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The influence of fire interval on community structure in the Greater Yellowstone Ecosystem

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Abstract With fires becoming more common in the intermountain West, understanding patterns of post-fire succession and the role of fire interval in shaping community responses has become critical. In 2016, the Berry Fire burned through 4 study grids which have been the focus of a long-term fire succession project started after the massive 1988 fire season. We investigated the effects of this fire with respect to repeatability of post-fire succession patterns (i.e., does succession after the 2016 fire match patterns observed after the 1988 fire) and the role of burn interval in shaping community structure of small mammals, invertebrates, and plants. Preliminary results indicate that sites with short burn intervals had greater diversity and abundance across all three taxonomic groups, although these differences were not always significant. Whereas the dominant taxa (deermice and ants) were the same 1 year after the 1988 and 2016 fires, we documented greater abundance of invertebrates and mammals and greater diversity of mammals after the 2016 fires. Taken together, these results highlight the importance of understanding fire regime (i.e., fire timing and intensity) in shaping these ecological communities into the future.

Introduction

Fire disturbances are predicted to become an increasingly frequent force shaping ecological communities in the Intermountain West (Riley and Loehman, 2016). Through the removal of old-growth and the redistribution of important nutrients, fires shape ecological community composition (reviewed in Wallace, 2004). Despite the widely recognized importance of fire in western ecosystems (e.g., Romme et al., 2011), few studies have followed long-term population responses (>10 years). Even less common is the opportunity to study a site well characterized before a burn or for repeat studies of fire at the same location. The 2016 fire season in the Greater Yellowstone Ecosystem (GYE) was the most active since the now iconic 1988 fires. One of the 2016 fires, the Berry Fire, burned through study sites that have been the focus of research on small mammal and invertebrate communities since 1988. This event provides the unprecedented opportunity to (1) *contrast community dynamics of post-fire succession based upon burn interval* as well as (2) *to evaluate the degree to which post-fire recolonization follows a predictable and repeatable trajectory*.

Building on initial studies on the impacts of the 1988 Yellowstone fires (Miller et al., 1989), data from the 28-year succession interval collected from our set of

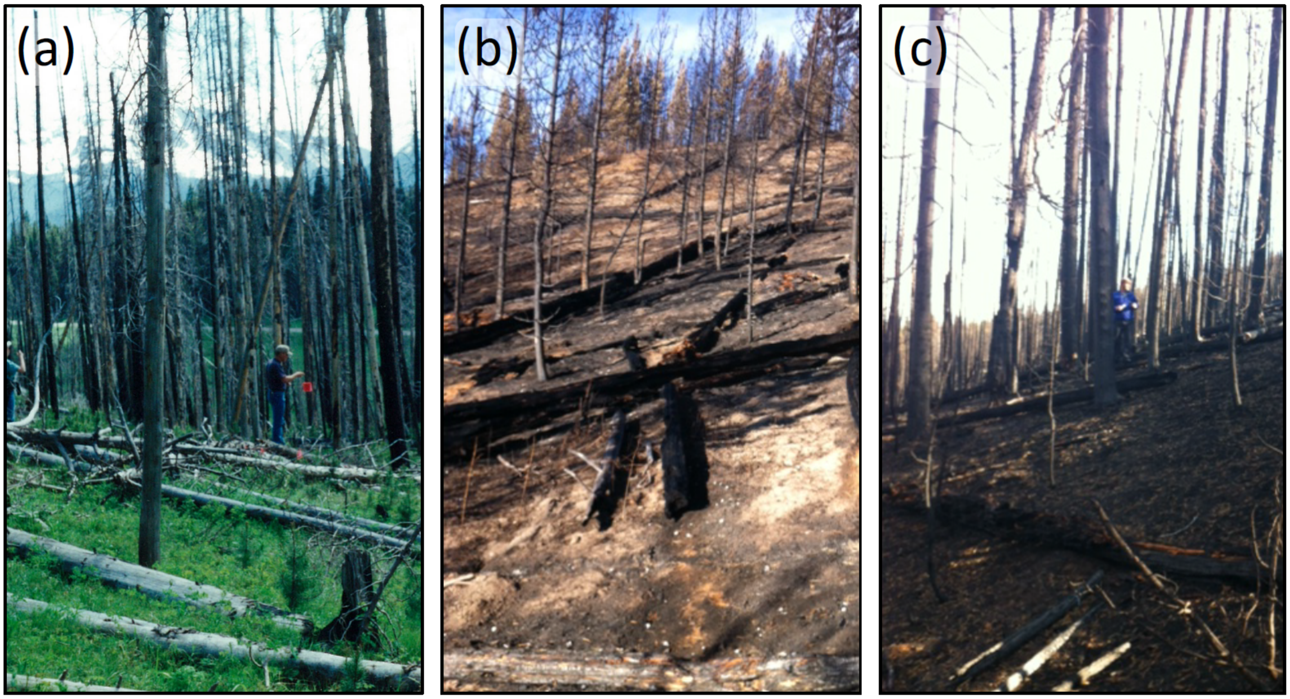

Figure 1. Standing and downed dead trees from the 1988 fire (a; photo taken in 1997) are much larger than those on the grids burned in *both* 1988 and 2016 (b). Grids that burned in 2016 only (c) are much more similar to those from the 1988 burn.

four study grids along the John D. Rockefeller Memorial Parkway illuminate the short- and long-term effects of fire disturbance on community dynamics and faunal structure (Stanton et al., 1990, 1991; Spildie, 1994; Seville et al., 1997; Stanton et al., 1998; Burt et al., 2009, 2011; Lanier et al., 2014, 2015). Started by lightning in July 2016, the Berry Fire burned ~8,500 hectares from west of Jackson Lake into the Bridger-Teton Wilderness, engulfing all four of our study grids and killing all of the live trees. In addition, much of the coarse woody debris (CWD) was completely reduced to ash leaving charred depressions where logs had lain. Prior to burning, the two 28-year interval grids had more CWD and many young trees, mostly of small diameter (<15 cm), whereas trees from the two old growth grids were 1.59 times greater in diameter, suggesting that past fire history may continue to influence the decomposition processes and thus, biotic community structure in the region (Figure 1).

The 2016 fire provides the opportunity to directly test questions related to the consistency of these successional trends in community structure as well as the role of fire interval on plots which have been well-characterized over the past 28 years. Specifically, we addressed two questions. First, does community structure differ among grids based upon burn interval (28-year vs. old growth) or is community structure post-fire simply re-set to a standard baseline, with few biologically relevant differences by burn history? Second, does post-fire succession from the 2016 fire match patterns previously observed on these study sites? We focus specifically on small mammals, invertebrates, and plant communities, all three of which have been the focus of our previous research (e.g. Lanier et al., 2014). This work is significant in understanding: (1) the long-term role of fire in shaping community dynamics in small mammals and invertebrates, (2) the role of fire interval on successional pattern and trajectory, and (3) impacts of post-fire succession on biodiversity in the GYE. Furthermore, this project contributes to a long-term knowledge of small mammal and invertebrate responses to natural fires in Rocky Mountain boreal forests.

Methods

Overall study design

Initially part of a smaller investigation by Miller et al. (1989), the current sampling design has been maintained since Stanton et al. (1990). The overall study layout consists of four 1-ha trapping grids, with two on west-facing slopes (WF) and two on east-facing slopes (EF). Each slope has one grid that burned in the 1988 Yellowstone fires (WFB and EFB grids) and an adjacent grid, which was unburned in the 1988 Yellowstone fires (previously referred to as 'control' grids; WFC and EFC). All four grids were burned during the 2016 Berry Fire, yielding two grids with a short burn interval (i.e., burned in 1988 and 2016; SBI) and two grids with a long burn interval (burned in 2016; LBI). Within each grid there are 100 trap stations at 10 m intervals, forming the basis for community surveys and faunal trapping.

Animal survey techniques

Trap effort (number of traps/grid, trap nights, and location) consisted of four-night trapping sessions in June, July, and August. Each night's effort consisted of 100 Sherman traps placed on each of the four grids (1 per trap station), baited with rolled oats and peanut butter. Total trapping effort was 1,600 trap nights per month, or 4,800 trap nights for the entire season. Traps were opened between 1530 and 1730 and checked between 0500 and 0830 the following day. Captured animals were uniquely ear- and pit-tagged for later identification; classified by species, sex, age class (juvenile or adult) and reproductive condition; weighed to the nearest gram and released where caught. Animals and traps were handled in accordance with current IACUC guidelines for handling small rodents (UW IACUC Permit #20170517ZR0071-01). In addition to live traps, a small pitfall trap with propylene glycol was placed at ground level at every fourth trap station (25 pitfalls/grid) to capture small insectivores, primarily shrews, as well as to sample invertebrate communities. In addition to matching established trapping protocols on these sites, this design provides a vouchered record of community change and targets species not readily recovered in Sherman traps. Mammal and invertebrate samples are vouchered at the Sam Noble Oklahoma Museum of Natural History (Norman, OK).

Vegetation surveys

To align data collection with previous work, vegetation structure was evaluated in several ways. First, for continuity with previous work (Stanton et al., 1990), we recorded 25 different microhabitat characteristics at a stratified subset of the 100 trap stations (25 per study grid) following Dueser and Shugart Jr (1978) and Daubenmire (1959). These characteristics included the distance from trap station to the nearest tree, sapling, seedling, and shrub, and whether the tree or sapling that was closest was alive or dead. Although all trees and saplings on our study sites were killed in the 2016 fires, they provide vertical structure for predators as well as some cones, which had recently been consumed by small mammals (pers. obs.), suggesting they may be important for small mammal habitat selection. In addition, we evaluated the ground cover in a m^2 quadrat around each chosen trap as to the nearest quartile: 0%, <25%, 26–50%, 51–75%, 76–100%. Ground cover classes were forbs, grasses, woody plants, logs, bare ground, litter, and ground that was disturbed by the presence of a pitfall. We also evaluated canopy cover (in this case from dead trees and remaining needles) using a convex spherical densitometer, directly over the chosen trap station following Lemmon (1956). In a 5 m transect in each cardinal direction from the trap station, we evaluated each piece of CWD >7.5 cm diameter by measuring the distance to trap, height from the ground, diameter, and decay state following Brown (1974) and Harmon (1996).

Targeted vegetation surveys were also undertaken in August, when most herbaceous vegetation was at maximum height and in flower or fruit. This consisted of a stratified-random sampling of understory vegetation within each grid, focusing on twenty-five 1 m x 1 m plots per grid. Each plot was sampled for species cover, density, frequency, and species composition using a modified Daubenmire method (Daubenmire, 1959; Diggle, 1975; Elzinga et al., 1998). Class midpoints were used to calculate average canopy coverage for each species. Cover data was summarized by grid, burn-interval, and by individual trap. Total vegetation, bare ground, and CWD cover data were normalized for the trap level analysis. Second, all plant species within study grids were identified onsite, where possible. Voucher specimens were collected and processed as per protocols established by the Rocky Mountain Herbarium (Hartman, 1992). In addition, soil and plant tissue were collected for later elemental analyses.

Analyses

To evaluate questions related to abundance and diversity, we used different proxies for abundance based upon the standards for the taxa in question: raw counts for each invertebrate order (family in the case of Formicidae), the number of unique mammals captured, and % species coverage for vegetation sampling. Differences among small mammal communities by burn interval were tested with the GTest of independence, with the Williams correction for small sample size, implemented in the R package DescTools (Signorell, 2017). Differences based upon burn interval were tested with non-parametric Kruskal-Wallis rank-sum tests. Invertebrate and plant community composition based upon grid and history was compared using principal coordinates analysis (PCoA) implemented in vegan (Oksanen et al., 2013), using the Bray-Curtis distance for invertebrate communities and the Jaccard distance for the presence/absence data from plant species. Data on invertebrates from the 1989 samples is from an unpublished honors thesis by Chris Vanterpool examining samples collected by Stanton and colleagues (Miller et al., 1989; Stanton et al., 1990, 1991; Vanterpool, n.d.).

Preliminary Results

In 2017, we had 402 mammal captures over the 3 trapping periods, of which 151 represented unique individuals. By far the most common small mammals were deermice (*Peromyscus maniculatus*), accounting for 85% of all captures but 75% of all unique captures (2). Red-backed voles (*Myodes gapperi*) were the second most abundant small mammal species, comprising 7% of all captures but 11% of unique captures. Jumping mice (*Zapus princeps*), shrews (*Sorex* spp.), voles (*Microtus* spp. and *Phenacomys intermedius*), chipmunks (*Tamias amoenus*) and pocket gophers (*Thomomys talpoides*) were also present, but at lower abundance (Figure 2). Out of the 18,218 macroinvertebrates collected in July of 2017, ants (Formicidae) made up the majority of captures (37%), followed by flies (Diptera; 6%), beetles (Coleoptera), and wasps and bees (non-ant hymenopterans). Each of the other macroinvertebrate orders comprised less than 1 individual/trap, and less than 1% of the total captures.

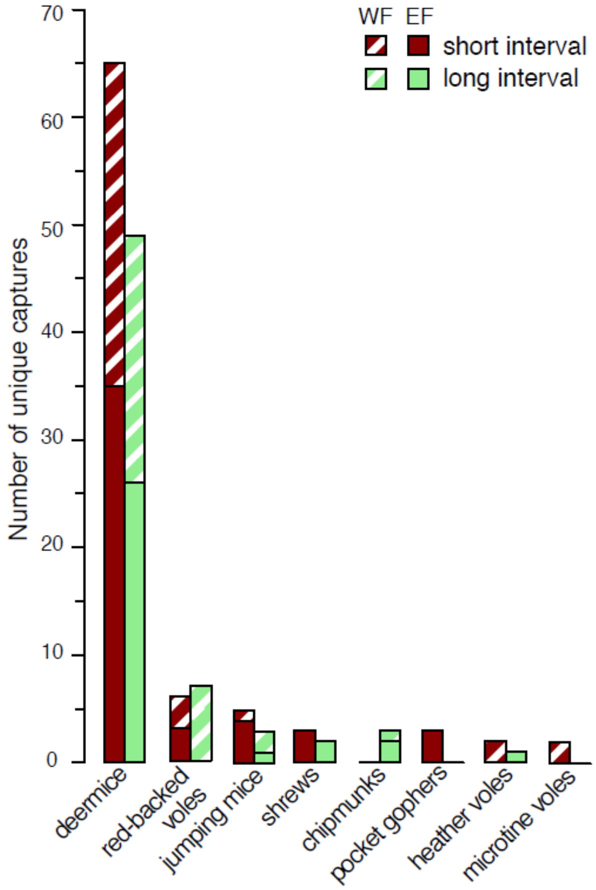

Figure 2. Across all 4 grids, and both burn intervals, deermice were the most commonly captured species. Red-backed voles, jumping mice, shrews, pocket gophers, heather voles, and microtine voles (*Microtus* spp.) were recovered in 2017 but were not recovered in the 1989 sampling.

Plant collection across all 4 grids yielded 74 species of plants represented by 89 voucher specimens. Of the 74 species, the most common families were the Asteraceae (28%) and the Poaceae (14%). Across all 4 grids, cover was dominated by 2 graminoid species: pinegrass (*Calamagrostis rubescens*; 10.4%) and elk sedge (*Carex geyeri*; 3.3%); 1 shrub: shiny leaf spirea (*Spiraea lucida*; 4.9%); and 4 forbs: lupine (*Lupinus argenteus* spp. *rubricaulis*; 5.5%), fireweed (*Chamerion angustifolium*; 4.8%), arnica (*Arnica cordifolia*; 4.5%), and wild hollyhock (*Iliamna rivularis*; 2.2%). There was also a strong influence of aspect, with higher species richness in the east facing grids vs. the west facing grids (65 east facing vs. 41 west facing). This includes species such as the noxious weed, Canada thistle (*Cirsium arvense*), which was documented on the east-facing grids but not the west-facing grids, although it was observed in the west-facing, short-interval grids prior to the fire.

Community differences based on fire interval

Mammals were more abundant on the short burn-interval grids, with 31% more unique captures than the long burn-interval grids (Figure 2). While most species appeared on both grids, microtine voles (*Microtus* spp.) and pocket gophers were only captured on short burn-interval grids, and chipmunks were only captured on long burn-interval grids.

Short burn-interval grids contained significantly more macroinvertebrates per pitfall overall ($\bar{X}_{\text{LBI}} = 51.5$, $\bar{X}_{\text{SBI}} = 136.1$; $p < 0.001$), a pattern largely driven by the greater abundance of ants in the short burn-interval pitfalls ($\bar{X}_{\text{LBI}} = 28.3$, $\bar{X}_{\text{SBI}} = 109.8$; $p < 0.001$). These differences contributed to distinguishable separation of short and long burn-interval sites in a PCoA (Figure 3).

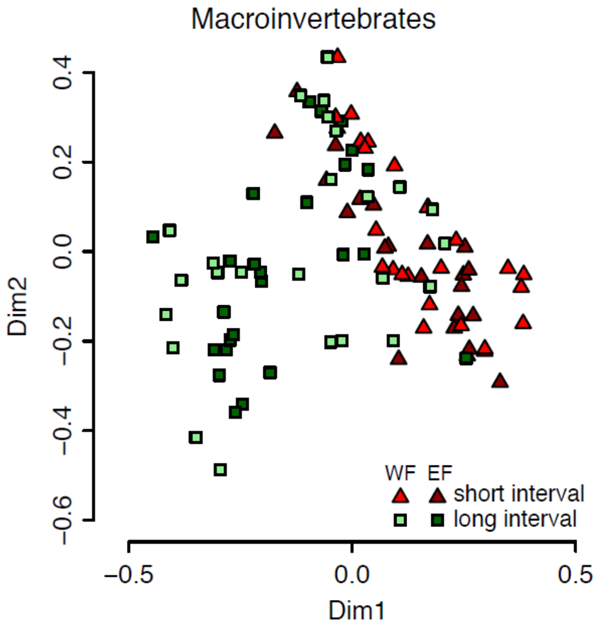

Figure 3. Long burn-interval sites clustered separately from short burn-interval sites in the July invertebrate data, a trend partially due to the greater abundance of all taxa in the short burn-interval sites. The long burn-interval sites also were typically more dissimilar from one another than the short burn-interval sites.

Although there was a similar eleven-species difference in plant communities between the short and long interval burns for both the east (38 vs. 27 species) and west facing (26 vs. 16 species) grids, the number of species in short burn-interval samples was not significantly higher. In addition, whereas the long burn-interval sites were relatively similar to one another with respect to plant taxa presence/absence, the short burn-interval sites were easily distinguishable across a PCoA (Figure 4).

2017 fire succession compared to 1989

Similar to observations in 1989, deermice were the most numerically dominant species one-year after the 2016 fire. However, in contrast to the 1989 data, when only deermice and chipmunks were recovered in the first year post-burn (Miller et al., 1989), we identified a minimum of 8 mammal species across all 4 grids in the first year post-burn in 2017 (Figure 2).

Although the 3 most abundant groups of invertebrates were consistent across both 1-year post-fire samples (i.e., in 1989 and 2017), their total and relative rank abundance differed, with more ants and more flies in the 2017 samples.

Conclusions

Across mammals, plants, and invertebrates, our results indicate that abundance and diversity were con-

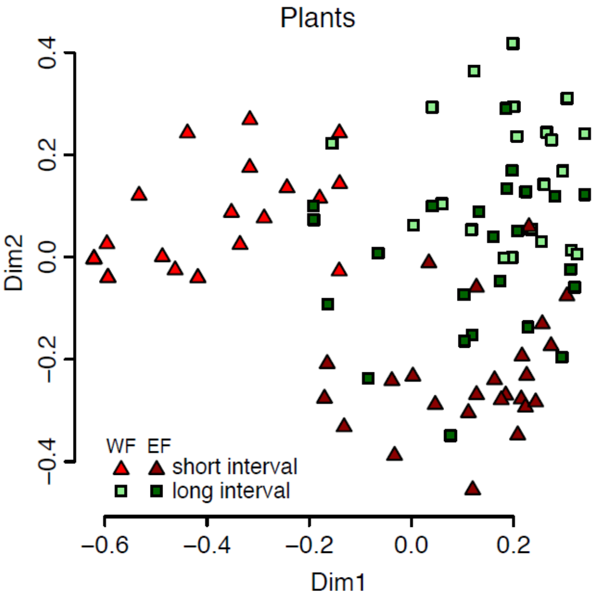

Figure 4. Plant communities can be separated out by both burn interval and aspect, with the greatest similarities between the long burn-interval sites. Communities from short burn-interval sites showed greater dissimilarity to one another, with very little overlap in plant species presence/absence data.

sistently (although not always significantly) higher in the short burn-interval grids. In addition, plant community structure differed based upon burn interval and grid in ways which may support the influence of community membership before the burn. Taken together, this suggests effects of burn interval on both abiotic and biotic factors that govern community assembly, possibly related to nutrient availability, diversity in the seed-bank, and/or fire intensity which may scale up to interactions between species within the communities.

When comparing the post-1988 succession and the post-2016 succession we observed a few common trends. While the dominant mammals and invertebrate groups (deermice and ants) remained the same, the relatively high mammal species diversity and greater abundance of invertebrates in 2017 was surprising.

This work highlights the importance of long-term research in studying ecological disturbances, particularly those which are likely to be repeated as part of a regular cycle. With a long-term fire succession study already in place, we were able to harness existing information to test predictions regarding the repeatability of successional patterns. In addition, the comparisons based upon burn-interval reveal community patterns which have implications for the mosaic of fire regimes across the GYE and the intermountain West.

Future Work

Ongoing work on this project includes analysis of elemental composition of plants, soils, and fungi samples, to better understand the role of fire interval in shaping available nutrients. In addition, invertebrate samples from June and August are still being sorted and identified, to better understand trends across the entire season in community structure. Vouchers from cryptic mammals (shrews and voles) are being identified through morphological techniques, and these vouchers are being compared to specimens from the original survey work following the 1988 fire. Next summer we anticipate returning to our study sites to continue to study the effects of burn interval and burn year on community structure.

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