Prescribed fire and other fuel-reduction treatments alter ground spider assemblages in a Southern Appalachian hardwood forest

Joshua W. Campbell [a,*], Steven M. Grodsky [b], Marc A. Milne [c], Patrick Vigueira [d], Cynthia C. Vigueira [d], Emily Stern [c], Cathryn H. Greenberg [e]

[a] USDA Agricultural Research Service, Northern Plains Agricultural Research Laboratory, 1500 North Central Ave., Sidney, MT 59270, United States
[b] U.S. Geological Survey, New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources and the Environment, Cornell University, Ithaca, NY 14853, United States
[c] University of Indianapolis, Shaheen College of Arts and Sciences, Department of Biology, 1400 East Hanna Ave., Indianapolis, IN 46227, United States
[d] High Point University, Biology Dept., One University Parkway, High Point, NC 27268, United States
[e] USDA Forest Service, Southern Research Station, 1577 Brevard Road, Asheville, NC 28806, United States

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ABSTRACT

Prescribed burns and understory thinnings are forest management practices aimed at reducing fuel loads to lessen wildfire threat in the Southern Appalachians, USA. Spiders play a critical role in forest ecosystems by controlling insect populations and providing an important food source for vertebrates. We used pitfall and colored pan traps to investigate how abundance, species richness, and diversity of spiders differed among three fuel reduction treatments administered repeatedly over a 15-year period and untreated controls. Additionally, we examined how spiders responded to one round (before and after) of fuel reduction treatments. We established treatments within the 15-year period as follows: mechanical understory removal (twice; M), prescribed burning (four times; B), mechanical understory removal followed one year later by high-severity prescribed burns and three subsequent burns (MB), and untreated controls (C). Our study period (2014–2016) occurred after multiple prescribed burns and two rounds of mechanical understory removal had occurred. Salticidae and Lycosidae were the two most commonly collected spider families in Southern Appalachian hardwood forests. Generally, we found increased spider abundances within all fuel-reduction treatments compared to controls. Individual spider families and species showed variable responses to treatments, but abundance of several spider families was greater in one or more fuel-reduction treatments than in controls. Additionally, abundance of several spider families and hunting/web building guilds (webs built for hunting purposes or defense) exhibited yearly differences to the last round of fuel-reduction treatments. Overall, our results suggest that changes in the overstory and understory of a forest are important drivers of regional spider abundance and assemblages, and forest management practices that modify forest structure can dramatically alter spider abundance and richness, usually in a positive manner.

1. Introduction

Natural (e.g., wildfires, pest and disease outbreaks, storms) and anthropogenic (e.g., prescribed burns) disturbances cause forest ecosystems to be dynamic. Severe disturbances that result in high tree mortality can result in a cascade of successional stages to occur, that given enough time, eventually result back to a closed canopy (Hilmers et al., 2018). Forest disturbances have often been associated with increased resource heterogeneity resulting in higher biodiversity but this often depends on the severity and type of disturbance (Michalko

et al., 2021a). Disturbances like fire can alter ecological processes and determine distributions of organisms. Indeed, prescribed burns have been utilized as an important tool in management of forests and grasslands (Mitchell et al., 2006, Valkó et al., 2014, Hamřík and Košulič, 2021). Small-scale/low intensity prescribed burns or other disturbances may promote biodiversity via intermediate disturbance (IDH) and patch mosaic burn (PMBH) hypotheses (Pastro et al., 2011). The IDH predicts that moderate disturbances will enhance and maintain biodiversity due to landscape and resource heterogeneity that are created, whereas the PMBH predicts a mixture of successional habitats after a burn will exist,

thus creating habitat for a multitude of species (Brockett et al. 2001).

Historically, fire was frequently used throughout the Southern Appalachians by Native Americans to achieve various goals, including clearing forests for agriculture and improved visibility for better defense, travel, and hunting (Williams, 1989). Euro-American settlers later continued to use fire to convert forests for improved livestock forage and for growing row crops. Ultimately, fire suppression policies and changing cultural practices greatly reduced burning in the Southern Appalachians starting in the late 1800s (Arthur et al., 2021, Fowler and Konopik, 2007, Yarnell, 1998). Today, the goal of fuel reduction techniques, including prescribed fire, is to limit understory fuel buildup to minimize wildfire risk (McIver et al., 2013) and to maintain wildlife habitat for hunting purposes and conserve biodiversity (Lashley et al., 2011). However, in many areas of the Southern Appalachians, increasing human populations (e.g., Weaver and Barrett, 2018) and an expanding wildland-urban interface present new challenges to burning, prompting forest managers to seek alternative fuel-reduction methods. Several studies have attempted to elucidate potential effects of forest management practices on vertebrate food chains and arthropods as bioindicators for forest health. In the Southern Appalachians, invertebrates, including pollinators, beetles, ants, and overall invertebrate communities have been examined following various forest management practices (Greenberg et al., 2010, Campbell et al., 2018a, Campbell et al., 2018b, Campbell et al., 2019a). The aforementioned studies found variable trends for different arthropod groups among fuel reduction treatments, which were largely taxa dependent. Thus, how other taxa (e. g., spiders) respond to these fuel reduction treatments is unknown.

Distributions and relative abundance of spiders (Araneae) and other animals in forested habitats can be influenced by heterogeneity occurring locally and across landscapes. Vegetation structure can affect spider community composition due to different requirements of species related to foraging strategies and web designs (Gunnarsson, 1990, Gómez et al., 2016). Similarly, increased shrub density and diversity can result in increased number of spider species and guilds present (Hatley and MacMahon, 1980). However, most spiders are predominantly predators, and thus most spiders should be indifferent to the actual species of plants, with some exceptions. Thus, overall vegetation structure can influence the structure of spider assemblages in forested habitats (Pajunen et al., 1995). However, we do caution that numerous spiders have been documented to supplement their diet with various plant products (e.g., nectar, pollen, sap, etc.) and, thus, some spiders may be attracted to certain plants over others (Nyffeler et al. 2016). Forest management practices can create changes in canopy cover, understory vegetation, abundance of flowering plants, and leaf-litter cover and depth, potentially altering forest spider communities directly or indirectly by changing the abundance and composition of their invertebrate prey (Grodsky et al., 2016).

Invertebrates are useful bioindicators of ecosystem response to disturbance (Grodsky et al., 2015), and spiders have been used as bioindicators for air quality (Horváth et al., 2001), impacts of livestock grazing (Gibson et al., 1992), agricultural practices (Campbell et al., 2019b), and various forest management practices (Pearce and Venier, 2006, Maleque et al., 2009). Additionally, reforestation practices (after deforestation and silviculture harvest) have used spiders as a proxy to determine how successful the practices are in restoring biodiversity (Košulič et al., 2021, Michalko et al., 2021b). We compared spider abundance, richness, and diversity among three, repeated fuel reduction treatments and untreated controls in a Southern Appalachian forest. We hypothesized that spider abundance, richness, and diversity would differ among fuel reduction treatments and the controls due to altered vegetation structure/density, and that these changes would differ among spider taxa in relation to their hunting strategies (e.g., coursing hunters versus web builders).

2. Materials and methods

2.1. Study site and design

Our study was conducted on the 5841-ha Green River Game Land [(35° 17′0900 N, 82° 19′42″W), blocks 1 and 2; (35°15′42″N, 82° 17′27″W), block 3] in Polk County, North Carolina and was part of the National Fire and Fire Surrogate study (McIvor et al., 2013) (Fig. 1). The Green River Game Land is in the mountainous Blue Ridge Physiographic Province of western North Carolina and is managed by the North Carolina Wildlife Resources Commission to promote conservation and wise use of the state's natural resources. Average annual precipitation is 164 cm and is distributed evenly throughout the year; average annual temperature is 17.6 °C (Keenan, 1998). Soils were primarily of the Evard series (fine-loamy, oxidic, mesic, Typic Hapludults), which are very deep (>1 m) and well-drained in mountain uplands (USDA Natural Resources Conservation Service, 1998). Elevation ranged from approximately 366–793 m. Oaks (*Quercus* spp.) and hickories (*Carya* spp.) are the dominant trees of the upland hardwood forest. Shortleaf pine (*Pinus echinata*) and Virginia pine (*P. virginiana*) occurred on ridgetops, and white pine (*P. strobus*) occurred in moist coves. Forest age within experimental units ranged from about 85–125 years old. Mountain laurel (*Kalmia latifolia*) found along ridge tops and on upper southwest-facing slopes and rhododendron (*Rhododendron maximum*) found in mesic areas were the predominant shrubs. Prior to our first prescribed burns in 2003, none of the sites had been thinned or burned (Greenberg et al., 2018).

Our experimental design was a randomized block design that contained three study areas (blocks) within the Green River Game Land. We randomly assigned three fuel-reduction treatments and an untreated control (C) within each of the three study blocks for a total of 12 experimental units (minimum 14 ha each). We established treatments as follows: (1) repeated mechanical felling of all shrubs and small trees ≥ 1.4 m tall and < 10.0 cm diameter at breast height (dbh) with a chainsaw with cut fuels left scattered onsite (M); (2) repeated dormant season prescribed burns (B); and (3) initial mechanical understory reduction, followed by four dormant season prescribed burns (MB). See Table 1 for application times and years for all treatments. The high intensity of the initial burn in MB killed many trees and dramatically altered forest structure in our field sites (Greenberg et al., 2018). By 2014 (when our study was established), 72% of trees in MB were dead, and canopy cover was greatly reduced compared to other treatments (Greenberg et al., 2018). Shrub-sized stem density also was much higher in MB (3–10 times higher compared to the other treatments) due to stump sprouting and growth of blackberry (*Rubus* spp.) and other shrubs. Leaf litter depth was reduced in B and MB after each burn but was rapidly replenished by leaves falling from deciduous trees each autumn (Greenberg et al., 2018). See Greenberg et al. (2018) for means of live tree density, canopy openness, shrub stem density, and leaf litter depth found within our study plots. Our study period (2014–2016) occurred after multiple prescribed burns and two rounds of mechanical understory removal had occurred.

We conducted prescribed burns (B and MB) by various means, including hand ignition using spot fire and strip-headfire techniques, and spot fire via helicopter. During the initial prescribed burns (March 2003), fine woody fuel loading in MB, where the shrub layer was felled a year prior (2002), was approximately double that on C and B units. Fire temperatures (30 cm above ground) of the initial burns were hotter in MB ($\bar{x} = 517$ °C) than B ($\bar{x} = 321$ °C) (Waldrop et al., 2010, 2016). Subsequent prescribed burns in MB units were less intense compared to the first burn (Waldrop et al. 2010).

2.2. Sampling procedure

Within each treatment unit, we established two pitfall trap arrays spaced > 50 m apart. Arrays consisted of a 118-ml cup filled half-way
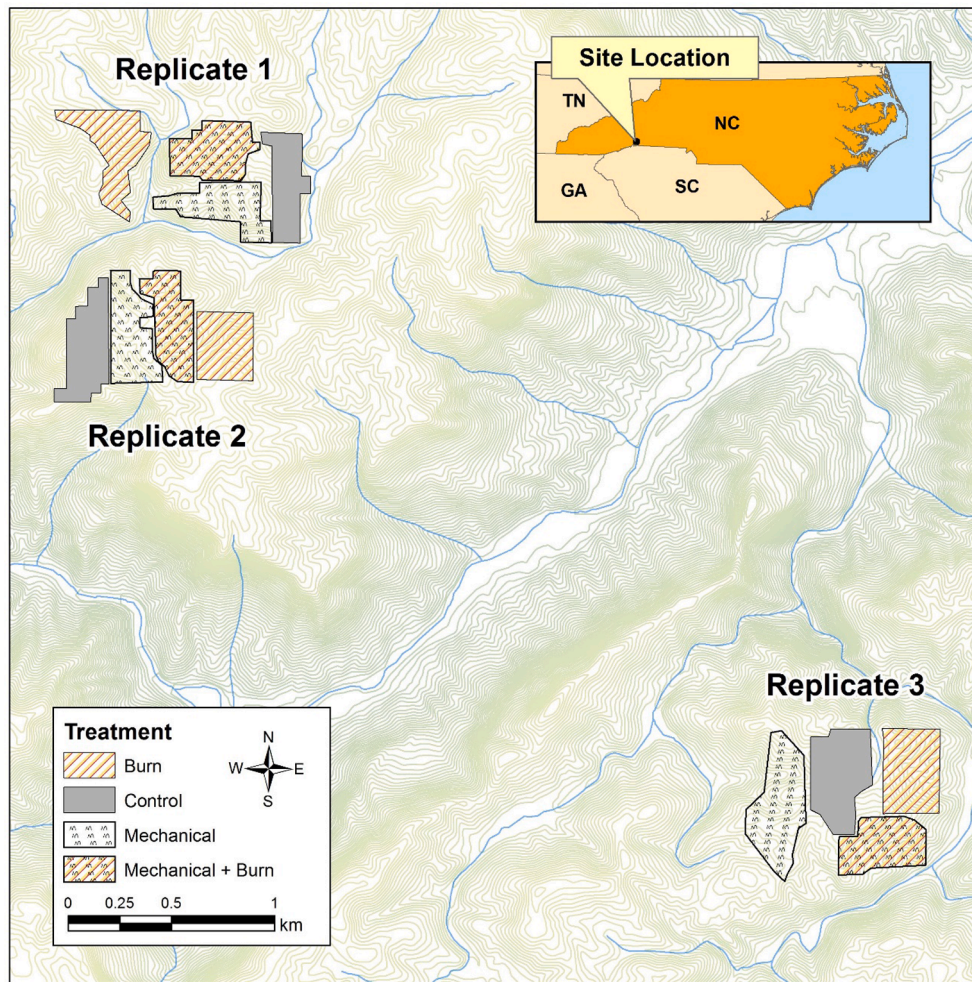
Fig. 1. Map of study area within the Green River Game Land, Polk County, North Carolina, in which we applied the experimental units of prescribed burn only (B), mechanical thinning only (M), and prescribed burn + mechanical thinning (MB) in three replicates (blocks) and control units (C), which had no forest management.

Table 1

Dates of mechanical understory felling and prescribed burn[*] treatments applied to experimental units, Green River Game Land, Polk County, North Carolina, 2001–2015. "x" indicates implementation of treatments; blank cells indicate no treatment implementation. Spider sampling occurred May/June – September/October 2014–2016.

	Winter 2001/ 2002	Winter 2002/ 2003	Winter 2005/ 2006	Winter 2011/ 2012	Winter 2014/ 2015
Mechanical felling	x			x	
Prescribed burns		x	x	x	x

[*] Prescribed burns were conducted only in burn-only (B) and mechanical and burn (MB) treatment units

with soapy water, with three, 30-cm long aluminum flashing drift fences trenched into the ground that radiated from the center of the cup oriented at 120° to the neighboring drift fence. We also used sets of colored pan traps filled with soapy water that we concurrently deployed for a separate project investigating pollinating insects (Campbell et al., 2018a, 2018b). Although not normally used for collecting spiders, pan traps have been successfully used to sample spiders in several studies (e. g., Buddle and Hammond, 2003, Cristofoli et al., 2010). We set pan traps both in the midstory and on the ground to capture bees but also collected spiders that may not be commonly captured in pitfall traps. Indeed,

different spider assemblages have been documented from forest canopies and understories (Larrivée and Buddle, 2009). For the colored pan traps, we attached blue, red, white, and yellow bowls at each corner of a 66-cm square of metal remesh (Nucoar) with binder clips (Campbell et al., 2018a, 2018b). At each of the two locations (>50 m apart) within each treatment unit, we hoisted one bowl set (one square wire remesh with four bowls) into the midstory (mean height 9.1 m ± 0.3 m) and placed another set on the forest floor. At a given trapping site, we spaced the pitfall trap array, midstory bowl set, and forest floor bowl set < 10 m (horizontal distance) apart. We sampled monthly for a 72-hour period, beginning in late spring (May/June) through early fall (September/October) each year from 2014 to 2016. We chose to sample during these months because they coincide with the primary growing season in the region and because most spiders are active during this time period and other studies have also focused spider collections only during growing seasons (Niemelä et al., 1994). We accomplished a total of 11 trapping periods during the three-year study (three in 2014 and four in 2015 and 2016, respectively). We used adult and juvenile spiders to determine spider abundance and guild trends, and we used adult spiders for diversity and richness analyses among the treatments.

2.3. Statistical analysis

We plotted relative abundances of all captured spider taxa and visually binned them into one of the following three abundance levels: 1) superabundant; 2) abundant; and 3) rare (see Grodsky et al., 2018a).

We set the cutoff for inclusion of individual spider taxa in analyses at the break between abundant and rare spider groups, thereby excluding all rare spiders with relatively low relative abundances from taxa-specific analyses (but not community-level analyses). For example, the cutoff between abundant and rare spiders in treatments was n = 16 because counts of individual spider taxa dropped from n = 16 to n ≤ 5 at that point on the plot. We placed spiders into hunting/web-building guilds based on family (sensu Uetz et al., 1999). See Table S1 for a list of spider taxa collected and the guilds to which they were assigned.

We conducted Poisson generalized linear models (GLMs) with counts of captured individuals for each spider taxon and guild and spider taxa richness as dependent variables to test response of spiders to fuel-reduction treatments (see Grodsky et al., 2018b). For all models, we tested for correlation among covariates and assumed overdispersion when the residual deviance divided by the residual degrees of freedom was > 1.0. We ran quasi-Poisson GLMs when we detected over-dispersion. We considered a sampling plot as the collection of two pitfall traps on the ground, four pan traps on the ground, and four pan traps in the midstory in each treatment unit (n = 10 traps/plot). We used treatment as the experimental unit and number of captured individuals of each spider taxon and guild and spider taxa richness pooled over all traps in each plot in each treatment unit as dependent variables. We first included a year × treatment interaction term, treatment, year, and block as explanatory variables in each model. If we detected a significant year × treatment interaction, we consequently developed a model for each year separately and included treatment and block as explanatory variables. Otherwise, we included treatment, year, and block as explanatory variables.

We followed the same procedure outlined above to test effects of treatments on spider diversity, with Shannon-Weaver Diversity Index as the dependent variable and a GLM with a Gamma distribution. We performed likelihood-ratio tests on all GLMs to identify significant treatment effects. For categorical treatment covariates (e.g., treatment) in all models, we performed *post hoc* Tukey's pair-wise comparisons of means using general linear hypothesis testing with a Holm adjustment (glht function; single-step method) in the R package "multcomp" (Hothorn et al., 2017). We set α = 0.05.

3. Results

We collected 1,600 spiders (790 adults) during the three-year study, comprising 31 families, 110 genera and a minimum of 151 species (Table S1). Salticidae was the most collected family (22.7% of captures), followed by Lycosidae (15.5%), Linyphiidae (11.6%), Theridiidae (7.7%) and Gnaphosidae (7.6%). The most collected genera/species

were *Naphrys pulex* (33.6% of all salticids collected), *Schizocosa* spp. (37.0% of all lycosids collected), and *Maevia inclemens* (14.0% of salticids collected). Canopy pan traps accounted for 24.2% of overall spider captures, whereas pitfall traps and pan traps situated on the ground accounted for 40% and 35.8% of overall spider captures, respectively. We collected two previously likely undescribed species: (Theridiidae-*Wamba* probable n. sp. and Linyphiidae- *Maro* probable n. sp.).

Total spider abundance was significantly higher in M and MB compared to C (Fig. 2a), and spider taxa richness was significantly higher in M compared to C (Fig. 2b). Among hunting guilds, ground hunters generally had higher abundances in all fuel-reduction treatments compared to C in all three years, whereas sheet spiders displayed the opposite trend (Table 2). Stalkers were more abundant in MB compared to C and B in 2014 (before burn 4), but we detected no differences among treatments in 2015 and 2016 (Table 2). Wandering spiders were more abundant in MB and M compared to B but not C. Ambushers, foliage runners, orb weavers, and space web builders showed no treatment-level responses (Table 2). We detected no treatment effect on spider diversity although a similar trend as species richness was noticed.

Some individual spider families also responded to fuel reduction treatments, and we observed some treatment × year effects. For example, Lycosidae abundance increased in MB compared to all other treatments in 2015 (after burn 4), and, in 2016, their abundance was greater in B compared to C and M (Table 2). Salticidae did not show treatment × year effects but were more abundant in all treatments compared to C (Fig. 3a). One commonly collected salticid, *Maevia inclemens*, showed a different trend with greater abundances in C, M, and MB compared to B (Fig. 3b). However, the Salticidae treatment trends were largely driven by *Naphrys pulex*, the most commonly collected spider species (Fig. 3c). Neither of these two salticid species showed treatment × year effects. *Erigone autumnalis* (Linyphiidae) was collected in significantly more in MB compared to all other treatments (Table 2).

4. Discussion

Our results support the concept that vegetation structure is an important driver of regional spider assemblages and corroborates results of several other studies on forest spiders (e.g., Bonte et al., 2003, Bowden and Buddle, 2010, Prieto-Benítez and Méndez, 2011, LaFage et al., 2019). Generally, spider abundance increased in all fuel reduction treatments compared to controls, likely due to increased structural heterogeneity within the forest understory and overstory. Greater availability of microhabitats may also explain the greater spider taxa richness observed within the fuel reduction treatments. Indeed, shrub
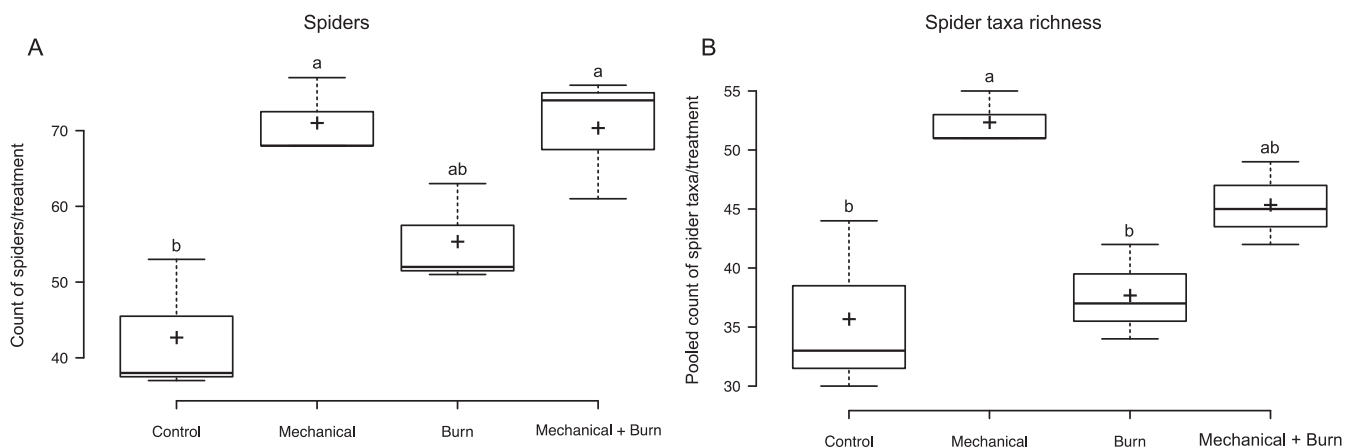

Fig. 2. Counts of total spiders (A) and spider taxa richness (B) in fuel-reduction treatments and controls, Green River Game Lands, Polk County, North Carolina, 2014–2016. Different letters indicate significant differences among treatment means at α = 0.05. Box plots show medians (thick black lines), treatment means (plus signs), interquartile ranges (boxes), and minimum and maximum counts (whiskers).

Table 2

Spider taxa diversity and mean number of spiders (± 95% CI) from common families and guilds captured within three fuel reduction treatments and controls at Green River Game Land, Polk County, North Carolina, 2014–2016. Spider taxa and guilds with an * indicate a significant treatment effect at $\alpha = 0.05$ and § indicates a treatment × year interaction. For each guild, family, genera, and species, different letter superscripts denote significant differences among treatments and controls.

Spider community and taxa	[1]LRT^{TRT}	PR(Chi)$_{TRT}$	Control	Mechanical	Burn	Mechanical + Burn
Shannon-Weaver Diversity Index	4.97	0.18	2.17 ± 0.12	2.42 ± 0.06	1.97 ± 0.07	2.20 ± 0.08
Ambusher	1.65	0.65	7.67 ± 2.85	8.67 ± 5.58	8.33 ± 3.64	10.67 ± 4.71
Foliage§						
2014	3.97	0.26	2.33 ± 2.35	4.00 ± 2.26	4.33 ± 0.65	2.00 ± 1.13
2015	4.22	0.24	6.67 ± 2.36	9.00 ± 4.93	7.00 ± 7.07	4.67 ± 2.85
2016	2.58	0.46	6.00 ± 4.08	5.00 ± 1.96	3.67 ± 3.97	6.33 ± 0.65
Ground§*						
2014	15.68	0.001	6.33^b ± 2.36	9.67^{ab} ± 5.70	16.67^a ± 9.42	12.67^{ab} ± 6.43
2015	9.20	0.03	7.33^b ± 5.81	12.67^{ab} ± 3.27	10.67^{ab} ± 3.46	15.33^a ± 8.57
2016	8.11	0.04	6.33^b ± 5.70	14.67^{ab} ± 8.64	24.00^{ab} ± 13.77	14.33^a ± 2.85
Orb§						
2014	1.27	0.74	3.00 ± 2.99	2.33 ± 0.65	1.67 ± 2.36	2.00 ± 1.13
2015	1.53	0.68	3.00 ± 3.92	4.67 ± 3.64	3.33 ± 2.36	3.00 ± 0
2016	6.83	0.08	3.33 ± 1.73	1.33 ± 0.65	4.00 ± 2.99	2.00 ± 3.92
Sheet*	9.87	0.02	6.00^a ± 4.53	3.00^{ab} ± 1.96	5.33^{ab} ± 6.63	1.67^b ± 1.73
Space	3.03	0.39	12.33 ± 5.58	13.00 ± 5.19	8.67 ± 2.61	11.67 ± 5.70
Stalker§*						
2014	21.12	>0.001	4.00^b ± 2.26	8.67^{ab} ± 3.46	4.67^b ± 2.36	13.33^a ± 1.56
2015	1.52	0.68	9.00 ± 7.42	11.67 ± 6.91	11.67 ± 6.23	11.67 ± 6.53
2016	4.80	0.19	6.67 ± 4.57	11.00 ± 9.26	13.33 ± 3.97	17.00 ± 5.19
Wanderer*	11.45	0.01	14.33^{ab} ± 6.63	19.67^a ± 2.85	11.33^b ± 1.73	21.00^a ± 14.13
Araneidae§						
2014	6.68	0.08	3.33 ± 3.64	2.67 ± 1.73	1.00 ± 1.13	1.33 ± 0.65
2015	2.32	0.51	1.33 ± 0.65	2.33 ± 2.61	1.0 ± 1.96	1.00 ± 0
2016	5.64	0.13	3.00 ± 1.96	0.67 ± 0.65	2.33 ± 1.73	1.33 ± 1.73
Castianeira	4.91	0.18	2.00 ± 1.13	2.33 ± 2.85	2.33 ± 2.35	1.00 ± 1.13
Elaver excepta	4.08	0.26	1.67 ± 1.73	3.67 ± 2.85	1.33 ± 1.31	2.00 ± 1.13
Gnaphosidae§*						
2014	10.72	0.01	2.33^{ab} ± 0.65	1.33^{ab} ± 1.31	0.67^b ± 0.65	4.33^a ± 4.71
2015	5.12	0.16	2.00 ± 1.13	5.33 ± 3.46	3.00 ± 1.99	3.00 ± 2.26
2016	22.23	>0.001	0.67^b ± 0.65	8.00^a ± 5.19	5.00^a ± 1.13	5.00^a ± 7.84
Leucauge venusta	2.78	0.43	2.00 ± 2.26	2.67 ± 1.73	4.33 ± 0.65	3.00 ± 3.39
Linyphiidae*	9.70	0.02	12.67^{ab} ± 6.82	18.33^{ab} ± 2.36	10.67^b ± 1.31	20.00^a ± 12.85
Agyneta	1.92	0.59	2.67 ± 1.73	5.33 ± 1.31	2.33 ± 1.31	2.33 ± 1.31
Erigone autumnalis*	55.38	>0.001	0^b	0^b	2.00^b ± 2.26	8.33^a ± 8.19
Lycosidae§*						
2014	4.17	0.24	7.33 ± 13.41	7.00 ± 2.99	6.67 ± 9.15	11.00 ± 8.98
2015	17.00	>0.001	3.33^b ± 3.63	5.00^b ± 1.13	4.00^b ± 2.99	11.00^a ± 9.05
2016	13.95	0.003	2.33^b ± 1.73	2.33^b ± 2.36	15.67^a ± 15.19	7.00^{ab} ± 2.26
Phrurolithidae	5.17	0.16	3.33 ± 1.31	5.33 ± 2.85	4.00 ± 2.26	2.00 ± 2.99
Phrurotimpus	3.72	0.29	3.00 ± 1.13	3.67 ± 1.73	1.33 ± 1.73	1.67 ± 2.36
Schizocosa§						
2014	6.44	0.09	7.33 ± 13.41	3.00 ± 1.13	4.67 ± 8.19	4.00 ± 6.88
2015	11.22	0.01	0.67 ± 1.31	2.67 ± 2.85	0.33 ± 0.65	3.00 ± 2.26
2016	3.55	0.31	1.00 ± 1.13	1.00 ± 1.13	2.33 ± 1.73	0.67 ± 1.31
Schizocosa ocreata§						
2014	4.98	0.17	2.67 ± 1.73	4.00 ± 4.53	6.33 ± 6.82	3.67 ± 6.32
2015	6.95	0.07	0.33 ± 0.65	2.00 ± 2.99	0.33 ± 0.65	1.67 ± 0.65
2016	10.24	0.02	1.00 ± 1.96	0.67 ± 1.31	2.33 ± 1.73	0
Theridiidae	3.16	0.37	11.33 ± 5.58	11.67 ± 6.82	7.33 ± 2.85	10.67 ± 6.82
Dipoena	1.62	0.66	3.00 ± 2.99	4.00 ± 2.99	3.00 ± 1.13	4.67 ± 3.27
Xysticus	2.63	0.45	2.00 ± 1.13	1.67 ± 2.36	1.00 ± 1.96	0.67 ± 0.65

[1] Scaled deviance reported for Shannon-Weaver Diversity Index.

average stem density was three times greater in MB than B, and 8.7 × and 5.7 × greater than in M and C, respectively, during the duration (2014–2016) of our study (Greenberg et al. 2018). Increased shrub density was primarily due to stump sprouting and shrub growth in response to heavy tree-kill and reduced canopy cover in MB, beginning with the initial high-severity fires. Between 2014 and 2016, canopy openness (measured at breast height) was nearly 30% in MB compared to < 10% in all other treatments (Greenberg et al., 2018). Reduced canopy cover in MB allowed more sunlight to reach the forest floor and resulted in significantly more herbaceous (e.g., forbs), shrub, and small tree growth (Waldrop et al. 2016); repeated burning impeded forest development in MB, likely prolonging open conditions (Greenberg et al., 2018). Greater abundance of herbaceous plants and flowers (i.e., forbs and shrubs) may have attracted insect prey for spiders (Campbell et al., 2019a, 2019b, 2019c), potentially explaining the increases in overall spider abundance and abundance of ground spiders. Additionally, an increase in lush foliage and young sprouts following a burn (Elliot et al., 1999) could also have attracted many herbaceous insects, resulting in more prey for spiders.

Our study and numerous others show that fire and other forest disturbances can alter spider abundance and diversity (Buddle et al., 2000, Niwa and Peck, 2002, Gillette et al., 2008, Vickers and Culin, 2014, Milne et al., 2021). Additionally, other studies have shown that canopy openness can be an important factor controlling spider abundance and diversity within broadleaved forest ecosystems (Košulič et al., 2016, Vymazalová et al., 2021). However, an earlier study within our study units and design found no difference in overall spider or Lycosidae abundance after initial fuel reduction treatments (2002–2003) (Greenberg et al., 2010). Similarly, Love et al. (2007) found no difference in spider abundance immediately following prescribed burns compared to
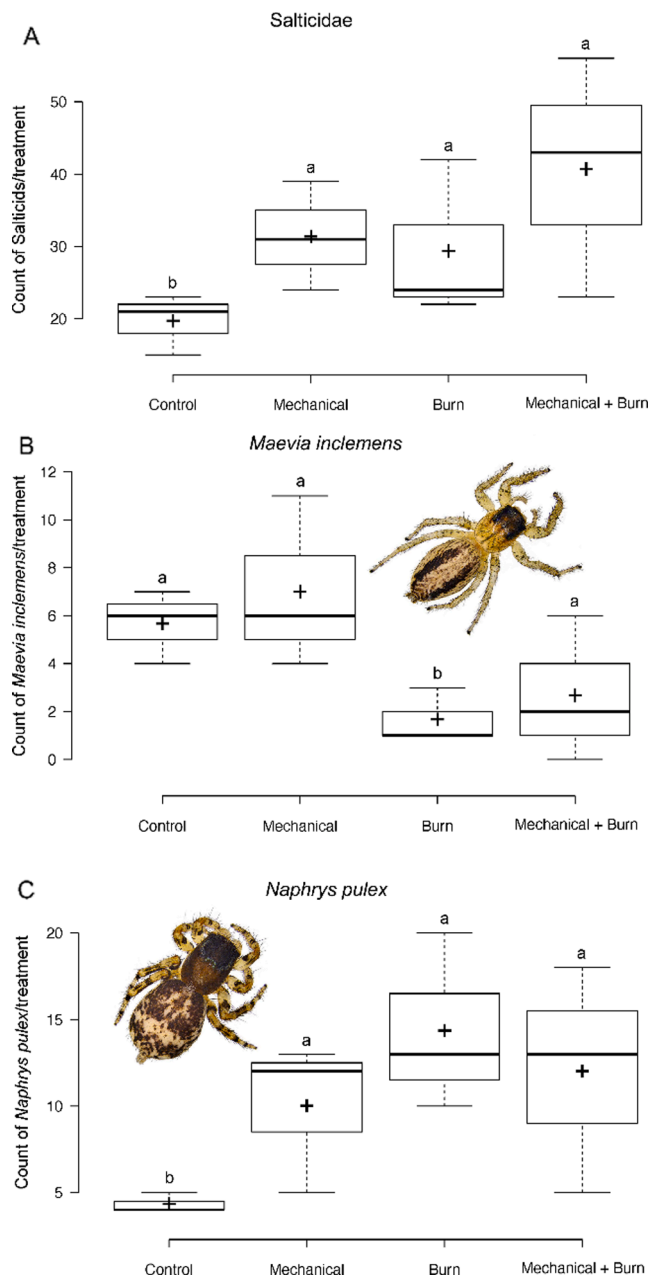
Fig. 3. Counts of Salticidae (A), *Naphrys pulex* (B), and *Maevia inclemens* (C) in fuel-reduction treatments and controls, Green River Game Lands, Polk County, North Carolina, 2014–2016. Different letters indicate significant differences among treatment means at $\alpha = 0.05$. Box plots show medians (thick black lines), means (plus signs), interquartile ranges (boxes), and minimum and maximum counts (whiskers).

controls in the Southern Appalachians. These findings may imply that it takes time, and/or repeated disturbances, for fire and other forest management techniques to alter spider communities. However, most studies listed above that found no treatment differences largely looked at spiders collectively (i.e., order level) whereas those examining spiders at the family or genus/species level did find treatment differences. These contrasting results among studies highlights the importance of using finer taxonomic resolution (*see* Grodsky et al., 2015) when examining spider assemblage response to forest management actions, as different taxa may respond to disturbances and altered forest structures in different ways. However, Milne et al. (2021) found that spider abundance decreased post-fire and their study had fine taxonomic resolution similar to the current study. Additionally, the timing of studies in

relation to time-since-disturbance might also factor into spider responses to fuel reduction and other forest disturbance treatments. For example, we found no treatment effects for Lycosidae in 2014 (3 years after the previous round of fuel reduction treatments), but their abundance increased in MB in 2015 (after the fourth burn in B and MB) and in B in 2016 compared to M (last treated in 2011) and undisturbed C.

Our study generally showed higher abundance of most spider taxa in fuel reduction treatments than controls; in contrast, Vickers and Culin (2014) found that prescribed burning and understory forest thinning in hardwood forests of the southeastern United States Piedmont region can reduce spider abundance. Although vegetation structure is likely a primary factor contributing to spider abundance in forested habitats (Pajunen et al., 1995), volume of coarse woody debris and leaf-litter depth can also play a role (Buddle et al., 2000, Abbott et al., 2003, Castro and Wise, 2009). Leaf litter adds structural complexity to a forest floor resulting in higher diversities of spiders and that many spider species may utilize different portions of leaf litter (e.g., vertical distribution) (Uetz, 1979, Wagner et al., 2003). In our study, leaf litter depth did decrease sharply after prescribed burns but rebounded in subsequent years (Greenberg et al., 2018).

Other studies have reported different responses among spider taxa to various forest management practices. Coyle (1981) reported that in the Southern Appalachians, clear-cutting did not affect *Maevia inclemen* abundance, but *Naphrys pulex* abundance dramatically increased. Our results corroborate Coyle's (1981) in suggesting that *N. pulex* increases in disturbed forest habitats, regardless of disturbance type (e.g., burns, harvests). The positive response by *Naphrys pulex* to fuel-reduction treatments in our study was not likely due to increased prey, as abundance of ants—their primary prey (Li et al., 1996) —was highest in C (Campbell et al., 2019a, 2019b, 2019c). Despite decreased ant numbers within MB and M, there still may have been ample ants to sustain *N. pulex* populations. Abundances of other species, such as *Erigone autumnalis*, were also greater in MB and B, suggesting that burns may improve habitat features and/or prey availability for this species. *Erigone autumnalis* avoids forested habitats (Draney, 1997), generally prefers disturbed habitats, and has the ability to disperse long distances (see Forster, 1971). Thus, these traits may have allowed it to colonize remote areas such as our B and MB. Although *M. inclemens* may be unaffected by clear-cutting (Coyle, 1981) and forest thinning, our results indicate it is negatively affected by fire. Coyle (1981) found that *Leucauge venusta* abundance increased after clearcutting (Coyle, 1981). In contrast, we did not detect any response by *L. venusta* to fuel-reduction treatments. Although we do not know the exact reason for this difference, many spider assemblages have been shown to differ in beta-diversity (variation in species composition through space) within similar habitats (Jiménez-Valverde et al., 2010, Hacala et al., 2020). Additionally, due to the decrease in leaf litter depth after prescribed fires, spiders that depend on leaf litter for shelter space could be negatively impacted.

Although vegetation structure was a potential driver for overall spider abundance and richness (Gunnarsson, 1990, Halag et al., 1998, Prieto-Benítez and Méndez, 2011), several hunting/web building guilds showed no response to treatments. We did not expect this, especially for foliage and orb guilds that depend on vegetation structure for their webs. Small sample sizes relative to other guilds suggest that either our collection methods were inadequate for these types of spiders and/or that they were uncommon within our experimental units. This contrasts to Milne et al. (2021), which showed that response to fire was significantly influenced by guild. Other guilds were largely dominated by certain spider families and generally followed similar abundance patterns as the dominant spider family. For example, ground hunters were primarily composed of Lycosidae and Gnaphosidae.

The Southern Appalachians are a hotspot of diversity for many insectivorous vertebrates (Dobson et al., 1997, Merkel and Chandler, 2020) including numerous important game animals that utilize arthropods for food. Spiders are important food sources for many insectivorous and omnivorous birds (Gunnarsson, 2007, Johnston and Holberton,

2009), mammals (Hamilton, 1941), and amphibians (Clark et al., 2011). Most insectivorous vertebrates are not highly selective and choose prey based on availability (Redford and Dorea, 1984). Thus, it is imperative that forest management decision-making consider potential changes to invertebrate prey availability following forest disturbances. Our results indicated that all of the fuel-reduction methods tested may increase spider prey for vertebrate organisms. However, other studies using the same experimental treatments and plots have shown variable invertebrate responses (Greenberg et al., 2010, Campbell et al., 2018a, Campbell et al., 2019a, 2019b, 2019c, Milne et al., 2021). For example, ant abundance was lower in MB compared to C (Campbell et al., 2019a, 2019b, 2019c) whereas flower visiting insects were more abundant in all fuel reduction treatments compared to C.

However, with the increased tree mortality caused by multiple rounds of MB treatments, maintaining high levels of biodiversity of flora and fauna, may require periodic prescribed burning or forest thinnings but not combinations. Additional research can explore how dormant versus growing-season burns affect biodiversity and how often to conduct fuel reduction techniques within the Southern Appalachians. Although some spider taxa responded to the treatments differently (as with other studies that examined other arthropod groups), overall spider abundance or richness was not negatively affected by any treatments compared to controls. Thus, forest managers may consider fuel reduction techniques as having positive benefits for maintaining biodiversity.

5. Conclusion

Response to forest management practices by spiders and other invertebrates is likely dynamic and depends on numerous factors. Our experimental units underwent multiple rounds of prescribed burning and/or mechanical understory thinning over a 15-year period. Our results suggest that spider taxa respond differently to forest fuel reduction treatments, and responses may change with time since disturbance, highlighting the importance of both spatial and temporal considerations when including invertebrates in forest management planning. Our findings could also have implications for higher trophic levels considering the importance of spiders to the diet of multiple vertebrate animals (e.g., birds, small mammals, amphibians, etc.) that inhabit the Southern Appalachians.

CRediT authorship contribution statement

Joshua W. Campbell: Conceptualization, Methodology, Investigation, Funding acquisition, Writing – original draft. **Steven M. Grodsky:** Conceptualization, Methodology, Writing – review & editing. **Marc A. Milne:** Resources, Writing – review & editing. **Patrick Vigueira:** Methodology, Project administration, Writing – review & editing. **Cynthia C. Vigueira:** Methodology, Project administration, Writing – review & editing. **Emily Stern:** Resources. **Cathryn H. Greenberg:** Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120127.

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