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Effects of Fire Intensity on Litter Arthropod Communities in Ozark Oak Forests, Arkansas, U.S.A.

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ABSTRACT.—Fires are a significant source of landscape scale disturbance in forested ecosystems, but fire effects also vary on small spatial scales due to differences in fuel loads and local environmental conditions. We tested the hypothesis that such variation influences post fire arthropod communities and faunal recovery rates on a 1 m^2 scale. We measured the abundance and species richness of selected arthropod taxa pre- and post-fire in patches of leaf litter experimentally burned at different intensities. Arthropod abundance declined sharply immediately after a burn and decreased with increasing fire intensity. Consistent with other studies of this system, the effects of fire on arthropod communities were still apparent >4 w post burn. The abundance of epigeic beetles recovered more quickly than the abundance of ants or springtails in some treatments. Recovery rates also differed among treatments but did not consistently support the prediction that recovery would be faster in plots subject to low intensity burns. We conclude that small scale differences in intensity within prescribed fires have measurable effects on litter arthropod communities in Ozark forests; however, these differences appear to be overshadowed by the more general effects of fire on arthropods.

INTRODUCTION

Fire is a key source of disturbance in terrestrial ecosystems (Sousa, 1984; Pyne *et al.*, 1996) and will play an increasingly important role in shaping the ecology of forests over the next few decades (Dale *et al.*, 2001). Whereas the ecology of fire is often viewed in terms of landscape level patterns, fires are also highly variable at smaller scales, influencing local floral and faunal community structure (Catling *et al.*, 2001; Stephens *et al*, 2009; Myers and Harms, 2011). The two most ecologically important characteristics of fire as a mechanism of disturbance are frequency and intensity (*e.g.,* Whelan, 1995). Disturbance frequency has predictable effects on diversity (*i.e.*, the intermediate disturbance hypothesis; Connell, 1978; Sousa, 1984), but disturbance intensity is less often studied in a community context (Malanson, 1984; Burke and Grime, 1996; Kennard *et al.*, 2002). Large scale variation in fire intensity can be an important determinant of post fire plant community composition (*e.g.,* Oliver, 1980; Sousa, 1984; Myers and Harms, 2011), but the effects of small scale fire intensity on animal communities are less well known.

Leaf litter arthropods are a good focal taxon for studies of fire effects on animal communities because they are widespread in terrestrial ecosystems and occur in relatively high densities. Arthropods may experience high mortality during even mild fires, and community parameters (*e.g.,* abundance and species richness) are typically reduced immediately post fire (*e.g.,* Ahlgren and Ahlgren, 1960; Swengel, 2001; Wikars and

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Schimmel, 2001; Santos *et al.*, 2008). Within arthropods, litter inhabiting taxa should be particularly sensitive to the effects of fire (Ahlgren and Ahlgren, 1960; Hanula and Wade, 2003; Philpott *et al.*, 2006; Verble and Yanoviak, 2013); even low intensity burns consume leaf litter, and few litter arthropods are sufficiently mobile to escape advancing flames. However, not all litter burns in a fire, and fire intensity at ground level varies with fuel characteristics at spatial scales corresponding to variation in litter arthropod communities (*i.e.*, 1 m^2; Kaspari, 1996a, b). Moreover, some arthropod taxa (*e.g.,* those nesting in soil or large woody debris; Torgensen, 1995) are not exterminated by fire (Pryke and Samways, 2012), and some beetle species specifically inhabit unburned refugia within burned areas (Gandhi *et al.*, 2001). Consequently, local variation in fire intensity is likely to affect post fire arthropod community structure in predictable ways. Experimental tests of this hypothesis in natural communities are rare (*e.g.,* Wikars and Schimmel, 2001).

Faunal recovery rates (*i.e.*, the time required for community parameters to return to prefire levels) also are likely to vary with fire intensity and by taxon (*e.g.,* Pryke and Samways, 2012). High intensity fires convert virtually all litter microhabitats to ash, which is likely to delay recolonization by consumers like insects. In contrast low intensity burns leave many essential resources (*e.g.,* physical niches, seeds, shrubby vegetation) minimally scorched or wholly intact, potentially facilitating rapid recolonization (Canon *et al.*, 1987; Petersen and Best, 1987; Russell *et al.*, 1999; Turner *et al.*, 1999). Such patterns are evident in some boreal forests; in Sweden, arthropod abundance and species richness recovered within 1 y after low intensity burns, but required up to 5 y to recover from more intense fires (Malmström, 2006). Whereas other studies have examined fire severity (Gongalsky *et al.*, 2012) and thermal tolerance (Malmström, 2008), few have specifically explored the relationship between local fire intensity and arthropod recovery times (*e.g.*, Malmström *et al.*, 2008).

The principal goal of this study was to determine how variation in fire intensity at small spatial scales (1 m^2) affects the composition of leaf litter arthropod communities in Ozark forests. We predicted that post fire arthropod abundance would decrease with increasing fire intensity. We further predicted that arthropod recovery rates (*i.e.*, the difference in relative abundance of a focal taxon from one sampling period to the next) would be most rapid in forest patches experiencing the lowest intensity fires. Statistically, this prediction would be represented as a significant time*treatment interaction. Based on our prior experience with this system (Verble and Yanoviak, 2013) and similar studies in Australia (Pryke and Samways, 2012), we expected ant abundance and species richness to be minimally affected by fire intensity in the short term (*e.g.,* <60 d).

METHODS

STUDY AREA

Field work was conducted Mar.–Jun. 2011 in oak dominated forests of Arkansas, primarily in the Ozark ecoregion (35.80°N, 93.50°W). The Ozarks are characterized by nutrient poor soils, xeric slopes, and dense hardwood and mixed pine forests (Read, 1952). Prior to 20th century management, Ozark forests burned at high frequencies and low intensities (mean interval = 7 y; Foti, 2004), primarily as a result of anthropogenic ignitions (VanLear, 2004). Modern Ozark fire managers burn large contiguous areas of forests each year as part of protocols aimed at restoring historic patterns of diversity (Russell *et al.*, 1999).

EXPERIMENTAL DESIGN

Small scale experimental manipulations of fire intensity were established within five replicate prescribed fires in oak forests. The prescribed burns were managed by a

TABLE 1.—Forest stand characteristics of the five study sites. Data were obtained by measuring all trees >10 cm DBH within a 10 × 10 m plot located in the approximate center of all leaf litter plots within a site. *Species composition* = visual assessment of the 3 most abundant tree taxa at each site. *DBH* = average diameter at breast height (cm) of all trees >10 cm DBH within the stand. *Char1* = percentage of trees >10 cm DBH with char on the bole. *Char2* = percentage of trees >10 cm DBH with char at heights >1.5 m above ground on the bole

Site	Species composition	DBH	Char1	Char2
1	Oak-hickory-maple	24.0	20	7
2	Oak-pine-hickory	22.5	27	7
3	Oak-hickory-pine	24.5	13	0
4	Oak-hickory-maple	25.6	27	7
5	Pine-oak-hickory	23.6	27	13

professional crew using a ring fire and a combination of handlines and dozer lines. To our knowledge, these areas had not been burned in the past 50 y. Each focal burn covered >16 ha and occurred between Mar. and May, 2011. Hereafter, we refer to the five burned forests used in this study as *sites*.

Upon notification of a burn (usually <48 h prior to burning), we installed 70 small (1 m^2) experimental *plots* within the limits of the burn site and 10 plots adjacent to, but outside of the burn site, to serve as spatial controls. The 70 plots within a site were located at least 10 m away from each other and from the fire lines and were haphazardly distributed within areas similar in slope, accessibility, and ground cover. Haphazard placement was chosen due to the short time frame available prior to the burn for plot construction. Ten of the 70 within-site plots were designated prefire samples (*i.e.*, temporal controls). These plots were sampled immediately prefire to establish baseline arthropod levels for each site. The remaining 60 plots were divided among three litter depth treatments: coarse litter removed, litter depth unchanged, and coarse litter added to 3× normal depth. Litter was sterilized (heat) pre- addition to kill any arthropods that may have previously occupied it. When coarse litter was removed, it was sifted, and fine litter/arthropods were retained in the plot. Plots were haphazardly assigned to the different treatments and temporal controls. We used litter depth as a mechanism for manipulating fire intensity because fuel loads typically are correlated with fire intensity in temperate forests (Myers and Harms, 2011). Litter addition and litter depth unchanged plots were pooled; therefore, we used the following groupings for statistical analyses: control [unburned (pitfall traps), preburn and unburned (Berlese samples)], low (litter removed), and high (litter unchanged/added).

A thermal indicator plate (TIP) was placed in each of the 70 within-site plots to confirm differences in fire intensity based on temperature. TIPs consisted of aluminum flashing marked with Tempilaq® paints that melt at specified temperatures (Tempil, Inc., South Plainfield, New Jersey). TIPs provided coarse (±50 C) but reliable maximum fire temperature data. We also quantified leaf litter depth pre and post fire in all plots. Litter depth was measured to the nearest 1 cm by inserting a metal wire vertically through the litter in the center of each plot until it contacted mineral soil.

All plots within a site were burned on a single day. Composite site and stand characteristics [proportion of trees with char, proportion of trees with char at 1.5 m on the bole, and tree diameter at breast height (1.4 m above ground; DBH)] were measured in all plots (Table 1). Char was defined as blackening of the bark on the bole of the tree.

ARTHROPOD SAMPLING

We used a combination of Berlese extraction, pitfall trapping, and qualitative baiting to sample arthropod communities on the sites. Because fires were ignited by local agencies under relatively short notice, it was not possible to set up pitfall traps and place baits before burns. Consequently, we relied on comparisons between burned and unburned sites to determine fire effects on the ground-active fauna. This is a common approach in fire ecology studies (*e.g.,* Pryke and Samways, 2012).

Prefire leaf litter arthropod communities were sampled from the 10 temporal control plots within each site by Berlese extraction 1–2 h before ignition. Within 6 h post fire, Berlese samples were collected from 10 of the 20 plots corresponding to each litter depth treatment. Each Berlese sample was obtained by collecting litter and ash from a 0.25 m^2 quadrat in the center of each 1 m^2 plot. Collected litter was sifted through a 1 cm mesh screen due to large volumes of coarse litter (Bestelmeyer *et al.*, 2000) and the siftate was placed in a Berlese funnel (30 cm diameter, 25 W bulb) for 24 h (Southwood, 1978). Care was taken to retain mobile individuals that attempted to flee the litter sifter. Extracted arthropods were sorted and stored in 95% ethanol and identified to the lowest taxon possible within a reasonable timeframe. In summary Berlese collections consisted of $n = 50$ temporal control samples (10 plots per site × 5 sites) and 150 post fire samples (10 plots per treatment × 3 treatments × 5 sites).

After burning baits consisting of a mixture of canned tuna and honey were placed on the soil at haphazardly chosen locations within a site. All baits were examined for the presence of ants after ca. 60 min. When possible, a subset of the baits was examined every 10–20 min for evidence of ant foraging activity.

To quantify the abundance and recovery rates of ground dwelling arthropods, we installed pitfall traps (3 cm diameter × 12 cm depth, soapy water trapping fluid; Southwood, 1978) in the remaining 10 plots of each litter depth treatment (*i.e.*, plots not sampled by the Berlese method) and 10 plots in adjacent unburned forest (spatial controls) within 6 h post fire. Trap size considerations were based on previous studies of ants in similar environments (Verble, unpublished data). One pitfall trap was placed in the center of each plot and checked weekly for 4 wk post fire. Trap contents were fixed and identified as described above. In summary post fire pitfall trapping consisted of $N = 200$ samples from unburned spatial control plots (10 traps per site × 5 sites × 4 wk) and $n = 600$ samples from burned treatment plots (10 pitfall traps per treatment × 3 treatments × 5 sites × 4 wk).

DATA ANALYSIS

Quantitative analyses focused on the four most abundant macroarthropod and mesofaunal taxa in our samples (hereafter, ''target'' arthropods): ants (Hymenoptera: Formicidae), springtails (Collembola), spiders (Araneae), and beetles (Coleoptera). All of these taxa are functionally diverse, but ants exhibit relatively high interspecific variation in trophic ecology, body size, and behavior (*e.g.,* Hölldobler and Wilson, 1990); thus, we examined ants at a higher taxonomic resolution than the other taxa. Our pitfall traps captured primarily predatory beetles (*e.g.,* Carabidae and Staphylinidae; >80%); thus, we limit our conclusions about beetles to this subset. All data were checked for normality (Shapiro-Wilk W) and log transformed when necessary to correct variance heterogeneity.

We used nested ANOVAs to compare three variables: average arthropod abundance (pooled abundance of target taxa), ant species richness, and leaf litter depth among sites and among treatments (low intensity, high intensity, and control) nested within sites, using data from the Berlese method only. We used a repeated-measures ANOVA to assess differences in average recovery rates (the difference in relative abundance of taxa between each sampling point), arthropod abundance, ant species richness, and leaf litter depth among treatments over time. These analyses used data from pitfall traps only and treated site as a random factor (based on the lack of site effects in the nested analyses; *see* Results). Arthropod abundance and ant species richness data were regressed against leaf litter depth for all treatments to determine the effects of microhabitat availability on the litter fauna. Differences in forest stand characteristics were analyzed among sites with a multivariate analysis of variance (MANOVA). Medians and ranges were determined for maximum fire temperatures recorded in the different intensity treatments.

Analyses were conducted with SAS software (SAS Institute, 2008). We used Bonferroni-adjusted α as a correction for multiplicity. Ants used in species richness analyses were identified to species or morphospecies using published keys. Problematic specimens were confirmed by taxonomists and voucher specimens were deposited in the Watson Museum of Entomology at the University of Arkansas at Little Rock.

RESULTS

INTENSITY MANIPULATIONS

Experimental addition of leaf litter increased local fire intensity. Maximum temperatures recorded in litter addition and unchanged plots were higher (litter addition: median = 725 C; range = 480 to >870 C; unchanged: median = 650 C, range = 480–650 C) than in litter removal plots (median = 93 C, range = ambient to 204 C). Target arthropod abundance generally increased over time since burn, but the rate of increase was inconsistent among taxa over the 4 w (Fig. 2, Table 3).

ARTHROPOD RESPONSES

We collected a total of 6803 target arthropods (3271 ants, 1701 springtails, 1096 spiders, and 735 beetles). Data from pre and post fire Berlese samples showed a significant effect of fire on the abundance of target arthropod taxa. Specifically, the average abundance of each focal taxon was at least 66% lower in plots a few hours after the fire (Fig. 1). Local fire intensity also had significant effects on arthropod abundance. Specifically, total arthropod abundance and the abundance of each focal taxon were higher in the low fire intensity plots than in the high intensity plots (Fig. 1, nested ANOVA treatment effect: $F_{10,195} > 5.99$; $P < 0.0001$ for all tests). These results were consistent among sites (nested ANOVA site effect: $F_{4,195} < 3.48$, $P \geq 0.01$; Bonferroni $\alpha = 0.007$ for all tests).

Likewise, pitfall trap data showed that post-fire abundance and recovery rates of all focal taxa differed among treatments and over time (Fig. 2, repeated-measures ANOVA treatment effect: $F_{2,833} > 17.8$, $P < 0.0001$; time effect: $F_{1,833} > 8.49$, $P < 0.004$; time*treatment interaction: $F_{2,833} < 2.53$, $P > 0.08$; Bonferroni $\alpha = 0.007$ for all tests). As in the Berlese samples, the abundance of all taxa in pitfall traps was lower in burned treatments relative to controls, and was lower in the high intensity fire treatment than low intensity fire treatment (Fig. 2).

A total of 29 ant species was collected, and ant species richness increased with ant abundance in both pitfall and Berlese samples ($R^2 = 0.54$). Consequently, ant species richness responses to fire intensity generally followed ant abundance in Berlese samples (Fig. 1; nested ANOVA treatment effect: $F_{10,195} = 16.7$; $P < 0.0001$; site effect: $F_{4,195} = 0.68$; $P = 0.61$) and pitfall samples (Fig. 2) as described above. Although ants were regularly captured in pitfall traps (Fig. 2), no ants were observed at baits during the 4 wk following burns, even when baits were placed within a few cm of known nest entrances. The general absence of ant activity at baits was consistent among treatments and sites.

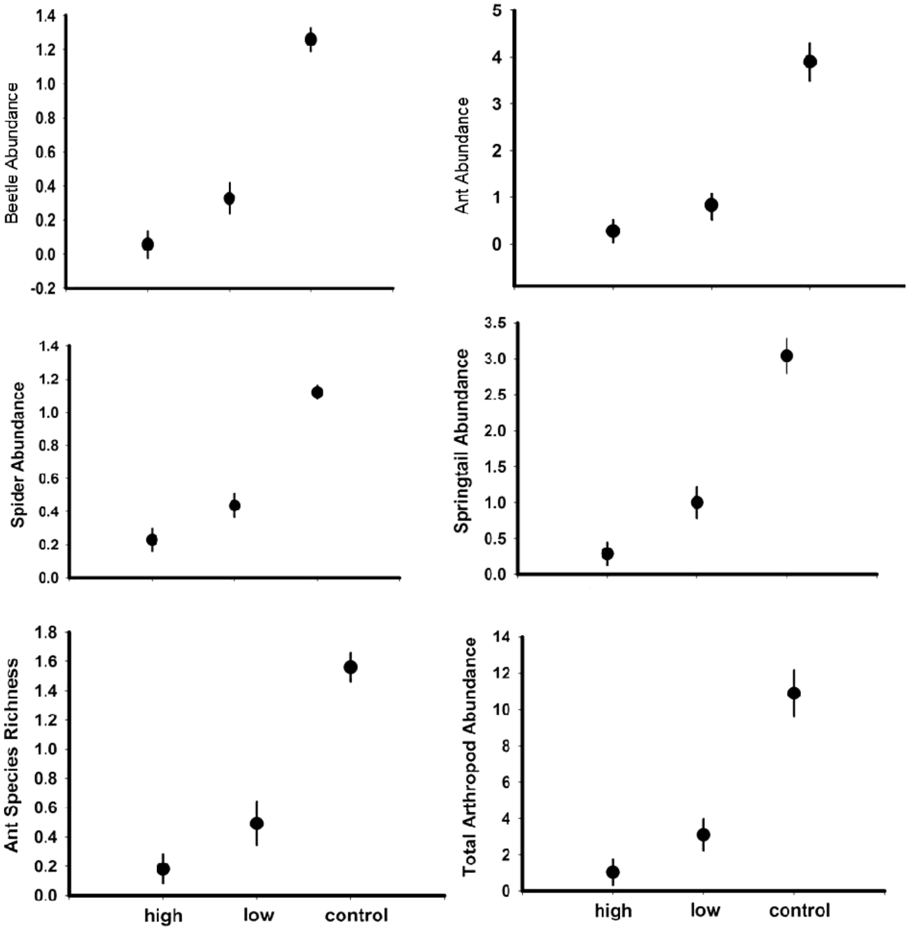

FIG. 1.—Least square mean (±SE) arthropod abundance (number of individuals per sample) and ant species richness (number of species per sample) among high, low, and unchanged (control) litter depths four weeks after prescribed fire in oak forests sampled by Berlese extraction. Within each plot, all means differ based on Tukey multiple comparison tests

Post fire leaf litter depth was low in all treatments but also differed significantly among them ($F_{2,833} = 1077$, $P < 0.0001$). Post fire leaf litter depth was not analyzed in control plots, since they were not burned. The abundance of ants, spiders, beetles, and springtails increased with leaf litter depth in all treatments ($F > 41.18$, $P < 0.0001$ for all tests); however, the relationships were generally weak (all $R^2 < 0.12$). Composite site and stand characteristics (tree species composition, DBH, char) were similar among sites (MANOVA; $F_{4,70} = 0.02$, $P = 0.90$; Table 1).

DISCUSSION

Here we show that prescribed fire alters litter arthropod community composition, abundance and species richness in Ozark oak forests over the short term. Specifically, fire

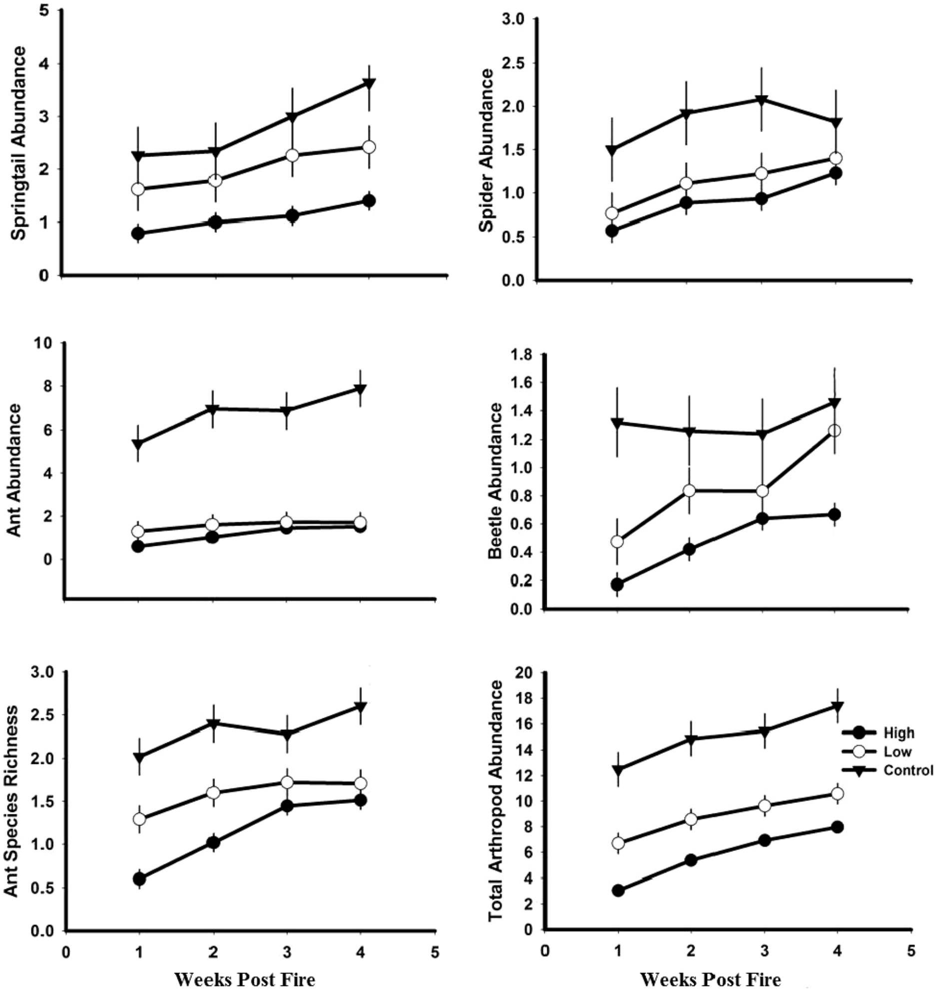

FIG. 2.—Least square mean (±SE) arthropod abundance (number of individuals per sample) and ant species richness (number of species per sample) among high, low, and unchanged (control) litter depths four weeks after prescribed fire in oak forests sampled by pitfall traps

dramatically reduced the abundance of common arthropod taxa and the species richness of ants relative to unburned sites. These effects appeared immediately after the burns and persisted as the communities began to recover over the subsequent 4 wk. This outcome is generally consistent with other studies that have explored the effects of fire on arthropod communities (*e.g.,* Ahlgren and Ahlgren, 1960; Greenberg and McGrane, 1996; Wikars and Schimmel, 2001; Santos *et al.*, 2008; Pryke and Samways, 2012; Verble and Yanoviak, 2013), although few such studies have specifically focused on short term effects or the potential role of variation in local fire intensity. In addition we observed seasonal increases in insect abundance in these forests, consistent with previous studies in the region (Verble and Yanoviak, 2013).

Results of this study reveal strong effects of differences in fire intensity on litter arthropod communities in the short term. Our field observations suggest that such differences arise from the ability of many litter dwelling taxa to escape low intensity fires by burrowing into the soil, seeking patches of high moisture, or occupying other refugia. Ozark forests have a long history of frequent low intensity burns, thus it is reasonable to expect that fire has shaped the composition and behavior of litter inhabitants, favoring taxa that can effectively avoid fire or rapidly recolonize burned sites. Related studies on this system showed minimal differences in ant species composition between burned and unburned areas over the short term (Verble and Yanoviak, 2013), and ants appear to be particularly adept at avoiding fire by moving deeper into soil (*e.g.,* Pryke and Samways, 2012). Our assessment of compositional differences was limited to ants, but responses to fire often are highly variable among taxa and functional groups (*e.g.,* Hanula and Wade, 2003), and more detailed studies of other diverse focal taxa (*e.g.,* beetles) may be more informative. In addition other studies have found that total arthropod abundance is a poor indicator of arthropod recovery (Lindberg *et al.*, 2002; Lindberg *et al.*, 2006); therefore, higher resolution taxonomy may better inform these questions, as responses may be guild or species specific. Likewise, we did not measure indirect effects of burning, such as post fire habitat conditions, which have important effects on faunal assemblages and recolonization patterns (Canon *et al.*, 1987; Petersen and Best, 1987; Russell *et al.*, 1999; Turner *et al.*, 1999).

The effects of fire on Ozark litter arthropods persist for >60 d (Verble and Yanoviak, 2013), which explains the lack of complete faunal recovery (*i.e.*, convergence of treatments with controls) over the short time frame of the current study. Although our expectation that short term community recovery rates would vary with local fire intensity was statistically supported, we did not observe dramatically faster recovery rates for low intensity burns relative to high intensity burns. Differences in patterns of recovery among focal taxa appear to reflect differences in their vagilities (*i.e.*, beetles are winged, whereas all other focal taxa are primarily cursorial).

Although leaf litter depth is a potentially important determinant of arthropod community structure (*e.g.,* Kaspari and Yanoviak, 2008), the lack of strong relationship between leaf litter depth and arthropod community parameters in this study is not surprising and is consistent with other studies (*e.g.,* Donoso *et al.*, 2010). Litter in Ozark forests is dominated by refractory detritus (tough oak leaves and pine needles) perched on rocky substrates. Thus, it does not tend to accumulate in thick layers that increase in density with depth. This relatively uncompressed litter structure is likely to have more conspicuous effects on the local abundance of macroarthropods (*e.g.,* spiders; Uetz, 1979) via the distribution of physical niches, than the abundance of microbivores and scavengers (*e.g.,* springtails and ants) which largely depend on local microbial processes (*e.g.,* Moore and Walter, 1988; Kaspari and Yanoviak, 2008; Donoso *et al.*, 2010). Moreover, we did not measure litter or soil moisture in this study and cannot account for their potentially confounding effects on litter quality or quantity.

Pitfall traps sample active epigeic insects (Woodcock, 2007) and are subject to behavioral bias (*i.e.*, species that are temporarily inactive are undersampled) and trap size constraints. Some differences in insect community structure observed in this study resulted not from the absence of species in the community, but their tendency to become inactive for prolonged periods after a fire. This was most evident in the very low activity of ants that persisted for weeks following a burn. Such low activity may be due to the toxicity of the surrounding environment (some types of ash are harmful or repellent to arthropods; Edwards and Schwartz, 1981). It is also possible the dietary needs of ants shift following a burn, such that tuna baits were unattractive in terms of nutrient composition. Further exploration of these patterns would be informative.

In conclusion here we show that arthropod abundance is reduced by prescribed burning in the short term and differences in fire intensity affect arthropod communities at the 1 m^2 scale. These results may help guide fire management practices in areas having rare or endemic invertebrate species. Mild fires account for a higher percentage of variation in insect composition than other forest management practices such as logging (Oliver *et al.*, 2000), suggesting that fires may exert strong selective pressure on forest dwelling insects. Future studies should examine other mechanisms by which faunal communities are shaped by fire disturbances, including habitat simplification, ash toxicity (Edwards and Schwartz, 1981) and decreased food availability.

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