



## Macroarthropod response to time-since-fire in the longleaf pine ecosystem



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### ABSTRACT

Fire is an important disturbance worldwide, and literature supports the use of prescribed fire to restore and maintain fire-dependent ecosystems. However, fire could alter the abundance and persistence of some arthropods, in turn influencing vertebrate taxa that depend on those arthropods as a food source. We used replicated prescribed fire treatments to evaluate macroarthropod response to time-since-fire in the fire-maintained longleaf pine (*Pinus palustris*) ecosystem. We sampled macroarthropod assemblages using vinyl gutter pitfall traps for 5 consecutive days in each month of the study (May–August 2014) in each replicate burn block. We identified macroarthropods to Order and dried and weighed the samples to determine biomass (g) of all taxa detected. We focused our analyses on 4 macroarthropod taxa important as food for wild turkey (*Meleagris gallopavo*): Araneae, Coleoptera, Hymenoptera, and Orthoptera. We used standard least squares regression to evaluate the effect of time-since-fire on total biomass of the 4 Orders (and we also evaluated those Orders independently). The analysis indicated that time-since-fire had no effect ( $p = 0.2616$ ) on combined biomass of these 4 taxa. Analyzing the 4 Orders separately, biomass of Araneae ( $p = 0.0057$ ) and Orthoptera ( $p = 0.0004$ ) showed significant effects of time-since-fire, while Coleoptera ( $p = 0.9465$ ) and Hymenoptera ( $p = 0.1175$ ) did not. Parameter estimates (Araneae = 0.0084; SE = 0.0029; Orthoptera = 0.0137; SE = 0.0036) indicated that greater time-since-fire resulted in greater biomass for those 2 Orders. Overall, time-since-fire did not appear to have substantial effects on macroarthropod biomass. However, responses by Araneae and Orthoptera provided evidence that longer time-since-fire may result in greatest levels of biomass for some taxa. Our results indicate the use of frequent prescribed fire to restore and maintain longleaf forests is unlikely to pose risks to overall macroarthropod biomass, particularly if heterogeneity in fire frequency and spatial extent occurs on the landscape.

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### 1. Introduction

Globally, fire is an important disturbance in many systems (Bowman et al., 2009), and literature supports the use of prescribed fire to restore and maintain fire-dependent ecosystems (Lashley et al., 2014b). Prescribed fire is used in the longleaf pine (*Pinus*

*palustris*) ecosystem (LLPE) for restoration and maintenance of plant communities and fire-dependent fauna (Aschenbach et al., 2010; Beckage et al., 2005; Fill et al., 2012; Van Lear et al., 2005). It is well-documented that endangered red-cockaded woodpeckers (*Picoides borealis*) and Bachman's sparrow (*Aimophila aestivalis*; a species of management concern) respond favorably to frequent growing-season fire regimes that maintain needed structural requirements (Cantrell et al., 1995; Tucker et al., 2004). Similarly, important game species' responses to prescribed fire effects are well-understood (e.g., white-tailed deer [*Odocoileus virginianus*] space use [Lashley et al., 2015], wild turkey [*Meleagris gallopavo*] brooding cover [McCord et al., 2014]). However, little focus has been given to arthropod responses to fire in this ecosystem even

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though many young vertebrates, especially gamebirds (Healy, 1985; Hill, 1985; Palmer et al., 2001; Park et al., 2001) and songbirds (Duguay et al., 2000), forage on arthropods in the understory.

Whether in soils (Paoletti et al., 1991), streams (Cain et al., 1992), forests (Iglay et al., 2012; Pearce and Venier, 2006), or rangelands (Hoffmann, 2010), invertebrates have proven useful for understanding bottom-up trophic interactions (Loreau et al., 2001). Because most land birds, many mammals, and herpetofauna use invertebrates for food (Greenberg, 1995), invertebrates are suitable study organisms for evaluating management practices at local or landscape-scale (Arribas et al., 2012). Despite relatively few documented instances of extirpations, concerns about localized population extinctions (i.e., extirpation without natural recolonization) of arthropod species following fire are widespread (Swengel, 2001). Thus, more research is needed to elucidate invertebrate responses to prescribed fire, particularly in forested systems managed for vertebrate species of conservation or management concern.

Given the necessity for, and interest in, managing fire-maintained, open forest systems with prescribed fire (e.g., Lashley et al., 2014b), our goal was to contribute to the growing literature on invertebrate responses to fire. Swengel (2001) reviewed insect responses to fire in the context of managing open vegetation communities, but less is known about how time-since-fire affects invertebrates. Thus, we addressed this need by quantifying macroarthropod response to time-since-fire at Fort Bragg Military Installation, North Carolina, USA. Because restoration and management of the LLPE depends on mimicking historically frequent growing-season fire, understanding effects of the fire-return interval are needed. Knowledge of macroarthropod responses to prescribed fire may lead to better habitat management for those vertebrates that depend on them as food sources (Grodsky et al., 2015), particularly in systems where frequent growing-season fires are common. We sampled for macroarthropods and reported counts and biomass (g) of all taxa by treatment. We focused our analyses on 4 Orders (Araneae, Coleoptera, Hymenoptera, and Orthoptera) that are important foods of wild turkey (Hurst and Stringer, 1975; Healy, 1985; Iglay et al., 2005; McCord et al., 2014) and comprised the majority of the biomass in the study. We hypothesized that greater time-since-fire would correspond to greater available biomass of the 4 Orders.

## 2. Material and methods

### 2.1. Study area

We conducted our study at Fort Bragg Military Installation (Fort Bragg), which was owned by the U.S. Department of Defense and located in the Sandhills physiographic region of central North Carolina. Fort Bragg comprised 73,469 ha in the LLPE, and uplands were dominated by longleaf pine forests and managed with growing-season prescribed fire on a 3-yr fire-return interval (Lashley et al., 2014b). Fort Bragg defined growing-season as April–September and dormant-season as October–March. During our study, burn blocks averaged 43 ha (Lashley et al., 2015). Burn blocks missed during their targeted growing-season were burned in the following dormant season (usually December–March), which resulted in a small area of Fort Bragg (~15% during the study period) being burned greater than 3 years prior and during the dormant season (Lashley et al., 2015). Drainages were dominated by blackgum (*Nyssa sylvatica*), with a densely vegetated understory stratum composed primarily of *Lyonia* spp. and *Ilex* spp.; drainages burned infrequently because of moist conditions (Lashley et al., 2015).

### 2.2. Prescribed fire treatments

In 2013 and 2014, we applied 4 prescribed fire treatments to 12 burn blocks (i.e., 3 replicates in each treatment) with known burn history and similar overstory and understory structure (Fort Bragg Forestry Branch). The 4 treatments were: (1) 1yrG: previous growing-season fire (i.e., replicates burned growing-season 2013); (2) 0yrD: previous dormant-season fire (i.e., replicates burned dormant-season 2013–2014); (3) 0yrEarlyG: same year early growing-season fire (i.e., replicates burned April 2014); and 4) 0yrG: same year growing-season fire (i.e., replicates burned June–July 2014). The 3 blocks selected for “previous dormant-season fire” (Treatment 2) had been burned every year in December–February since 1985; these blocks were burned annually, but not during the growing season, due to proximity to anthropogenic structures. The 9 blocks selected for the 3 treatments associated with previous or same-year growing-season fire were burned every 3 years since Fort Bragg initiated the growing-season fire regime in 1989; all 9 blocks had at least 4 consecutive rotations where fires were set in May–June. For each replicate block, we calculated time-since-fire in months (range: 0–24), relative to macroarthropod sampling (all of which was conducted in 2014; see next section) and the month the block was burned during its treatment window (or in previous years). For example, if a replicate block from the 1yrG treatment was originally burned in May 2013, then time-since-fire at the May 2014 macroarthropod sampling would be 12 months and at the June 2014 sampling it would be 13 months. Similarly, if a replicate block from the 0yrG treatment was originally burned in May 2012, then time-since-fire at the May 2014 macroarthropod sampling would be 24 months; however, when the “same-year” burn occurred in June 2014 for this treatment, then time-since-fire at the June 2014 sampling would be 0 months and at the July 2014 sampling it would be 1 month.

### 2.3. Macroarthropod sampling

We sampled macroarthropod assemblages using gutter pitfall traps for 5 consecutive days in each month of the study (May–August 2014) in each replicate burn block (see previous section). We chose gutter traps (Pausch et al., 1979) over conventional circular pitfalls because of increased sampling area (length), which should improve resolution. Additionally, suction sampling can introduce bias by damaging invertebrate samples (Iglay et al., 2005). We randomly assigned the gutter locations; however, to avoid potential bias associated with edge effects or military traffic, we constrained the random points to be  $\geq 50$  m from firebreaks (i.e., the edge of the burn block). At each point, we buried 2 10-ft vinyl gutters (fitted with watertight end caps) flush with the ground, leveled them, and replaced the disturbed litter layer to avoid biasing the captures. We buried the gutters 10–30 m apart, with 1 oriented north-south and the other oriented east-west. We filled the gutters approximately half-full with water and added several drops of dishwashing detergent to break surface tension. We checked traps daily to make sure water levels did not get too low from evaporation or too high following rain events. We left gutters open day and night from the time of deployment until sampling was complete 5 days later. We acknowledge that pitfall trap features influence their efficiency at capturing arthropods (Luff, 1975) and that our use of gutter traps is biased toward mobile, ground-dwelling macroarthropods. We acknowledge that a single method cannot sample all taxa important to the diet of birds or other vertebrates; however, gutter traps effectively capture taxa available to ground-foraging species like wild turkey and allow for standardized comparisons among treatments.

We used tweezers to collect all invertebrates until only small individuals remained. We removed small individuals using a tea strainer. We stored all samples in 70% ethanol until identification, at which time we separated specimens by Class and identified most to Order, acquiring a count of individuals by taxonomic groups of interest. After sorting and identification, we dried samples at 47 °C in plastic weighing boats in a stand-alone cabinet drying oven with continuous venting (commonly used to dry forage samples to avoid thermal decomposition; Lashley et al., 2014a). We weighed samples to the nearest 0.0001 g every 6–12 h until we achieved constant weight and used the dry weight of each taxonomic group per gutter as an estimate of biomass.

#### 2.4. Data analysis

Because our focus was on quantifying macroarthropod response to time-since-fire using taxa that were important foods of wild turkeys, we focused the statistical analysis on biomass (i.e., biomass was the response variable) of 4 Orders (Araneae, Coleoptera, Hymenoptera, and Orthoptera) that comprised the majority of biomass sampled in our study. First, we used standard least squares regression in JMP Pro 10 (SAS Institute Inc., Cary, North Carolina) to evaluate the effect of time-since-fire on total macroarthropod biomass (using all 4 Orders combined). We chose least squares regression because we expected the relationship between time-since-fire and macroarthropod biomass to be fairly linear, particularly over the short time scales evaluated in our study. For this analysis, we determined the total biomass for each Order by calculating the average biomass (i.e., average of 2 gutter traps) from each replicate burn block. Second, we performed the same analysis on each Order independently to determine if time-since-fire affected some taxa but not others. In all analyses, we determined the variance explained by time-since-fire when month of sampling was held constant in the models. For all analyses we used  $\alpha = 0.05$ .

### 3. Results

We detected 6 Classes of invertebrates (Arachnida, Chilopoda, Diplopoda, Entognatha, Gastropoda, and Insecta) and identified 22 Orders within Classes Arachnida, Chilopoda, Entognatha, and Insecta (Table 1). We did not identify to Order the few individuals detected from Classes Diplopoda and Gastropoda. Of the 24 taxonomic groups we detected in the study, 13 were in all 4 prescribed fire treatments (Table 1). The 13 taxonomic groups detected across all treatments comprised 10 Orders of Insecta, 2 of Arachnida, and 1 of Entognatha; in most cases, these Orders were the most prolific numerically (i.e., count of individuals) and in biomass (Table 1). Most Arachnids ( $\geq 95\%$ ) were from Order Araneae (i.e., spiders), so biomass was greater for Araneae than Trombidiformes (i.e., mites; Table 1). Coleoptera and Hymenoptera (primarily ants [Order Formicidae]) dominated the biomass of insect samples, though Diptera exceeded Coleoptera in count of individuals (Table 1). Collembola (Class Entognatha) was present at every sampling site across all treatments, but we excluded this Class from count and biomass measurements and analyses because of their small size and resultant low biomass.

The standard least squares regression model including all 4 Orders of interest indicated that time-since-fire had no effect ( $p = 0.2616$ ) on combined biomass of these taxa. Analyzing the Orders separately, biomass of Araneae ( $p = 0.0057$ ) and Orthoptera ( $p = 0.0004$ ) showed significant effects of time-since-fire, while Coleoptera ( $p = 0.9465$ ) and Hymenoptera ( $p = 0.1175$ ) did not. Parameter estimates (Araneae = 0.0084; SE = 0.0029; Orthoptera = 0.0137; SE = 0.0036) indicated that greater time-since-fire resulted in greater biomass for those 2 Orders. Indeed, greatest bio-

mass for Araneae and Orthoptera occurred during May sampling (the earliest sampling period) of the OyrG treatment, which meant time-since-fire was at its greatest (Figs. 1 and 2, respectively). Peaks in biomass for these 2 taxa were followed by lower levels post-fire.

### 4. Discussion

Time-since-fire had substantial short-term effects on the availability of 2 of the 4 taxa that dominated the macroarthropod biomass in the LLPE. Indeed, responses by Araneae and Orthoptera provided evidence that longer time-since-fire may result in greatest levels of biomass for some taxa. In longleaf pine forests, frequent fire-return intervals (i.e.,  $\leq 3$ -yr) commonly are recommended to restore and maintain ecosystem function (Fill et al., 2012; Glitzenstein et al., 2003). Thus, our study design was a reasonable approximation of the range of time-since-fire in management plans relying on the frequent application of fire (i.e., time-since-fire could vary between 0 and 24 months for any particular burn unit in our study). Our results indicate the use of frequent prescribed fire to restore and maintain longleaf forests could reduce available biomass of some macroarthropods, at least along the short-term spatiotemporal scales that we measured. However, when considering overall biomass of the 4 Orders combined, we did not detect an effect of time-since-fire. This result is consistent with conclusions reached by Greenberg et al. (2010), who determined that prescribed fire and mechanical fuel reduction treatments (conducted in winter or early spring) had little short-term effects on community composition, relative abundance, or biomass of total arthropods in southern Appalachian upland hardwood forests.

Our results indicate that Araneae, Orthoptera, Hymenoptera (particularly ants), and Coleoptera comprise a notable portion of biomass available for consumption by wild turkeys in the fire-maintained LLPE. Indeed, all 4 Orders are important taxa for wild turkey diet (McCord et al., 2014). Wild turkey poults require a diet of 28% crude protein (Marsden and Martin, 1955), which largely can be achieved through consumption of invertebrates. Research with other avian species has indicated that arthropod abundance was not a proximate factor in determining bird selection of habitat (Champlin et al., 2009). However, it is possible that certain phases of the turkey life cycle could be limited by food resources and that increasing frequency of fire in the longleaf pine ecosystem could shift those effects. Coleopterans have been studied more extensively regarding their response to fire and other management practices (Greenberg and Thomas, 1995; Gandhi et al., 2001; Cobb et al., 2007; Ulyshen et al., 2010; Iglay et al., 2012), but given the effects of fire that we detected for Araneae and Orthoptera, our results demonstrate that other taxa warrant attention as well. When considering changes to the fire-return interval in the LLPE, understanding taxa-specific responses to time-since-fire should help managers avoid unintended effects on available macroarthropod biomass for species like wild turkeys.

The timing of fire during the growing season, rather than time-since-fire, could have implications on availability of invertebrates as a food source. Fire can cause a short-term flush of insect carcasses, followed by a great reduction in food availability for insectivorous vertebrates (Daubenmire, 1968). Further, fire timing could kill eggs or larvae of some taxa, helping to drive responses that might otherwise be attributed to time-since-fire. Invertebrate declines can continue for some time post-fire, likely because mortality may occur not only during the fire but due to a 'shock phase' after the fire (i.e., from exposure and starvation; [Rice, 1932; Warren et al., 1987]). In our study, the responses of Araneae and Orthoptera were consistent with this premise. Without a solid

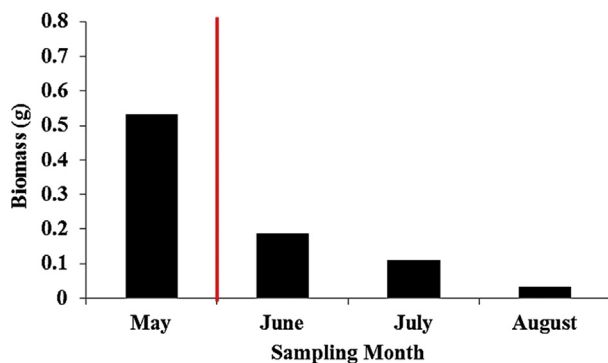
**Table 1**

Mean (and standard deviation) of count and biomass (grams) for arthropod taxonomic groups detected in each gutter pitfall trap deployed in 4 prescribed fire treatments at Fort Bragg Military Installation, North Carolina, May–August 2014. The 4 treatments were: (1) 1 yrG: previous growing-season fire; (2) 0yrD: previous dormant-season fire; (3) 0yrEarlyG: same year early growing-season fire; and (4) 0 yrG: same year growing-season fire. Biomass denoted as TL was too light to weigh or had a mean weight below 0.001 g.

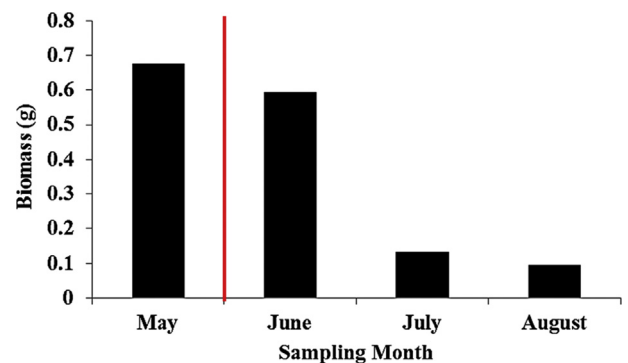
Taxa	Treatments							
	1yrG		0yrD		0yrEarlyG		0yrG	
	Count	Biomass	Count	Biomass	Count	Biomass	Count	Biomass
Araneae	24.6 (15.8)	0.149 (0.148)	20.6 (16.9)	0.102 (0.100)	21.9 (13.1)	0.155 (0.246)	26.4 (21.4)	0.207 (0.234)
Blattodea	3.0 (6.8)	0.048 (0.103)	2.3 (3.7)	0.050 (0.074)	1.0 (1.3)	0.020 (0.041)	5.3 (8.6)	0.079 (0.120)
Coleoptera	14.8 (12.2)	0.770 (0.815)	18.3 (18.9)	0.705 (0.772)	19.3 (13.2)	0.780 (0.638)	22.9 (16.9)	0.722 (0.597)
Collembola <sup>a</sup>	Detected	TL	Detected	TL	Detected	TL	Detected	TL
Diplopoda	0	0	0	0	0	0	0.04 (0.2) <sup>b</sup>	TL
Diptera	23.4 (24.6)	0.150 (0.123)	32.3 (22.9)	0.064 (0.078)	23.7 (19.0)	0.088 (0.099)	29.8 (35.7)	0.088 (0.119)
Gastropoda	0	0	0	0	0.04 (0.2) <sup>b</sup>	0.001 (0.006)	0.04 (0.2) <sup>b</sup>	0.001 (0.005)
Geophilomorpha	0.1 (0.4)	TL	0.1 (0.3)	TL	0	0	0.1 (0.4)	TL
Hemiptera	3.8 (5.0)	0.006 (0.011)	2.5 (3.2)	0.004 (0.013)	6.6 (6.3)	0.012 (0.017)	5.5 (8.0)	0.011 (0.019)
Hymenoptera	134.7 (91.9)	0.215 (0.126)	213.2 (254.1)	0.161 (0.153)	225.5 (198.9)	0.302 (0.313)	244.2 (280.1)	0.266 (0.167)
Isoptera	0.2 (0.6)	TL	1.8 (4.0)	TL	0.5 (1.7)	TL	0.8 (1.8)	TL
Lepidoptera	0.6 (1.0)	0.032 (0.074)	0.8 (1.0)	0.019 (0.035)	1.0 (1.6)	0.021 (0.043)	0.8 (1.2)	0.033 (0.080)
Mantodea	0	0	0	0	0	0	0.1 (0.3)	TL
Neuroptera	0.2 (0.7)	TL	0	0	0.2 (0.7)	TL	0.1 (0.4)	TL
Odonata	0.5 (0.7)	0.003 (0.005)	0.3 (0.7)	0.001 (0.003)	0.1 (0.3)	0.001 (0.003)	0.1 (0.3)	0.001 (0.003)
Opiliones	0	0	0.1 (0.4)	0.002 (0.009)	0.1 (0.4)	0.008 (0.029)	0.3 (0.9)	0.003 (0.006)
Orthoptera	7.1 (3.8)	0.197 (0.228)	9.8 (12.0)	0.186 (0.177)	9.2 (5.7)	0.206 (0.183)	9.8 (6.0)	0.368 (0.347)
Parasitiformes	0	0	0	0	0.04 (0.2)	TL	0	0
Pseudoscorpionida	0.04 (0.2) <sup>b</sup>	TL	0.2 (0.7)	TL	0	0	0.1 (0.3)	TL
Scolopendromorpha	0	0	0.4 (1.1)	0.013 (0.039)	0.1 (0.4)	0.001 (0.003)	0.1 (0.4)	0.006 (0.027)
Thysanoptera	0	0	0	0	0.1 (0.3)	TL	0.2 (0.6)	TL
Thysanura	0.1 (0.3)	TL	0.04 (0.2) <sup>b</sup>	TL	0	0	0.04 (0.2) <sup>b</sup>	TL
Trichoptera	0.04 (0.2) <sup>b</sup>	TL	0.3 (0.6)	0.001 (0.002)	0.1 (0.3)	TL	0.3 (0.8)	TL
Trombidiformes	3.1 (5.9)	TL	3.8 (5.1)	TL	0.7 (2.0)	TL	2.3 (3.9)	TL

<sup>a</sup> Collembola was detected in all gutter pitfall traps, but we did not attempt to weigh given small size.

<sup>b</sup> Only 1 individual detected.



**Fig. 1.** Araneae biomass (g) response to fire in the 0-yr growing-season treatment. During May sampling, it had been 24 months-since-fire. The vertical line corresponds to the timing of the fire in our study, which means August represents 2 months-since-fire.



**Fig. 2.** Orthoptera biomass (g) response to fire in the 0-yr growing-season treatment. During May sampling, it had been 24 months-since-fire. The vertical line corresponds to the timing of the fire in our study, which means August represents 2 months-since-fire.

understanding of how forest management practices (e.g., prescribed fire) affect some macroarthropod taxa, managers could cause unintended changes. However, heterogeneity in fire season, timing, frequency, intensity, and spatial distribution likely will support the greatest variety and biomass of macroarthropods at the landscape scale, which translates to more food for insectivorous vertebrates.

Araneae and Orthoptera maintained their greatest levels of biomass at the longest time-since-fire we studied, potentially suggesting that some macroarthropod taxa are negatively affected immediately following fire. Fire could cause direct mortality of eggs, larvae, or adults, or fire could change cover conditions, making it unfavorable for some taxa. For example, fire reduces leaf litter depth and therefore cover, which could reduce abundance and available biomass of spiders and other invertebrates, at least until leaf fall restores the litter layer (Savage et al., 2010). Additionally,

Gandhi et al. (2001) demonstrated that conservation of unburned areas in managed forests is important for refugia and landscape continuity for forest dwelling Coleopterans. Ground beetle response to wildfire and forestry-related disturbances can differ at the level of species, with some benefitting from what is detrimental to others (Cobb et al., 2007). Also, Andersen (1991) documented that many species of ant were common under one fire regime but rarely or never detected under others, demonstrating that different fire regimes could have major influences on one of the most important faunal groups in their study system (i.e., tropical savannas). Andersen (1991) attributed these differences to structural changes in habitat caused by fire, particularly levels of litter accumulation, which could have effects on availability of an important vertebrate food source. By contrast, forest insects can have inter-taxonomic differences in adult activity patterns (Greenberg and Thomas, 1995; Greenberg and McGrane, 1996).



Thus, trends we detected in biomass that we ascribed to fire-effects could be confounded with temporal differences in activity of some taxa.

Araneae and Orthoptera responded negatively to fire, though the responses did not suggest that fire was eliminating their populations at the shortest time-since-fire frequencies. As hypothesized, biomass was greater when time-since-fire was greater, which could have been due to direct mortality from fire (in eggs, larvae, or adults), movement away from the fire, or from changes in cover conditions post-fire. Though biomass of Araneae and Orthoptera declined in the month immediately post-fire in our study, it continued to decline over the following two months of sampling, potentially indicating a longer-term effect than direct mortality from the fire itself. Radford and Andersen (2012) documented that Orthoptera was the only taxonomic group in their savannah system that did not decline immediately post-fire. In our study, the consistent decline of Araneae and Orthoptera following fire could indicate high levels of direct mortality from fire followed by increased susceptibility to predation due to lack of cover, either of which could be combined with a need for longer recovery time via recolonizing individuals from adjacent unburned areas. Additionally, Orthopteran declines could be related to loss of herbaceous forage. It seems likely that managing for a variety of cover conditions, including fire excluded areas (Gandhi et al., 2001; Hanula and Wade, 2003) or areas that contain remnant long-lived vegetation (VanTassel et al., 2015), provides the best opportunity for maintaining diversity and biomass of arthropod taxa. However, the reason(s) that Coleoptera and Hymenoptera did not demonstrate significant changes in biomass relative to time-since-fire is unknown. We speculate that life history strategies, dispersal and re-colonization rates, and variation in the availability of refugia or unburned areas could play a confounding role in measurable responses to fire for some macroarthropod taxa.

We concur with Greenberg and Forrest (2003), who suggested that questions remain about whether or not observed reductions in macroarthropod biomass or abundance following fire (or other management practices) could potentially cause adverse effects on vertebrate predators and at what scale(s) those effects become a conservation issue. Recovery of arthropods following fire is still poorly understood, and studies are needed to quantify how their recovery could affect vertebrate predators. For example, a limitation of many studies is that when biomass “recovers” following fire, we do not know if this is because of changes in species composition within the arthropod group or just simple abundance of that arthropod group as a whole. This fact may help explain why different studies of the same arthropod group report conflicting results (Swengel, 2001). A study of native bees in the LLPE documented that abundance and species richness were greater in sites burned the same year of sampling and one year post-fire than in the control sites; however, diversity was similar between burned and unburned sites (Moylett, 2014). Moreover, the size of the burn may influence the rate and extent of arthropod immigration from adjacent unburned areas, particularly during the shock and recovery phases (Whelan and Main, 1979). Finally, the frequency of fire surely affects the level of recovery, such that recovery baselines are linked to fire-return interval.

## 5. Conclusions

Arthropods are an important food source for an array of vertebrate taxa of conservation or management concern in the LLPE. From a coarse perspective, frequent prescribed fire does not appear to cause negative effects on the biomass of macroarthropods. However, if certain macroarthropod Families or Genera are important food sources, future research could focus on the recovery level of

those taxa following fire, which is still poorly understood. Long-term effects of frequent fire could result in declines in the recovery level of important macroarthropod taxa. For example, if Fort Bragg increased fire frequency to every year, the “recovered” level of Araneae and Orthoptera following fire likely would be lower than levels we report from 2 years post-fire. Over longer time periods, fire-related suppression of “recovered” levels of macroarthropod taxa could negatively influence food availability for vertebrates. Nevertheless, current fire regimes in the LLPE that incorporate time-since-fire of 24 months or less are unlikely to eliminate important macroarthropod Orders. Heterogeneity in fire frequency and spatial extent likely provides a buffer against short-term negative effects of fire on macroarthropod communities, which should allow persistence of an important vertebrate food source in fire-maintained systems.

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