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✦ Abstract

Fires are an important and increasingly common driver of habitat structure in the intermountain West. Through an ongoing study of burned and adjacent unburned areas along the John D. Rockefeller, Jr. Memorial Parkway, we examine the long-term effects of the 1988 fire season on community assembly, succession, and ecological processes. We collected mark/recapture data on rodents, removal data for insectivorous mammals and invertebrates, and habitat measurements on four grids in 2014 and combined these results with previous survey data. In 2014, 4,800 trap nights yielded 13 species of small mammals, comprising 618 individuals. Macroarthropod abundance was higher on burned grids, but diversity was higher on unburned grids. In contrast, springtail (Collembola) diversity was higher on burned grids, but abundance was highest in unburned grids. Since the beginning of this long-term study, the total number of mammal species has increased across all sites, and relative abundance in burned areas has shifted from early successional species (*Peromyscus maniculatus*) to those more associated with old growth forests (such as *Myodes gapperi*). Other than in 1991, the burned grids have harbored more diverse small mammal communities than the unburned control grids. Significant, long-term differences in vegetation based upon burn history were observed, including different ground cover, less canopy cover, and more coarse woody debris in burned sites. This work provides a unique long-term picture of the interrelationships of small mammal and invertebrate communities and correlated habitat variables as these ecosystems undergo post-fire succession.

✦ Introduction

On 20 August 1988, a wind-blown tree touched a power line in the John D. Rockefeller, Jr. Memorial Parkway (JDRMP) and sparked the Huckleberry Mountain Fire (Huck Fire; Swinford 1989). This fire was one of many that grew and merged as part of the 1988 fire season in the Greater Yellowstone Area (GYA). As the beginning of an upsurge of more severe fires in the western US, the 248 fires that burned ~570,000 ha in the GYA comprised one of the most severe fire seasons documented to date in the region both in scope and intensity (Romme et al. 2011). This event has provided a natural experiment for examination of the short- and long-term effects of fire disturbance on community assembly, succession, and ecological processes in previously burned regions.

While our understanding of the short-term (0–10 years post burn [YPB]) effects of fire on small mammals has reached a level of maturity that allows researchers to try and synthesize results from many studies, we have very little data on the long-term (>10 YPB) impacts of fire on forest communities (Fisher and Wilkinson 2005, Fontaine and Kennedy 2012, Kennedy and Fontaine 2009). Although few studies

have longitudinally characterized changes due to post-fire succession for more than 10 years, previous work has identified and summarized what is known about common transitions during these successional stages (Fisher and Wilkinson 2005, Lee 2002). Expectations based upon previous studies suggest many communities are initially dominated by the North American deermouse (*Peromyscus maniculatus*), which often responds positively to fire disturbance. Over time, the southern red-backed vole (*Myodes gapperi*) gradually invades burned areas, and generally this old-growth specialist will become the dominant species within the small mammal community (Fisher and Wilkinson 2005).

Several stages have been identified and characterized in this process (Lee 2002). Immediately after the fire, the initiation stage (0–10 YPB) is marked by a general absence of canopy cover, and an abundance of coarse woody debris (CWD). In the initiation stage small mammal response is highly variable based on fire severity and its effects on food and cover availability and other microhabitat characteristics. This phase is followed by the establishment stage (11–25 YPB), when shrubby and herbaceous vegetation increase as grasses decrease, and grainivore abundance decreases while red-backed voles, typically omnivores, increase. The third phase, and the current stage of succession from the 1988 fires, is the aggradation stage (26–75 YPB). During this phase tree density and canopy cover increase, while shrubs and herbs continue to decrease in burned areas. During the aggradation phase deermice are predicted to be the most abundant small mammal, and overall abundance of mammal communities is predicted to be lower than the preceding stages (Fisher and Wilkinson 2005).

Comparatively little is known about long-term community shifts of arthropods during post-fire succession. Arthropods fill numerous ecological roles during succession. Adult members of macroarthropod orders such as Lepidoptera, Coleoptera, and Diptera are essential to pollination. The larvae of many insects are also important in mediating flora via herbivory (Carson et al. 1999). Arthropods represent an abundant food source for vertebrate colonizers, such as bats, during succession (Loeb et al. 2006). Particularly important are the ecosystem services provided by the mesoarthropods that occupy leaf litter and soil. These small but highly abundant organisms create a system of complex trophic interactions involving mycorrhizae, detritus, nematodes, and bacteria (Rusek 1998). Springtails (order Collembola) are among the most ubiquitous and abundant arthropod members of

this community and can reach numbers up to a 100,000 per m^2 (Hopkin 1997). Their diverse diet of fungi, bacteria, detritus, and other soil organisms coupled with sheer abundance has ramifications for larger ecosystem processes such as mitigation of nematode plant parasites (Heidemann et al. 2014) and the formation of soil microstructure during succession (Rusek 1998). Springtail interaction with arbuscular mycorrhizae, endomycorrhizae, and other non-mycorrhizal fungi competitors can affect plant growth both negatively and positively depending on taxa (Lileskov et al. 2005). These ecologically important roles make springtails an integral component of post-burn succession (Chauvat et al. 2003).

Previous studies by Stanton et al. (1991, 1998), Spildie (1994), Seville et al. (1997), and Burt et al. (2009, 2011) have examined the responses of small mammal communities and corresponding habitat structure on the same burned and unburned sites at regular intervals (3, 4, 9, 10, 21, and 22 YPB) in the Huck Fire region of the JDRMP. As these data can provide us with a unique longitudinal picture of successional changes in this community since a stand replacing fire event in the summer of 2014, we continued the Huck Fire region series of investigations to maintain this long-term dataset and determine the impacts of post-fire succession and habitat change on small mammal and invertebrate communities as these burned sites enter the aggradation stage of stand succession. Our specific objectives were to:

1. Determine the composition of small mammal and springtail communities at 26 YPB in adjacent burned and unburned sites following the methodologies and locations established by previous investigations.

2. Investigate relationships between small mammal community structure, habitat variables, and invertebrate communities.

3. Provide an overall summary of the 26 YPB change in mammal communities and habitat structure since the 1988 fire.

✦ **METHODS**

Trapping procedures

To match previous study design and effort, we sampled the same 4 trapping grids, 2 burned and 2 unburned, at similar times of the year to previous studies during the summer of 2014. Trapping grids are located in Teton County, Wyoming, in the JDRMP,

10.5 north of the junction with Leeks Marina Road along Highway 287. Specific UTM coordinates for each grid (all in zone 12) are: east facing burn (EFB) 44 3.210 N, 110 41.568 W; east facing control (EFC) 44 2.953 N, 110 41.260 W; west facing burn (WFB) 44 2.992 N, 110 41.348 W; west facing control (WFC) 44 3.105 N, 110 41.624 W. Each grid consisted of a 1 ha area of burned or unburned forest. One of each treatment grid type was on the east facing slope of Steamboat Mountain (EFB, EFC) and the west facing slope of Huckleberry Mountain (WFB, WFC), as originally established by Stanton et al. (1991, 1998), and used by Spildie (1994), Seville et al. (1997), and Burt et al. (2009, 2011). All grids were assessed simultaneously from 1–4 June, 6–8 and 9–12 July, and 2–6 August 2014. During each 4-night trapping period, grids of 100 Sherman traps were placed (100 stations/ha, 10 m apart) and baited with rolled oats and peanut butter. Cotton bedding was placed in each trap for insulation/nest material. Traps were opened between 1600–2000 h and checked between 0500–0930 h the following day. Traps were closed during the day, and then reopened and re-baited (if necessary) the same afternoon. Animals captured in live traps were uniquely ear tagged and classified by species, sex, age class (juvenile or adult) and reproductive condition, weighed to the nearest gram and released where caught. Trap efforts (number of traps/grid, trap nights, and location) followed protocol from previous work at these locations.

Arthropods and insectivorous mammals were collected concurrently with live trapping during each of the trapping periods, using the same sites and grids. Pitfall traps were placed every 40 m within the 4 grids, with a total of 25 pitfall traps per grid, 100 traps per month, and 300 traps total for the survey. Traps consisted of plastic cups filled with 15.24 cm of propylene glycol/ethanol/water mixture (commercially available "pet safe" RV antifreeze), and buried so their rims were flush with the ground. Arthropods were allowed to accumulate for 4 days per month. Mammals were removed at least twice per day and frozen until they could be processed. After invertebrate collection, the propylene glycol mixture was replaced with 70% ethanol for long-term storage and preservation of invertebrate specimens. Invertebrates were sorted and counted, with all arthropods identified to order and Collembola further identified to family based upon Christensen and Bellinger (1998) and sorted to morphospecies. Small mammals captured in pitfall traps were processed as described above, preserved as voucher specimens, and will be deposited in the University of Wyoming, Vertebrate Museum.

Habitat data were collected from 100 trap stations (25/grid) evenly spaced throughout the grid. Data gathered at each trap station included distance from trap to nearest tree, nearest sapling, nearest seedling, and nearest shrub (within 10 m of trap station), as well as diameter at breast height for nearest tree and sapling. A 5 m tape was laid down in the 4 cardinal directions (N, S, E, W), and at any point where CWD (>7.5 cm in diameter) crossed the tape, distance was measured from the trap station and the diameter, height above ground, and decay state of the debris was recorded. Cover class data gathered at each trap location included percent ground cover using a 1 m² square frame for herbs, grasses, woody plants, CWD, bare ground, leaf litter, and (where applicable) pitfall trap. Cover class categories were scored 0–4, with cover category 0 not represented, 1 representing 1–25% ground cover, 2 representing 26–50% cover, 3 representing 51–75% cover, 4 representing 76–100% cover.

Because these data are non-normal, and in many cases nonparametric, Kruskal-Wallis tests were used to examine vegetation community differences based upon fire history and year. Diversity among sites and between years was estimated using the Shannon-Wiener Index ($H' = -\sum p_i \log p_i$). Recursive, nonparametric conditional inference trees implemented in the R package 'Party' (Hothorn et al. 2006) were used to examine the relationship between habitat variables and capture history for *M. gapperi* and *P. maniculatus*. Analyses were run in the *R* statistical package (version 3.0.2; R Core Team 2013).

✦ **RESULTS**

Current mammal community composition

Thirteen species of mammals and 618 individuals were captured in 2014, including 322 *M. gapperi*, 71 *Sorex monticolus*, 67 *P. maniculatus*, 27 *Tamias amoenus*, 24 *Sorex cinereus*, 10 *Zapus princeps*, 5 *Thomomys talpoides*, 4 *Phenacomys intermedius*, 3 *Microtus longicaudus*, 3 *Microtus montanus*, 1 *Microtus pennsylvanicus*, 1 *Neotoma cinerea*, 1 *Lemmiscus curtatus, 1 Microtus* sp. and 78 *Sorex* spp. Total numbers of species by grid are provided in Table 1. Reported values are out of 4,800 trap nights. As in previous years, *M. gapperi* and *P. maniculatus* accounted for the majority (63%) of captures (Figure 1).

The east ($H' = 1.33$) and west ($H' = 1.51$) facing burned grids harbored more diverse small mammal communities than the east ($H' = 1.04$) and

west ($H' = 1.13$) facing unburned control grids. As it is difficult to definitively identify shrew species without examination of the skull, diversity indices were calculated with all species of shrews lumped together (*Sorex* spp.) to accommodate unknown live species and facilitate comparison with previous years investigations in which shrew species data is not available.

Table 1. Total number of each species captured per grid in 2014. EFB = east facing burn; EFC = east facing control; WFB = west facing burn; WFC = west facing control.

|	EFB	EFC	WFC	WFB
Myodes gapperi	58	96	109	59
Peromyscus maniculatus	25	14	6	22
Sorex monticolus	29	18	15	9
Sorex cinereus	2	8	7	7
Tamias amoenus	4	3	6	14
Zapus princeps	1	1	6	2
Thomomys talpoides	1	1	2	1
Phenacomys intermedius	0	0	1	3
Lemmiscus curtatus	0	0	0	1
Microtus longicaudus	3	0	0	0
Microtus montanus	1	0	0	2
Microtus pennsylvanicus	0	1	0	0
Neotoma cinerea	0	0	1	0
Microtus sp.	0	0	1	0
Sorex spp.	18	19	25	16
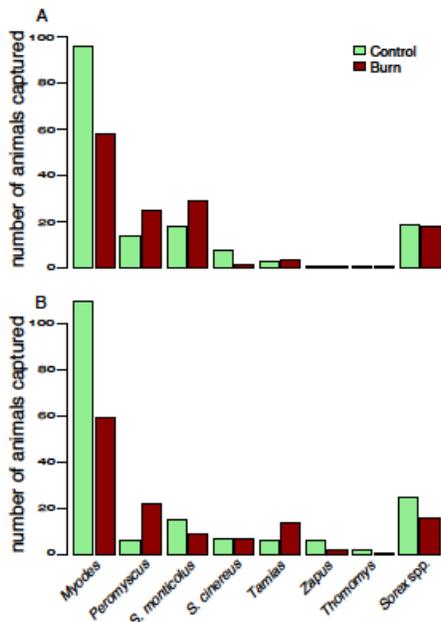
Figure 1. Relative abundance of most common small mammal species in (A) east-facing sites and (B) west-facing sites based upon burn history.

Current invertebrate community composition

Burned grids yielded 18,278 total macroarthropods, while 8,456 were collected from unburned grids. All major arthropod orders were included in the samples, with the most abundant captures coming from Hymenoptera (11,157 burned, 2,794 unburned, primarily ants), Diptera (1,009 burned, 598 unburned), Coleoptera (909 burned, 1,040 unburned), and Araneae (675 burned, 775 unburned). Burned grids had significantly higher abundance overall ($p = 0.0374$; Figure 2). However, unburned grids had higher diversity ($H' = 1.58$) than burned grids ($H' = 1.03$; Figure 2).

Over 5,470 Collembola were collected in the EFB, while 49,164 were collected in EFC (west-facing samples are still being identified). Across these grids, a total of 18 morphospecies from 4 different Collembola families (Entomobryidae, Isotomidae, Hypogastruridae, and Sminthuridae) were collected throughout the study area on burned and unburned grids. Individual stations within unburned grids exhibited much higher abundance ($\overline{X} = 664.38$ individuals/trap) than burned grids ($\overline{X} = 72.93$ individuals; $p = 0.0495$). Burned grids, had higher diversity ($H' = 1.139$) than unburned grids ($H' = 0.617$; Figure 3), and this effect was most pronounced in June and July. Differences among family abundances in burned and unburned sites were also observed. Hypogastruridae were more abundant in unburned sites, whereas Sminthuridae and Entomobryidae were more abundant in previously burned habitats (relative to their abundances in unburned habitats; Table 2).
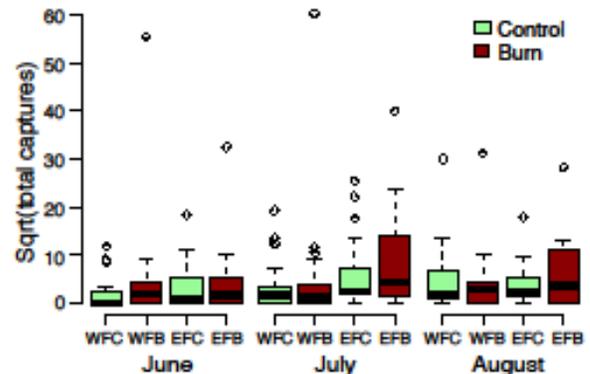

Figure 2. Boxplot of macroarthropod abundance over the entire survey period (note y-axis is square root transformed). Kruskal-Wallis test indicate a significant trend ($p = 0.0374$), with greater abundance in burned grids.

Table 2. Average (above) and range [below] of collembolans from particular families collected per pitfall trap in June, July, and August in 2014.

| June	Sminthuridae	Entomobryidae	Isotomidae	Hypogastruridae
Burn	2.83	3.67	14.88	0.58
	[0-18]	[0-19]	[0-63]	[0-4]
Control	0.17	3.04	7.91	203.35
	[0-3]	[0-30]	[0-105]	[0-2,730]
July				
Burn	41.24	8.6	2.12	5.64
	[0-154]	[0-25]	[1-11]	[0-119]
Control	6.52	4.12	2.96	1193.80
	[0-58]	[0-11]	[0-20]	[0-20,044]
August				
Burn	2.58	3.00	1.54	138.83
	[0-23]	[0-7]	[0-9]	[0-2,217]
Control	0.58	1.92	1.58	580.92
	[0-4]	[0-17]	[0-11]	[0-4,508]

Changes in mammal communities since the fire

Over the past 26 years, the number of mammal species trapped has increased across all sites (both burned and unburned), and relative abundance has shifted. Initially, *P. maniculatus* dominated burned sites whereas *M. gapperi* was dominant in unburned sites (Figures 4 and 5). Gradually the community composition in burned sites has shifted, so that relative abundance more closely resembles control sites. *M. gapperi* became dominant in the WFB between 1998 and 2009 (Figure 4), and in EFB between 2010 and 2014 (Figure 5).

Trends for other species are more difficult to discern, due to low capture rates or difficulties with identification of live individuals. Shrews have become more abundant in both burned and unburned areas, and constitute 25–30% of captures on all grids (Figures 4 and 5). *Tamias* has been present on both burn grids in low numbers shortly following the fire, but is more abundant on the WFB (Figures 1, 4 and 5). Recently, *Tamias* has become more common in the control grids especially on the WFC (Figure 1). *Zapus princeps* and *Thomomys talpoides* have been captured on all grids, but are most abundant on the WFC grid (Figure 1). Other species with ≤5 individuals captured are generally scattered among different grids (Table 1).

Small mammal community diversity has increased in the 26 YPB history in both burned and unburned sites, but it appears to be impacted by annual fluctuations as well as slope aspect. Diversity indices for burned sites have been consistently higher than adjacent unburned areas beginning the 4th YPB (Figures 4 and 5). In most years, there have been more rare species on burned sites than unburned sites, contributing to the persistent differences in diversity.
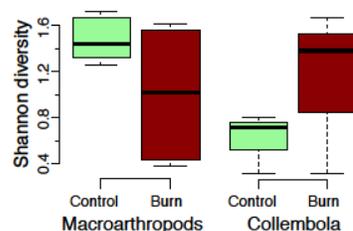
Figure 3. Macroarthropod and Collembola diversity, as measured by the Shannon-Weiner index. Macroarthropod diversity was greater in unburned grids relative to burned grids, whereas collembolan diversity was greatest in burned grids.
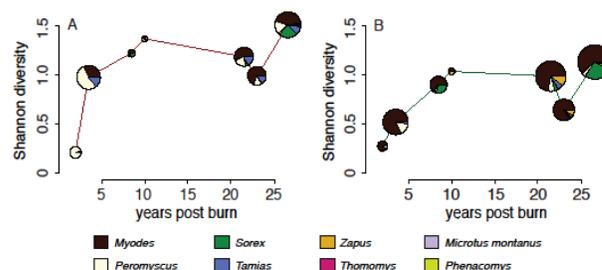
Figure 4. Diversity, abundance, and species composition in: (A) the west facing burn sites, and (B) the west facing control sites. Initially, deermice (*Peromyscus maniculatus*) were predominant in the burned sites, whereas red-backed voles (*Myodes gapperi*) have consistently dominated the adjacent unburned sites. Across most years, abundance has been higher in unburned grids whereas diversity has been higher in burned grids.
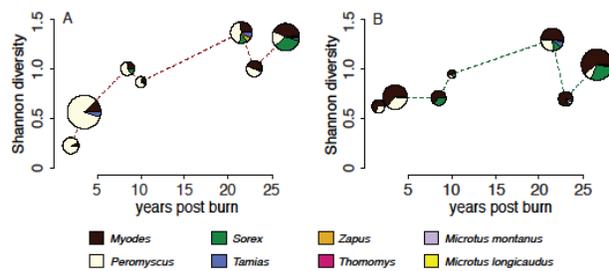
Figure 5. Diversity, abundance, and species composition in: (A) the east facing burn sites, and (B) the east facing control sites. Deermice (*Peromyscus maniculatus*) were initially predominant in the burned sites, whereas red-backed voles (*Myodes gapperi*) have consistently dominated the adjacent unburned sites. Generally, shrews and other small mammals have increased in frequency and abundance over time in both sites.

Microhabitat differences

Persistent and significant differences were observed between burned and unburned sites in terms of habitat, ground cover, canopy cover, and CWD. Previously burned areas have significantly less canopy cover (50% closure burned vs. 71% closure in unburned grids), fewer shrubs, more bare ground and more grasses than unburned areas (Figure 6). There was also significantly more CWD in burned areas, but that CWD was more decayed and closer to the ground than CWD in unburned areas (height from ground $\overline{X}_{burned}$ = 4.5 cm, $\overline{X}_{unburned}$ = 7.8 cm; Figure 8). Differences in standing vegetation around traps are also evident, with trees, seedlings, and shrubs closer to traps in unburned areas relative to the distances in burned areas (Figure 7).

While microhabitat differences are evident over time, many habitat changes captured by our data have not been linear with respect to burn history or time period. Not surprisingly, trees and saplings were significantly closer to traps in burned sites than in past years (results not shown). In terms of ground cover, herbaceous cover has increased in burned sites (Figure 9), while the amount of bare ground has decreased (Figure 10).

The regression tree approach indicated the best explanatory variable for capturing *M. gapperi* was the presence of shrubs near the trap site (Figure 11), without considering burn history. For the subset of sites where we captured *P. maniculatus* and measured habitat variables, none of the habitat characteristics we examined (or combinations of those characteristics)

significantly explained capture probability, despite the significantly higher number of deermice captured in previously burned habitats and the significant differences observed among habitats based upon burn history (Figures 6–10).
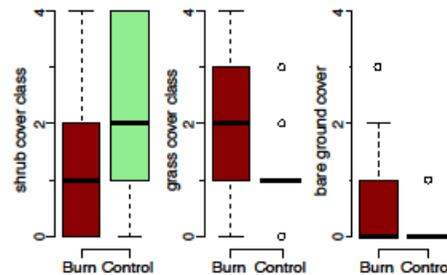

Figure 6. Persistent differences in ground cover surrounding trap sites exist between burn and control sites, with fewer shrubs and more grasses and bare ground in unburned areas.
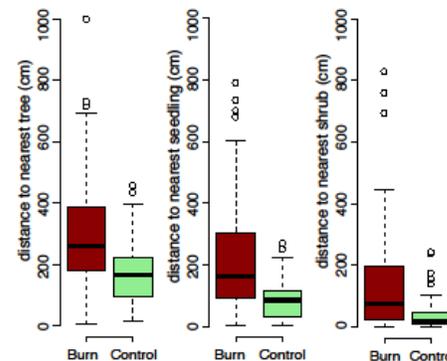

Figure 7. Differences in vertical habitat between burn and control sites. Trees, seedlings, and shrubs are all closer to traps in unburned (control) areas relative to previously burned habitat).
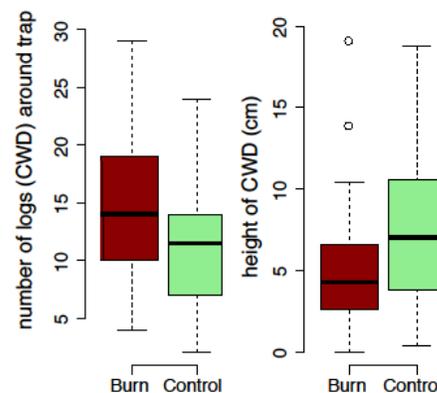

Figure 8. Coarse woody debris (CWD) is more prevalent in previously burned sites than in control sites, but CWD is higher off the ground in control sites.
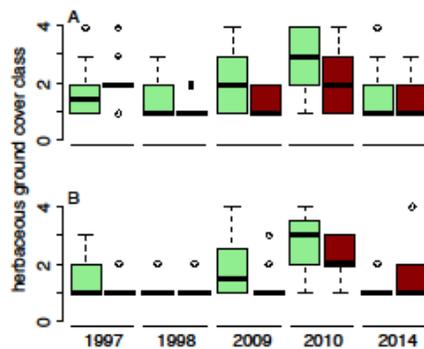
Figure 9. Herbaceous ground cover has generally, and significantly increased in burned sites over time on both (A) east facing and (B) west facing grids.
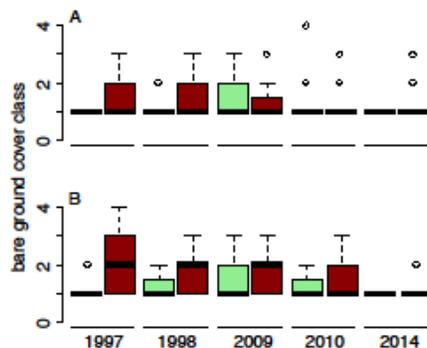

Figure 10. Bare ground cover has generally, and significantly decreased in burned sites over time on both (A) east facing and (B) west facing grids.
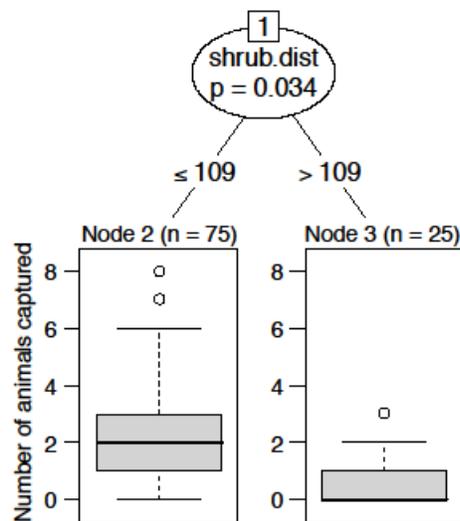

Figure 11. Recursive partitioning identifies distance to nearest shrub as the most important factor impacting capture success for *Myodes gapperi*, with more animals captured when shrubs are less than 109 cm from the trap, regardless of burn history.

✦ DISCUSSION

Our findings speak to broadscale patterns in succession occurring as the areas impacted by the 1988 Yellowstone fires transition into the aggradation phase (26–75 YPB). While 26 years have passed since the Huck Fire, persistent differences remain among burned and unburned sites in terms of mammal communities, invertebrate communities, and vegetation structure. In terms of major changes in mammalian communities, *M. gapperi* have increased in abundance in burned sites, and have become the most numerically abundant species in all 4 grids. *Peromyscus maniculatus*, which was initially dominant in burned sites, is no longer most abundant, but still makes up 17% of captures, and shows a preference for previously burned areas. Similar shifts in small mammal abundance during successional processes have been documented (e.g., Fisher and Wilkinson 2005); however, some of the hallmarks of those transitions, such as the dominance of deermice 26–50 YPB, are not supported by our results. In our sites, shrew species have become more abundant, now accounting for 24–35% of captures in burned sites and 26–28% of captures in adjacent unburned areas.

We also observed significant differences in macroarthropods between burned and unburned grids, suggesting habitat differences due to burn history are shaping abundance at the aggradation stage of succession, though the higher abundance in the burned grids (Figure 2) does not translate to greater diversity at the ordinal level (data not shown). Given the predominance in the number of ants collected in burned areas, it is possible that predation by ants, which were highly abundant in previously burned areas, are shaping community structure of the burned grids by limiting overall arthropod diversity. To thoroughly investigate differences in abundance and diversity further analysis of the macroarthropod community will need to be performed at the level of genus and species.

Differences in Collembola abundance were also observed to be significant between burned and unburned grids but interestingly trends in diversity were inverse from macroarthropods (Figure 3). Collembola appear to be more diverse in burned areas, and less diverse, but more abundant, in unburned areas. This may be due to observed mixed vegetative structure allowing for a broad range of canopy cover in burned areas, selecting for species with the ability to handle dryer and patchier climates. Comparisons by family suggest that differences in abundance exist which might be explained by the habitat tolerances of

each family (e.g., some species and some families may be better at traversing open habitat). However, further study is needed to examine whether functional differences in collembolan traits may be underlying these differences in abundance.

Trends in succession over time

Successional trends observed in our sites are similar to those observed in other burned areas. During the early phases of succession (Lee 2002), deermice dominate community abundance on burned sites; chipmunks correspondingly tended to be more abundant than in adjacent unburned habitat (e.g., Barmore et al. 1976, Wood 1981, Zwolak and Foresman 2007). More than a decade after a fire, during the establishment stage (11–25 YPB; Lee 2002), voles and shrews have increased on previously burned sites (Figures 4 and 5). However, the abundance of red-back voles and masked shrews continues to be greatest in old-growth areas compared to nearby burned areas (Figure 1; Roy et al. 1995), similar to the trend observed previously on the Huckleberry Mountain sites (Burt et al. 2009, 2010).

One other commonly observed trend is that abundance of small mammals increases with stand age after a fire (Fisher and Wilkinson 2005). In our sites, abundance has generally increased. However, fluctuations in abundance are evident across all 4 grids (Figures 4 and 5). The number of rare species has increased in all 4 grids, suggesting a potential regional impact of the succession across the GYA.

✦   **ACKNOWLEDGEMENTS**

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