Fig. 3C). In contrast with surface stakes, termites had an important role in wood stake mass loss in mineral soil, but only on some burned plots. Of the 100 mineral soil aspen stakes sampled over 5 yr, 26 had termite damage or were totally gone, while only 4 of 100 stakes in unburned plots were attacked by termites. After 2 yr, aspen stake mass loss from termite attack in mineral soil was significantly greater in the burned plots as compared with the unburned plots, and from only microbial decay by the end of the

Table 5
Prescribed burning effect on the incidence of subterranean termite and resulting number of stakes with mass loss > 50% in aspen and pine stakes placed in mineral soil or on the soil surface at the Red Mountain study site near Montpelier, Idaho.

Unit[3]	Aspen				Pine			
	Mineral		Surface		Mineral		Surface	
	Total[1]	Mass[2] loss > 50%	Total	Mass loss > 50%	Total	Mass loss > 50%	Total	Mass loss > 50%
Unit 6								
Subplot 1	8	7	0	—	8	1	0	—
Subplot 2	8	2	0	—	0	—	0	—
Unit 11	12	8	11	9	7	0	6	< 10
Subplot 1	12	8	0	—	1	0	0	—
Subplot 2								

[1] Number of the 25 stakes in each subplot that were attacked by termites.
[2] Number of stakes with termite damage having greater than 50% mass loss.
[3] No termite-damaged stakes were found in Unit 16.

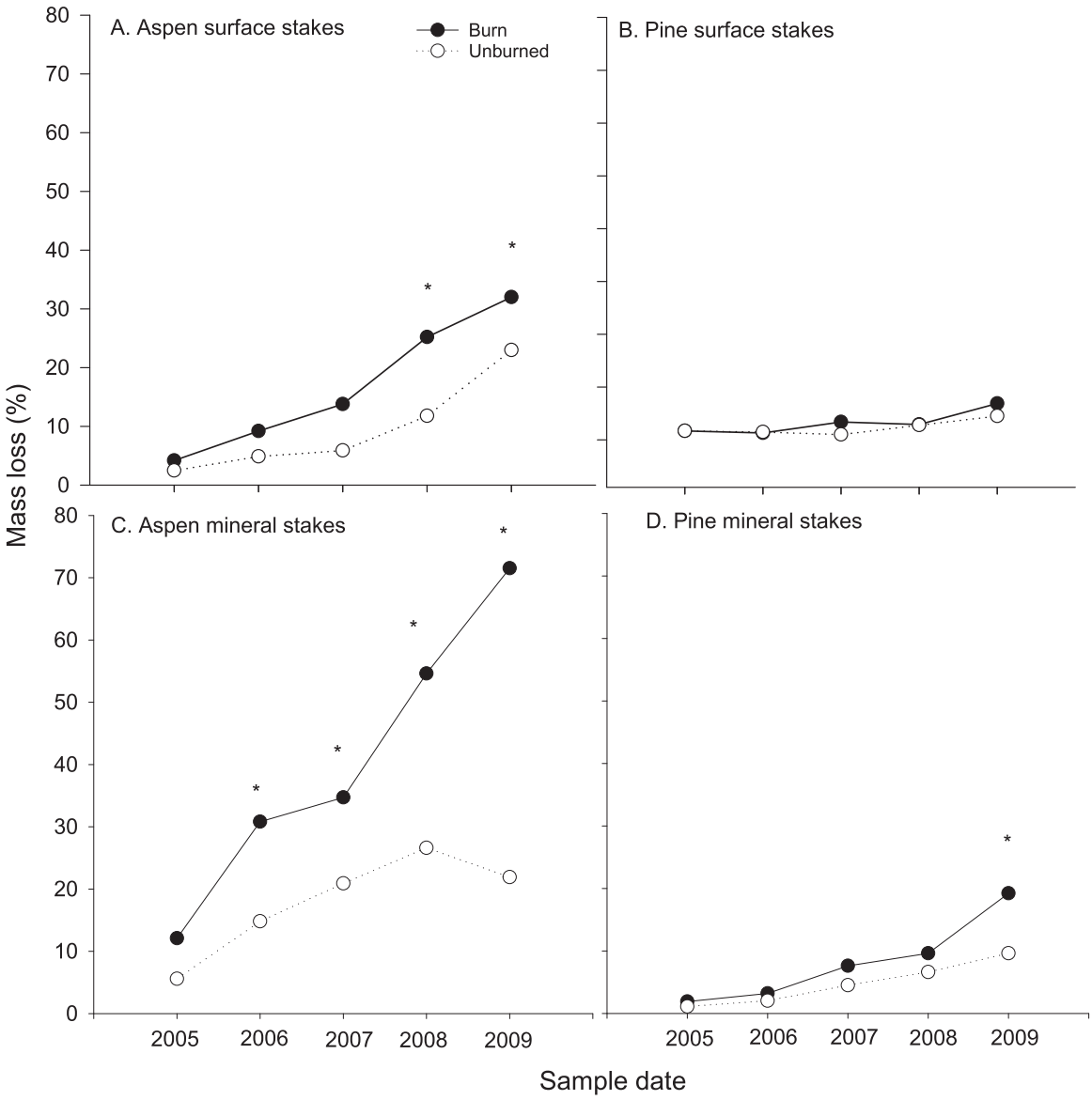

Figure 3. Mass loss of wood stakes. Mass loss from surface and mineral wood stakes in adjacent burned and unburned plots at the Red Mountain study site near Montpelier, Idaho, for **A,** surface aspen stakes, **B,** surface pine stakes, **C,** mineral aspen stakes, and **D,** mineral pine stakes. Mass loss values in burned plots marked with an asterisk (*) are significantly different from the unburned plots in that year ($P \leq 0.05$). Mass loss is inclusive of stakes with fungal decay and termites.

third yr. While not significantly different, aspen mass loss from termite damage in burned soil after 5 yr was > 70% compared with 50% from only microbial decay ($P = 0.250$).

Mineral pine stake mass loss (see Fig. 3D) was slower as compared with mineral aspen stakes in both burned and unburned plots. Significant pine stake mass loss from microbial decay in both burned and unburned plots was not evident until the end of 3 yr. Termites had less effect on pine decomposition than on aspen, as only 8 of the 100 pine stakes in the burned plot mineral soil and two stakes in the unburned plot soil sustained termite damage. Fall prescribed burning did not have a significant impact on pine stake mass loss in each year sampled, but when averaged over 5 yr, decomposition was greater in the burned treatment as compared with the unburned treatment for microbial decay ($P = 0.054$) and microbial decay plus termites ($P = 0.006$). However, pine stake mass loss in mineral soil across all plots was < 20%.

We were not able to obtain adequate information on soil water content during the study, but stake moisture content reflects recent precipitation events and confirmed that the soil was drying throughout the study (see Table 1; Fig. 4). As expected, aspen and pine stakes on the soil surface (see Fig. 4A) were significantly drier than stakes inserted into mineral soil (see Fig. 4B; $P < 0.0001$). Water contents of surface and mineral soil stakes of both aspen and pine on burned and unburned plots soil were not significantly different. In addition, stake water contents were not significantly different when averaged by species across treatments: 1) aspen surface, $P = 0.1923$; aspen mineral, $P = 0.0963$, and 2) pine surface, $P = 0.7526$; pine mineral, $P = 0.1696$.

Stake-soil depth

The impact of soil depth on wood stake decomposition was confounded by termite activity and, therefore, we used stakes with microbial decay only in this analysis. Soil depth and the interaction terms were statistically not significant in both burned and unburned soil for aspen ($P = 0.446$), pine ($P = 0.528$), or when both treatments were combined (aspen: $P = 0.475$; pine: $P = 0.506$). The trend for aspen stakes was that there was greater mass loss deeper in the soil in the burned plots while greater mass loss in the unburned plots occurred closer to the soil surface. For example, in yr 5, aspen stakes in the burned soil had 51.6% mass loss at the 15.7 cm depth as compared with 49.5% at the 5.7 cm depth while in the control plots mass loss at the 5.7 cm depth was 25.5%, but at the 15.7 cm depth it was 16.7%.

Termite incidence

Subterranean termites were actively feeding on pine and aspen stakes, causing steadily increasing damage. As shown in Table 5, wood stake mass loss among the burned treatment replicates was highly significant, which would likely decrease the precision of our fire effects analysis on wood stake decomposition. This replicate effect on stake mass loss was due to the incidence of termite attack and varied among burned and unburned plots. Of 68 aspen and pine surface and mineral soil stakes sustaining termite damage, 49 (72%) stakes extracted from burned plots had termite activity. Termite attack on wood stakes was highly variable (see Table 5) with stakes in the mineral soil having greater mass loss. The possible impact this large spatial variability of termite occurrence across the treatment plots could have on the study results is addressed in the Discussion section. All termites obtained from stakes in burned and unburned soil were identified as *Reticulitermes tibialis* Banks (Blattodea: Isoptera: Rhinotermitidae), commonly known as the "arid land subterranean termite" and are adapted to high-altitude rangeland soils.

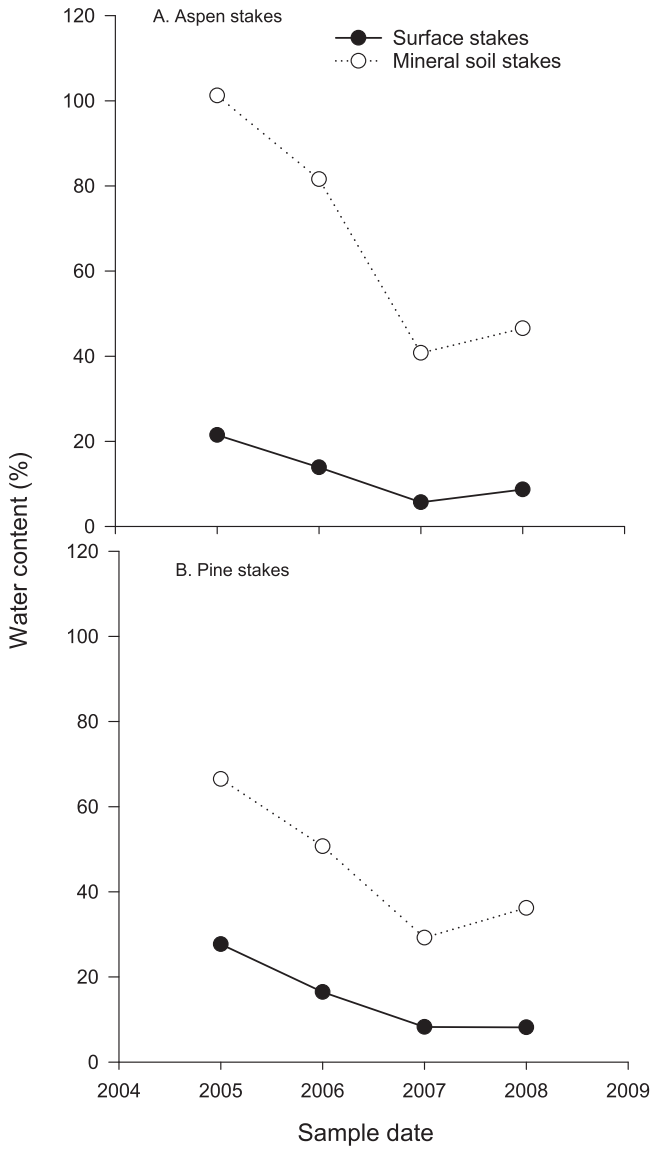

Figure 4. Wood stake water content. Water content of **A,** aspen and **B,** pine stakes averaged across burned and unburned plots at the Red Mountain study site near Montpelier, Idaho.

Discussion

Climate, soil, and vegetation cover

The use of fall prescribed burning within sagebrush-steppe habitats in southwestern Idaho is used to reduce surface woody residues, woody and invasive plants, and increase establishment and productivity of herbaceous plants (Bunting et al. 1987; Wrobleski and Kauffman 2003; Rau et al. 2008) while also reducing invasive species (Bunting et al. 1987). Fall prescribed burning created a mosaic of burned and unburned areas, which generally increased grass cover and decreased forb and shrub cover. However, both the unburned and postburn sagebrush cover amounts were greater than the targeted shrub cover of 15% (Johnson 2003).

Forb cover and soil C, N, and OM declined significantly after the prescribed burning when compared with unburned plots. However, other researchers have shown that fire can increase or maintain total C and N depending on fire severity, soil texture, plant species, and soil moisture conditions at the time of burn-

ing (e.g., White and Currie 1983; Davies et al. 2007; Hess and Beck 2014). In sagebrush-steppe communities there is a risk of annual grasses sprouting, particularly invasive cheatgrass (Bunting et al. 1987; Dumroese et al. 2015). However, regrowth of perennial native grasses can be encouraged with low-severity fires when there is an adequate seedbank (Bunting et al. 1987; Fuhlendorf et al. 2011). Six months after the fire, most grass cover was composed of native fescue species, but Beck et al. (2009) pointed out that prescribed burning did not enhance forage required by greater sage-grouse and, after 9 yr, resulted in increased cheatgrass abundance. Alterations in vegetation amounts and structure can also result in changes in the amount of water and light reaching the soil surface (Daubenmire 1967), which likely contributed to a reduction in soil surface OM. As noted in Table 2, prescribed burning also reduced soil N, C, and OM, at least in the short term.

Insect communities

After 5 yr, many insect families had significant increases in burned plots, reflecting a more favorable habitat (Southwood et al. 1979; Strong et al. 1984), which could provide a higher level of food that may influence a variety of birds reproduction and survival. We found ants, grasshoppers, and beetles were not adversely affected by burning, with beetle numbers enhanced 3½ yr after prescribed burning.

Changes in vegetative cover after burning (see Table 2) did not result in significant declines in three orders of insects (see Table 3). In Oregon, prescribed burning resulted in a longer growth period of herbaceous species, resulting in an extension of the period of photosynthesis and plant succulence for foraging insects (Wrobleski and Kauffman 2003). In addition, several species of plants flowered earlier, which increased high-quality reproductive plant parts early in the growing season for pollinators. The number of insect families were not different in unburned plots compared with adjacent burned areas. Insect families we collected all had a strong connection to soil habitats during at least a portion of their lives. Acridids typically oviposit in the soil, halictids usually nest in the soil, and tenebrionids are often found associated with the soil throughout their lifetime.

Orthopteran captures were dominated by acridid grasshoppers, a common prey item for greater sage-grouse (Wallestad and Eng, 1975; Drut et al. 1994; McAdoo and Back 2001; Hess and Beck 2014). Grasshoppers tend to be more abundant in areas the year following a fire (Nagel 1973; Bock and Bock 1991; Chambers and Samways 1998; Hess and Beck 2014). This study demonstrated that increased grasshopper abundance can remain for at least 4 yr following prescribed burning, which suggests that these areas will likely provide grasshoppers as food for birds and small mammals for several years. In addition to the grasshoppers, one family of bees (Halictidae) had significantly higher numbers in burned plots compared with unburned plots. Like acridids, halictids tend to have an intimate association with soil because they predominantly nest in the ground (Triplehorn and Johnson 2005).

One of the five beetle families captured in higher numbers from burned plots were darkling beetles, another of the previously identified insect families frequently fed upon by greater sage-grouse (Wallestad and Eng, 1975; Drut et al. 1994; McAdoo and Back 2001). Of the remaining four beetle families, two are intimately associated with each other, as well as the grasshopper and ground-nesting bee populations. Six species of meloids, *Linsleya sphaericollis* (Say), *Epicauta pruinosa* LeConte, *E. sericans* LeConte, *E. ferruginea* (Say), *E. puncticollis* Mannerheim, and *Lytta nuttalli* (Say), were captured. Meloids in the genera *Linsleya* and *Epicauta* typically feed on eggs of grasshoppers, while members of the genus *Lytta* are associated with nests of ground-nesting bees (Werner et al. 1966). Blister beetles produce cantharadin as a defensive compound that occurs in the blood of adults (Arnett 1993). Use of cantharadin as a defensive compound is of note because of an anthicid captured during our study (*Anthicus melanicholicus* Laferte) (Cook et al. 2009). Male anthicids in the genus *Anthicus* are attracted to cantharadin, which they present to females as a nuptial gift (Chandler 1976). The significantly higher number of meloids captured after burning may explain the significantly higher capture of anthicids (see Table 5). However, the anthicids may have been attracted to dead meloids present in the traps and may not be resident within the areas in which the prescribed burns occurred. The remaining two beetle families captured in higher abundances in burned plots were ground beetles (eight species captured) and rove beetles (seven species captured). Both families are potentially useful indicators of habitat change because they have high species richness and diversity and are habitat generalists (Arnett 1993).

Wood stakes

High-severity wildfire can increase mass loss rates from wood stakes, especially in mineral soil where soil moisture may remain higher than on the soil surface (Page-Dumroese et al. 2019). Similar to other studies, aspen stakes in and on this sagebrush-steppe soil generally lost mass at a faster rate than pine because aspen has lower stake cellulose:lignin and C:N ratios (Jurgensen et al. 2006; Wang et al. 2018). Wood decomposition in mineral soil was greater after prescribed burning than in adjacent unburned plots, and this is similar to other studies that examined wood decay following prescribed burns in forests (Page-Dumroese et al. 2019) or prairie soils (O'Lear et al. 1996) and after a wildfire in chaparral (Jurgensen et al. 2020). There is little information on wood decay in sagebrush habitats; however, sagebrush wood can act as a sink for nutrients because of its slow decomposition rate (Rickard 1985). Nitrogen release from soils after prescribed burning is considered to be less, and vegetation recovery faster, as compared with a high-severity forest wildfire (Choromanska and DeLuca 2001; Alcañiz et al. 2018).

In addition to N release, prescribed burns can result in higher available soil moisture due to reduced evapotranspiration following loss of shrub overstory (Wrobleski and Kauffman 2003). Stake moisture content generally declined throughout the study, which indicates that soil moisture likely followed this same trend. Stake water content reflects the previous 2 wk of climatic and soil moisture conditions. Although there were no significant differences in stake water content between the site treatments, it is interesting to note the steady decline of stake moisture across all sampling years. In particular, stakes on the soil surface were near or below the fiber saturation point of approximately 30% for the entire study and this low moisture content limits microbial wood decay (FPL 2010).

Termites

In some ecosystems, termites process 70% of the annual input of plant litter (Whitford 1991; Mando et al. 1999; Ouédraogo et al. 2004), but 7 yr after the prescribed burn, there was no significant difference in litter ground cover between the burned and unburned plots (Elliot et al. 2020). Termite activity can also influence soil bulk density as soil is moved between horizons (Li and Su 2008), resulting in greater infiltration rates and lower runoff rates (Elkins et al. 1986; Mando and Stroosnijder 1996). We did find that soil bulk density was significantly lower after burning and this could have been due to termite activity or the increased activity of other ground disturbing fauna (Elliot et al. 2020).

Soil microorganisms are important for ecosystem function as they contribute to nutrient cycling (Gustine et al. 2021) and OM decomposition (Dangi et al. 2010), and termite foraging may also

affect soil OM, soil nutrient cycling, and soil porosity (Elkins et al. 1986; Nash and Whitford 1995; Myer and Forschler 2019) by redistributing C and OM during their excavation and tunneling activities (Kard et al. 2022). In this study both microorganisms and termites contributed to wood stake mass loss (see Fig. 3 and Table 4). Wood stake mass loss associated with termites was highly variable, with greater incidences of termite damage in burned plots and with aspen stakes, with 28.5% of the aspen stakes and 11.5% of the pine stakes showing termite damage.

Termites can escape rangeland fires by moving downward, as their tunnels are often vertical within soil horizons (Nutting and Jones 1990; Brown et al. 2009; Morris et al. 2016). Soil heating associated with prescribed burns indicate soil temperature could reach nearly 100°C at 0.3 m deep in the mineral soil (Massman and Frank 2006). Peterson (2010) reported that in a Nevada rangeland study, 75% of termite colonies were found in the top 0.5 m of soil, but colonies could be found as deep as 8 m. Soil temperatures above 50°C are likely to be lethal to termites; thus, a severe wildfire could potentially kill 75% of the termites residing near the surface (Peterson 2010). Our work suggests, however, that the surviving termite colonies were sufficiently viable after the fall prescribed burn and that they likely either migrated into the burned plots from the unburned areas or survived deep in the soil profile, thereby making a significant impact on mineral wood decomposition by the fourth yr (see Fig. 3).

Termite distribution is controlled by temperature (King et al. 2013; Zanne et al. 2022). Actively foraging termites at this elevation demonstrates their adaptability to harsh winter climates on a sagebrush-steppe rangeland. Termites have been found at a high-elevation sagebrush-steppe site in southeastern Wyoming with a mean winter air temperature of −8°C but were associated with *Pogonomyrmex occidentalis* (harvester ant) nests (Crist and Friese 1994). In addition, *R. tibialis* has been shown to tolerate winter temperatures < −2°C (Haverty and Nutting 1976). Average soil temperatures at both 2 and 8 cm deep in the mineral soil did not get below freezing (see Table 1) at Red Mountain because of a deep snowpack, and this likely facilitated termite survival through the winter.

During swarming season in late spring, thousands of winged termite reproductives (alates) fly from the underground colonies. Termite swarming generally occurs in late spring in this northern part of this termite's range (Fumapest 2005), which would likely be weeks before greater sage-grouse chicks would hatch in mid-June and begin foraging for food (Beck et al. 2006; Dinkens et al. 2012). Adult greater sage-grouse, other birds, and small mammals may benefit from this late spring flush of winged termites occurring before the presence of many other insects in their diet, but there are no studies to date confirming this to be the case.

Management Implications

Our study evaluated short- and longer-term responses of fall prescribed burning on soil cover and chemical properties, insects, and the impact of microbes and termites on wood decay. This work provides an understanding of postfire responses for making management decisions. Fall prescribed burning is an important tool that can be used to enhance both aboveground and belowground properties and processes in sagebrush-steppe ecosystem. At this site, fall burning was conducted when the soil was moist, which left many unburned patches that likely promoted postfire forb and grass recovery. Shrub canopy cover declined after burning, but only a few soil chemical properties were affected and will likely recover quickly. In addition, fall prescribed burning generally enhanced insect availability with the unburned areas providing a refugia, allowing insects, including termites, to quickly repopulate the burned units. The use of wood stakes as an index of soil microbial changes is an effective method for determining prescribed fire impacts.

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Research Data

Wood stake decomposition data are available from the Michigan Technological University, Houghton, Michigan, and the USDA Forest Service, Forestry Sciences Laboratory, Moscow, Idaho. Insect data are available from the University of Idaho, Moscow, ID, and Oklahoma State University, Stillwater, OK.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.06.002.

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