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Effects of Fire on Ground-Dwelling Spider (Araneae) Assemblages in Central Indiana Forests

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Abstract

Fire is a natural disturbance that occurs in many temperate and tropical ecosystems worldwide. As ubiquitous members of these ecosystems, spiders (Araneae) are often affected by fire, and their response to this disturbance has been shown to be dependent on taxonomy, functional diversity, seasonality, and a variety of environmental factors. We examined the effect of fire on ground-dwelling spider assemblages in temperate forests in central Indiana over 5 yr and found that spider assemblages were significantly affected by fire disturbance. Overall spider abundance decreased, whereas species richness and diversity remained unaffected. We also found that spider response depended heavily on the family and/or guild to which the spider belonged. We suspect that altered habitat heterogeneity, the patchy nature of fire's effect on leaf litter, and the high rate of recolonization by spiders all played important roles in these observed patterns.

Key words: disturbance, resilience, fire, spider, Indiana

Disturbance is the destructive change of an ecosystem by altering key elements. They can be small or large, with a wide range of effects. Small disturbances may include an animal digging a burrow or a tree falling, whereas large disturbances may include fires, floods, or significant human habitat alterations (Wilcove 2009). Disturbance can cause death, population displacement, and destruction of habitats (Dornelas 2010). Ecosystems may change in the face of such disturbance. Oftentimes, an ecosystem resists—or mediates—this change, a term coined resistance. In other instances, the ecosystem does change, and the time that it takes for that ecosystem to return to its predisturbed state has been termed resilience (Abella et al. 2018). Ecosystems will often return to their normal state unless the disturbance is severe, and this recovery depends on the severity of the disturbance and native species abundance and diversity (Fu et al. 2017).

Arthropods have been shown to be significantly affected by environmental disturbances (Englund 1991, Paquin and Coderre 1997, Kalisz and Powell 2000, Death 2002, Pryke and Samways 2012). For example, deforestation and fire commonly decrease species richness, abundance, and diversity. This is largely caused by immediate loss of life and the degradation of critical habitats and vegetation that arthropods use for survival (Kalisz and Powell 2000, Ohwaki et al. 2008, Prieto-Benítez and Méndez 2011, Haddad et al. 2015). Even though disturbance often results in these negative effects, many arthropod assemblages have been shown to recover rather quickly in these metrics (Buddle et al. 2000, Abbott et al. 2003, Pryke and Samways 2012). The most common measurement used to determine whether a population has recovered from a disturbance is primarily based on a single life-history property or ecological interaction such as reproductive rates or sex ratios (Gårdmark et al. 2003). However, invertebrate recovery commonly requires a more dynamic approach (Pryke and Samways 2012). Different guilds (functional diversity; e.g., pollinators or web-building spiders) or taxonomic groups (e.g., Coleoptera vs. Hymenoptera) may recover at different rates (Pryke and Samways 2012).

Functional diversity aims to quantify the functional traits within a species assemblage and is a critical measure in determining the ecological dynamics, stability, and nutrient balance of an ecosystem (Tilman 2001). Guilds are nonphylogenetic groups of species that share one or a series of important resources and may be used to measure functional diversity (Blondel 2003). Our analysis of spider resilience to wildfire follows nine guilds of spiders slightly modified from Cardoso et al. (2011). Each of these guilds tends to display common behaviors. For example, GRO (Ground spiders) consist of wandering spiders that are normally on the ground, commonly found in leaf litter, and do not use webs to hunt, but forage for insects, whereas ORB (Orb web weavers) consists of spiders that normally utilize elevated spiral webs between branches and trees to capture flying and winged prey. Species diversity and functional diversity are both significant indicators of how well an ecosystem is functioning (Tilman et al. 1997). However, as Cardoso et al. (2011) explained, the abundance of species or family diversity does not always indicate higher functional diversity. This can be viewed in the comparison of tropical and temperate environments where there is a higher family richness in tropical environments but relatively similar functional diversity between the two environments, possibly indicating functional role redundancy (Cardoso et al. 2011). Also, increased functional role redundancy in an environment could allow for a higher resilience of any single taxon when another taxon in the guild is reduced because of the likelihood of the two taxa sharing functional traits (Tilman et al. 1997).

Spiders disperse into new habitats through a variety of means, one of which is by ground movement. Wandering spiders often enter novel habitats by walking after disturbance (Riechert and Reeder 1972, Vogl 1973). Spiders also enter novel habitats—often after disturbance—by a process called ballooning (Bishop and Riechert 1990, Malumbres-Olarte et al. 2014). Spiders are able to construct a silk parachute-like structure that allows them to surf rising air and electrical currents to travel up to hundreds of kilometers (Morley and Robert 2018). This behavior is common in both male and female immatures and has been linked to avoiding excessive intraspecific competition, avoiding predation, and helps in searching for a mate (Simonneau et al. 2016). This mate searching is predominately done by males, whereas females are often in webs and burrows and do not search for mates (Wise 1995, Foelix 2010). This behavioral dichotomy increases the rate of male dispersal compared with females into new environments (although linyphiid females, especially erigonines, have often been found ballooning; Wise 1995, Blandenier et al. 2013, Foelix 2010).

Although there have been many studies on the effect of fire on spider assemblages, some of these studies have investigated only short-term (≤1 yr) effects (Riechert and Reeder 1972, Paquin and Coderre 1997, Kalisz and Powell 2000, Niwa and Peck 2002, Larrivée et al. 2005, Hore and Uniyal 2008, Vickers and Culin 2014), are studies of vastly different habitats (e.g., grassland; Merrett 1976, Polchaninova 2015, Rose and Goebel 2015, Brantley 2020), or are focused on a different suite of spider taxa that only slightly overlap with ours (Merrett 1976, Moretti et al. 2002, Hore and Uniyal 2008, Pryke and Samways 2012, Haddad et al. 2015, Polchaninova 2015). This is not to say these studies cannot be used for comparisons; however, these study differences may influence their results in ways that did not influence ours and vice versa. Studies that have examined similar timelines and environmental factors show that burned areas are quickly colonized by vagrant spiders and that spider assemblages are rather resilient and recover relatively more quickly from fire than do other site characteristics such as vegetation structure (Buddle et al. 2000). A review of similar studies revealed that fire causes a reduction in species richness and abundance, probably caused by a reduction in habitat heterogeneity (Prieto-Benítez and Méndez 2011).

Our study was part of the Hardwood Ecosystem Experiment (HEE), a long-term field experiment initiated by the Indiana Department of Natural Resources-Division of Forestry and a collaborative effort among multiple academic institutions in the Midwest (Kalb and Mycroft 2013). Designed to study the impacts of forest management, the HEE conducts periodic prescribed burning of its sites. In collaboration with the HEE framework, we utilized these periodic prescribed burns to study their effect on spider assemblage composition, abundance, and diversity in central Indiana forests.

Materials and Methods

Site Locations

Two locations were used for this study: Morgan-Monroe State Forest (MMSF; Morgan and Monroe Counties, Indiana) and Yellowwood State Forest (YSF; Monroe and Brown Counties, Indiana). These locations possess rolling, dry hills covered in temperate forests. Vegetation commonly consists of oak, hickory, chestnut, tulip poplar, American beech, maple, and sassafras (Kalb and Mycroft 2013). Between 2015 and 2020, July maximum air temperatures ranged from 34.4 to 32.2°C, whereas January minimum air temperatures ranged from −11.7 to −22.8°C (data from Bloomington, IN; Time and Date AS 2020). Precipitation varied some by sampling period (January–October), with 2017 being the wettest (107.6 cm) and 2018 the driest (93.3 cm) during the sampling period with a SD among years of 5.8 cm. On average, within our sampling period, the wettest month was July (16.2 cm) and the driest month was January (7.52 cm; precipitation data are for Indianapolis; NOAA 2020).

Two sites were located at MMSF: U3-05 and U3-16. Six sites were located at YSF: U6-06, U6-10, U6-14, U6-18, U9-13, and U9-20. Sites were at least 150 m apart and consisted of three sections. Each section was located at least 80 m apart from adjacent sections within the same site. This design created a total of 24 sections spread out among eight sites. Each section consisted of two pitfall traps placed approximately 5 m apart. Data from each pair of pitfall traps within each section were pooled.

Treatments

Burns were conducted by the Indiana Department of Natural Resources (IDNR) Fire Headquarters. Each site was burned separately on various dates. Fires were ignited using drip torches with flame targets of 2–3’ and were generally of low intensity. When higher intensities were observed, strip fires were used to reduce and ring the head fire. Sections left unburned from the first fire were burned in small sections afterward.

Collection

Spiders were collected at all sites five times a year between January 2015 and February 2020. Collection dates occurred in late January, March, May, July, and September of every year, resulting in 27 collection instances for all 24 sections. Collecting was spread throughout the year rather than summer alone, as past studies have shown that year-round sampling is important to adequately and efficiently sample ground-dwelling spider assemblages (Steffen and Draney 2009). However, to ensure data reflected yearly blocks for each site (five sampling dates in each with equal sample size), some data were eliminated from the analysis (Table 1). In this way, data were organized by year for each site, staggered over years since burned. By using this methodology, detected patterns should more likely reflect

Table 1. Date ranges of spider collection used from each site

Site	Section	Unburned	Postburn		
			<1 yr	1–2 yr	2–3 yr
U3-05	C13 E8 H5	5 April 2015–20 Mar. 2016	21 Jan. 2017–6 Oct. 2017	28 Jan. 2018–7 Oct. 2018	27 Jan. 2019–14 Oct. 2019
U3-16	F5 F12 H8	23 Jan. 2015–4 Oct. 2015	21 Jan. 2017–6 Oct. 2017	28 Jan. 2018–7 Oct. 2018	27 Jan. 2019–14 Oct. 2019
U6-06	C3 D6 H11	7 Feb. 2015–23 Jan. 2016	28 May 2017–22 April 2018	28 May 2018–6 April 2019	N/A
U6-10	D5 D11 E15	6 Feb. 2016–22 Jan. 2017	28 May 2017–22 April 2018	28 May 2018–6 April 2019	N/A
U6-14	C6 F9 I12	7 June 2015–30 May 2016	21 Jan. 2017–8 Oct. 2017	28 Jan. 2018–8 Oct. 2018	27 Jan. 2019–12 Oct. 2019
U6-18	D4 D12 E8	7 Feb. 2015–23 Jan. 2016	20 Mar. 2016–4 Feb. 2017	19 Mar. 2017–11 Feb. 2018	8 April 2018–24 Mar. 2019
U9-13	D6 G3 M3	5 April 2015–20 Mar. 2016	24 Mar. 2019–15 Feb. 2020	N/A	N/A
U9-20	F8 L6 S3	7 June 2015–30 May 2016	28 Jan. 2018–7 Oct. 2018	27 Jan. 2019–14 Oct. 2019	N/A

response to disturbance and minimize seasonal differences due to correlated sampling dates, which has been shown to significantly affect spider abundance and diversity (Pryke and Samways 2012).

Spiders were collected using two different methods: pitfall trapping and Berlese funneling of collected leaf litter. The two pitfall traps at each section were filled with a 50/50 mixture of water and ethylene glycol-based antifreeze. In addition, 0.5 g of denatonium benzoate, a strong bitterant, was added to prevent ingestion of pitfall trap liquid by nontarget vertebrates. This created a denatonium benzoate concentration of 124 ppm. Pitfall traps consisted of 88.7 ml (3 oz) plastic cups recessed into the soil, so that they were flush with the ground. Pitfall trapping occurred on each collection date. These traps were left in situ for 2 wk before being collected, returned to the lab, and placed in cold storage (~3°C) to slow decomposition. Trap contents were then examined over the next month using a Leica S6E stereomicroscope, and spiders were removed and preserved using 90% ethanol for later identification.

Berlese funneling of collected leaf litter began with collecting two to three handfuls of leaves at each section on every collection date. Leaves were put into plastic bags and returned to the lab where they were then put into Collapsible Berlese funnels (BioQuip, Product No. 2832). An LED light (Triangle Bulbs, 13-Watt PAR30 Flood Light Bulb, Model No. T97005-4) was placed at the top of the funnel, and a vial of ethanol (70%) was placed at the bottom of each trap. Traps were left to extract over 2–3 d before the ethanol, and contents were removed. Trap contents were examined using the same process that was used for the pitfall trap contents. Pitfall and Berlese funnel-collected spiders were pooled within sampling dates and locations.

All spiders were sexed and identified to the deepest taxonomic level possible using Ubick et al. (2017), the World Spider Catalog (WSC 2020), and many other associated species keys with a Leica M165C stereomicroscope. All spiders that could be identified at least to family, regardless of maturity, were used in all nonfamily to family comparisons. All specimens are held in the lead author's private collection.

Statistical Analysis

The analysis of functional diversity was aided by grouping spider families (and sometimes specific subfamilies and genera) into guilds according to Cardoso et al. (2011), with a slight modification to Linyphiidae. Although we only targeted ground spiders (e.g., pitfall traps and Berlese funnels), a small amount of nonground spiders were also captured; all collected spiders were analyzed. Using this methodology, spiders fell into nine guilds: Ambushers (AMB: Thomisidae), Ground hunters [GRO: Corinnidae, *Cicurina* (Hahniidae), Gnaphosidae, Liocranidae, Lycosidae, and Phrurolithidae], Other hunters 1 (OT1: Anyphaenidae, Miturgidae, Ctenidae, Philodromidae, Salticidae, and Cheiracanthiidae), Other hunters 2 (OT2: Clubionidae and Oxyopidae), Specialists (SPE: Mimetidae), Orb web weavers (ORB: Theridiosomatidae, Araneidae, Uloboridae, and Tetragnathidae), Space web weavers (SPA: Dictynidae, Theridiidae, Pholcidae, Mysmenidae, Nesticidae, and Titanoecidae), Sheet-web weavers (SHE: Agelenidae, Pisauridae, Linyphiidae, Cybaeidae, and non-*Cicurina* Hahniidae), and Sensing web weavers (SEN: Antrodiaetidae, Atypidae, Segestriidae, and Halonoproctidae). Since guilds grouped families, this organization method was considered our broadest taxonomic level.

Taxonomic communities of spiders over all sites were grouped and organized by date in relation to the burn date. This created four groups: Unburned, <1 yr postburn, 1–2 yr postburn, and 2–3 yr postburn. Due to the staggering of burn dates, each of these groups had a different number of sites represented within each: Unburned (all eight sites), <1 yr postburn (all eight sites), 1–2 yr postburn (seven sites; U9-13 excluded), and 2–3 yr postburn (four sites; U6-06, U6-10, U9-13, and U9-20 excluded; see Table 1). Sample size was equal across all treatments. Data were grouped by section. Each section in each treatment (time period) consisted of five Berlese collections and 10 pitfall trap collections (5 collection dates × 2 pitfall traps/date).

Estimates of sample coverage (fraction of the entire spider community represented in our sampling), degree of homogeneity (differences in abundance among species), and actual species richness (using the iChao1 model; Chiu et al. 2014) of the entire spider community were run using spadeR (Chao et al. 2015). All other statistical tests were done in R (R Development Core Team 2020) version 3.5.1 and the associated vegan and permute packages. Tests of homogeneity of variance and normality were done before all tests.

One-way ANOVAs with Tukey's HSD post hoc tests were used to compare the abundance of all spiders among the four treatments. Data that did not fit normality or variance were tested using a Kruskal–Wallis test and Wilcox post hoc test. This analysis was also conducted for each family (with a raw abundance higher than 100) and each guild (with a raw abundance higher than 100). Additionally, a one-way ANOVA was used to compare species richness among treatments and the Shannon–Weiner diversity index of the spider communities found among sections over the four time periods with diversity defined using species data. Finally, one-way ANOVAs or Kruskal–Wallis tests were used to compare the abundances of the species with the six highest abundances across treatments.

The similarities among taxonomic assemblages of spiders were compared using non-metric multidimensional scaling (NMDS) analyses. NMDS were run to compare the taxonomic assemblages (grouped by either species or guild) of spiders with years since burn as a grouping factor (unburned, <1 yr since burn, 1–2 yr since burn, and 2–3 yr since burn). Data were standardized prior to each NMDS by ln+1 transforming the data. Statistical significance between specific groups was determined using the pairwise.adonis package in R (Martinez 2017). Plots were created using R with the associated ggplot2 package. All data were considered significantly different at $P < 0.05$.

Results

Abundance, Richness, and Diversity

Throughout the study, 2,901 spiders were captured (see Supp Table S1 [online only] for full list). Of that number, 2,603 were able to be identified at least to family (immatures—especially ones of early instar—are often difficult to identify past order). There were 888 adult spiders that were identified to the species level. We found 114 species within 30 families, which represented an estimated 96.7% of the species located at our sites (estimated sample coverage). However, the spider community was estimated to possess a species richness of 166 species by a different metric (iChao1 estimator), a slightly higher estimate than what is suggested by the estimated sample coverage. The spider community was considered highly heterogeneous with a coefficient of variation of 2.70 (aka degree of homogeneity). The number of spiders captured in each guild and family is reported in Table 2. Since guilds were largely constructed from family-level taxonomic identifications, this sum value is also represented at the guild level (minus the specimens of unknown family designation).

The most common species over all sites and years was *Phrurotimpus palustris* (Banks 1892), a guardstone spider that commonly lives in the leaf litter and is common in deciduous forests throughout Eastern North America (Platnick 2019). The second, third, and fourth most common species were all erigonines within Linyphiidae: *Mermessus maculatus* (Banks 1892), *Origanates rostratus* (Emerton 1882), and *Tapinocyba emertoni* Barrows & Ivie 1942, respectively. Erigonines, a distinct subfamily within Linyphiidae, are typically smaller, mostly found in the leaf litter or in crevices on the ground, and generally feed on soft-bodied insects such as collembola (Ubick et al. 2017). The fifth most common species was *Cicurina arcuata* Keyserling 1887, a hahniid spider that is commonly found in forested regions under rocks and logs (Paquin and Hedin 2004, Ubick et al. 2017). Unburned and burned sites of various times after burn varied only slightly in the most common species found (Table 3). When compared across treatments, none of these abundant species were significantly more abundant in any treatment compared to any other.

The abundance of spiders significantly decreased after fire and was significantly different among years following fire ($F = 12.07$; df = 3,77; $P < 0.00001$) with unburned sections having a greater abundance of spiders than any postfire treatment (unburned vs <1 yr: $P < 0.0005$; unburned vs 1–2 yr: $P < 0.0005$; unburned vs 2–3 yr: $P < 0.0005$; Fig. 1). With families as replicates, the mean variance of the abundance of family assemblages in the '<1 yr since burn' treatment had approximately double the variance (0.25) of any other treatment (unburned: 0.14, 1–2 yr: 0.14, 2–3 yr: 0.10). We found no difference in species richness after fire ($P = 0.08$) nor were any treatments different in diversity (Shannon–Weiner diversity index: $P = 0.055$).

Comparing Species Assemblages

Spider assemblages significantly differed when organized by species ($F = 2.24$; df = 3, 77; $P < 0.0001$; Fig. 2A) and by guild ($F = 3.83$; df = 3, 77; $P < 0.0001$; Fig. 2B) though with relatively high stress. In both organizing schemes, the spider assemblages that existed in the unburned sections were significantly different than all of the other treatments (for species: unburned vs <1 yr: $P < 0.05$; unburned vs 1–2 yr: $P < 0.01$; unburned vs 2–3 yr: $P < 0.05$; for guild: unburned vs <1 yr: $P < 0.01$; unburned vs 1–2 yr: $P < 0.01$; unburned vs 2–3 yr: $P < 0.01$). In addition, when assemblages were organized by species, the spider assemblage within the <1-yr treatment was significantly different than that which was in the 1- to 2-yr treatment ($P < 0.05$).

Family-Specific Analyses

The abundances of four families were significantly less abundant after the fire than before the fire. Specifically, Agelenidae ($\chi = 17.8$; df = 3; $P < 0.0005$) were significantly more abundant in the unburned section compared with 1–2 yr ($P < 0.005$) and 2–3 yr ($P < 0.005$) after the burn. Gnaphosids ($\chi = 13.5$; df = 3; $P < 0.005$) were significantly more abundant in the unburned sections compared with sections 1–2 yr after the burn ($P < 0.05$) and 2–3 yr after the burn ($P < 0.05$). Phrurolithids ($F = 5.29$; df = 3, 77; $P < 0.005$) were significantly more abundant before the burn versus <1 yr ($P < 0.005$) and 2–3 yr after the burn ($P < 0.05$). Lastly, thomisids ($\chi = 17.2$; df = 3; $P < 0.001$) were significantly more abundant in the unburned sections versus <1 yr ($P < 0.005$), 1–2 yr ($P < 0.005$), and 2–3 yr ($P < 0.05$) after the burn (Fig. 3).

Functional Diversity

There were also differences in functional diversity when spider assemblages were grouped as guilds. AMB (see Thomisidae above, since AMB = only Thomisidae), GRO ($F = 5.49$; df = 3, 77; $P < 0.005$), OT1 ($F = 12.7$; df = 3; $P < 0.01$), and SHE ($F = 4.46$; df = 3, 77; $P < 0.01$) showed significant differences among treatments. Specifically, the ground spiders (GRO) were more abundant in unburned treatments compared with <1 yr after the burn ($P < 0.05$), 1–2 yr after the burn

Table 2. Number of spiders captured by family and guild

Family	Number captured	Guild	Guild	Number captured
Agelenidae	104	SHE	AMB	118
Antrodiaetidae	14*	SEN	GRO	1,185
Anyphaenidae	14*	OT1	ORB	22*
Araneidae	13*	ORB	OT1	120
Atypidae	3*	SEN	OT2	14*
Cheiracanthiidae	1*	OT1	SEN	31*
Clubionidae	14*	OT2	SHE	954
Corinnidae	19*	GRO	SPA	158
Ctenidae	40*	OT1	SPE	1*
Cybaeidae	5*	SHE		
Dictynidae	41*	SPA		
Gnaphosidae	207	GRO		
Hahniidae	231	SHE/GRO		
Halonoproctidae	2*	SEN		
Linyphiidae	752	SHE		
Liocranidae	4*	GRO		
Lycosidae	181	GRO		
Mimetidae	1*	SPE		
Miturgidae	3*	OT1		
Mysmenidae	3*	SPA		
Nesticidae	8*	SPA		
Philodromidae	1*	OT1		
Phrurolithidae	634	GRO		
Pisauridae	2*	SHE		
Salticidae	61*	OT1		
Segestriidae	12*	SEN		
Tetragnathidae	9*	ORB		
Theridiidae	92*	SPA		
Thomisidae	118	AMB		
Titanoecidae	14*	SPA		
(Unknown)	298*	N/A		

AMB, Ambushers; GRO, Ground-dwellers; ORB, Orb web weavers; OT1, Other hunters 1; OT2, Other hunters 2; SEN, Sensing web weavers; SHE, Sheet-web weavers; SPA, Space-web weavers; SPE, Specialists.

*Families and guilds with abundances < 100 that were not analyzed individually.

Table 3. Most abundant species found in each treatment

Abundance rank	All sites	Unburned sites only	<1 yr since burn	1–2 yr since burn	2–3 yr since burn
1	*P. palustris*	*P. palustris*	*P. palustris*	*P. palustris*	*P. palustris*
2	*M. maculatus*	*T. emertoni*	*M. maculatus*	*M. maculatus*	*M. maculatus*
3	*O. rostratus*	*O. rostratus*	*O. rostratus*	*C. arcuata*	*O. rostratus*
4	*T. emertoni*	*M. maculatus*	*C. arcuata*	*Centromerus latidens* (Emerton, 1882)	*Centromerus latidens* (Emerton, 1882)
5	*C. arcuata*	*Neoantistea magna* (Keyserling, 1887)	*T. emertoni*	*T. emertoni*	*Anahita punctulata* (Hentz, 1844)

($P < 0.05$), and 2–3 yr after the burn ($P < 0.01$). For the OT1 assemblage, unburned sections had significantly more spiders than sections <1 yr after the burn ($P < 0.01$) and 1–2 yr after the burn ($P < 0.01$). Finally, the Sheet-web weavers (SHE) were also more abundant in unburned treatments compared with <1 yr after the burn ($P < 0.05$) and 1–2 yr after the burn ($P < 0.01$), but not 2–3 yr after the burn ($P = 0.34$; Fig. 4).

Discussion

Fire had a dramatic effect on spider assemblages within central Indiana forests. These effects were evident in some analyses of the collected data, but not in others. For example, the most dominant species within the forests, *P. palustris*, maintained its dominance regardless of treatment or year. Similarly, the other species rounding out the top five most abundant were almost always linyphiids or *C. arcuata*. Most of the linyphiids in these lists were within the subfamily Erigoninae: small, leaf litter-dwelling spiders that commonly consume smaller arthropods such as collembolans (Aitchison 1984). This may have been due to the bias in our sampling effort as we focused largely on litter-dwelling spiders by using pitfall traps and Berlese funnels of leaf litter. However, the dominance of erigonines in all of our habitats may also be due to their inclination to balloon, which increases their dispersive range (Bishop and Riechert 1990, Blandenier et al. 2013). Interestingly, although there were no significant differences found within each of these species abundances, clear patterns were visible in the abundances of *M. maculatus* and *T. emertoni* in that the former increased and the latter decreased in their ranked abundance after fire (Table 3). It is possible that these changes are linked to these species propensities to live in leaf litter or balloon, though due to the lack of research on their behavior this is just speculation.

As expected, overall spider abundance was reduced immediately after fire. This reflected the findings of most other similar studies (Paquin and Coderre 1997, Abbott et al. 2003, Hore and Uniyal 2008, Prieto-Benítez and Méndez 2011, Haddad et al. 2015) and is likely due to direct mortality, loss of prey, or a reduction in habitat heterogeneity (Riechert and Reeder 1972, Phillips et al. 2003). Even after 2–3 yr, abundance did not recover from disturbance (Fig. 1). Moretti et al. (2002) found similar results after 1–2 yr but noted that recovery did eventually occur and surpass previous abundances at 7–14 yr. Other studies saw a return to predisturbance abundance after 3 yr (Brantley 2020), suggesting that perhaps another year of sampling would have resulted in similar results. The lack of change in species richness after fire that we observed was similar to some studies (Buddle et al. 2000, Niwa and Peck 2002) but contrasted to most (Coyle 1981, Prieto-Benítez and Méndez 2011, Polchaninova 2015). However, as elucidated by Rose and Goebel (2015), these comparisons must consider the type of sampling conducted. Since our study focused on ground-dwelling spiders, those studies that gathered much of their data from sweep netting or hand collecting may not reflect the same spatially oriented fauna. When comparing studies that possessed some of these same characteristics, some also found no difference in species richness (Niwa and Peck 2002), whereas others found a reduction (Paquin and Coderre 1997, Larrivée et al. 2005), and still others an increase (Riechert and Reeder 1972). It has been suggested that this difference among studies in the effect of fire on species richness is due to the varying severity of the fires in these studies and differences in fire movement throughout various habitats (Moretti et al. 2002).

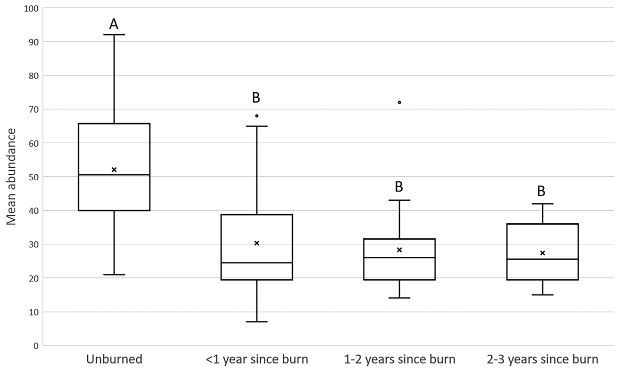

Fig. 1. Mean abundance of spiders captured from each treatment. Different letters represent significantly different values at α = 0.05.

Diversity was not significantly affected by the burn. Other North American spider-focused studies revealed similar results (Coyle 1981, Buddle et al. 2000, Niwa and Peck 2002), though, interestingly, they contrast with an Asian spider study (Hore and Uniyal 2008) and soil invertebrate studies (Englund 1991, Kalisz and Powell 2000). One very similarly structured study also noted that after 3 yr litter-dwelling spider diversity did not return to unburned levels even though the assemblage seemed to otherwise recover (Polchaninova 2015). Although a decrease in diversity has been linked to a decrease in habitat heterogeneity due to fire, thereby reducing the availability of suitable web locations, our calculation of spider diversity did not seem to be significantly affected by this change. A decrease in heterogeneity likely affects litter-dwelling spiders (those less likely to build webs) as fire is known to alter the microhabitats on the forest-floor (Prieto-Benítez and Méndez 2011). However, it is possible that the patchiness of the fire (Paquin and Coderre 1997) maintained enough habitat heterogeneity to allow for a diverse assemblage of spiders to remain within burned areas.

Unburned species assemblages were significantly different from all burned assemblages (<1, 1–2, and 2–3 yr), and there were also some significant differences among burned species assemblages. There was significant overlap among all treatments (Fig. 2A). It is likely that much of the noise (and likely high stress of this model) is at least partially due to wandering males and early-colonizing (possibly by ballooning) spiders. Adult male spiders often wander

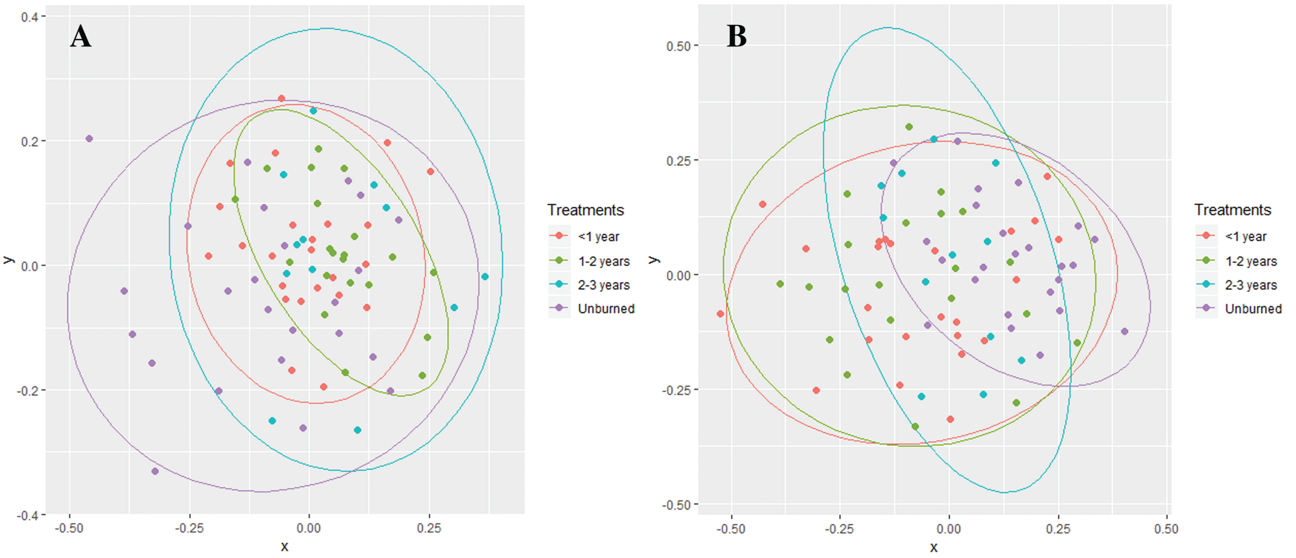

Fig. 2. (A) Non-metric multidimensional scaling (NMDS) of spider species assemblages over all sections over time since burn (stress = 0.27); (B) NMDS of spider guild assemblages over all sections over time since burn (stress = 0.21).

great distances, looking for females, whereas females are oftentimes more sedentary, especially if gravid (Foelix 2010). Moreover, spiders are incredibly efficient colonizers. In fact, spiders are often the first colonizers after disturbance (Bishop and Riechert 1990, Foelix 2010, Morley and Robert 2018), as quickly as 1 d postdisturbance (Vogl 1973). This may have contributed to the high variance we witnessed in the <1 yr treatments. As vagrants move in and out of newly disturbed habitats, sampled specimens may not accurately reflect a functioning, interactive assemblage. With this vagrancy—especially by males—burned spider assemblages still did not resemble their former unburned state even after 2–3 yr. This may indicate that the colonizing and wandering immigrants do not reflect the unburned assemblage, but only a subset. Indeed, some guilds are more vagrant than others, which may help explain this difference (Bultman et al. 1982, Foelix 2010).

Guild assemblages were also significantly affected by fire. When assemblages were organized by guilds, the unburned assemblage significantly differed from all other burned treatments, much as the species assemblages did. This suggests that the functional quality of the system (i.e., ability of the system to support prey that likewise support various hunting strategies; Cardoso et al. 2011) shifted upon burning and that the assemblage able to utilize the environment (via their different hunting strategies) differed postburn versus unburned. Since the guild assemblage in our longest treatments (2–3 yr after burn) still significantly differed from the unburned assemblage, this suggests that the system required more time to return to a predisturbed level of ecological

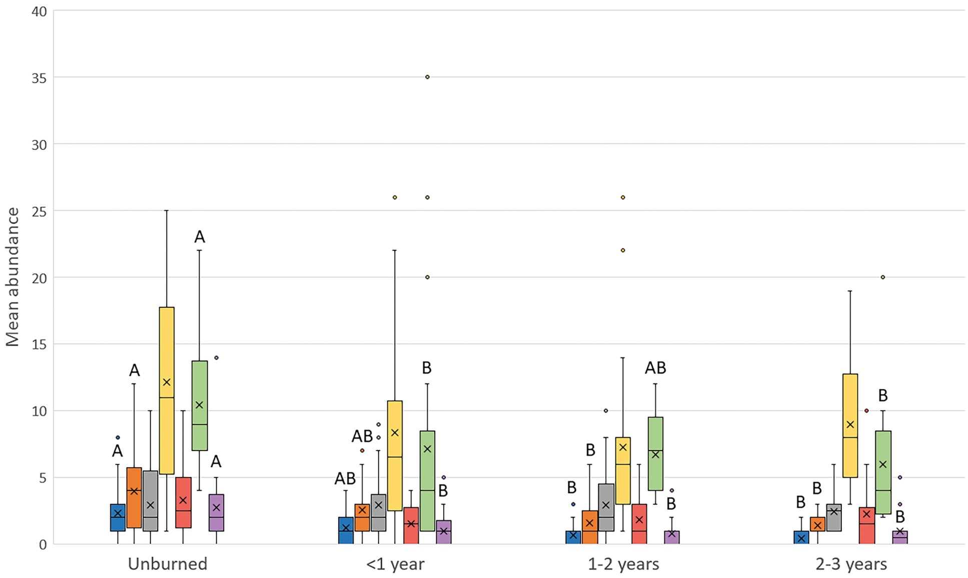

Fig. 3. Mean abundance of the seven most abundant families captured during the study. Families are in this order under each treatment: Agelenidae, Gnaphosidae, Hahniidae, Linyphiidae, Lycosidae, Phrurolithidae, and Thomisidae. Different letters represent significantly different values at $\alpha = 0.05$ within a family.

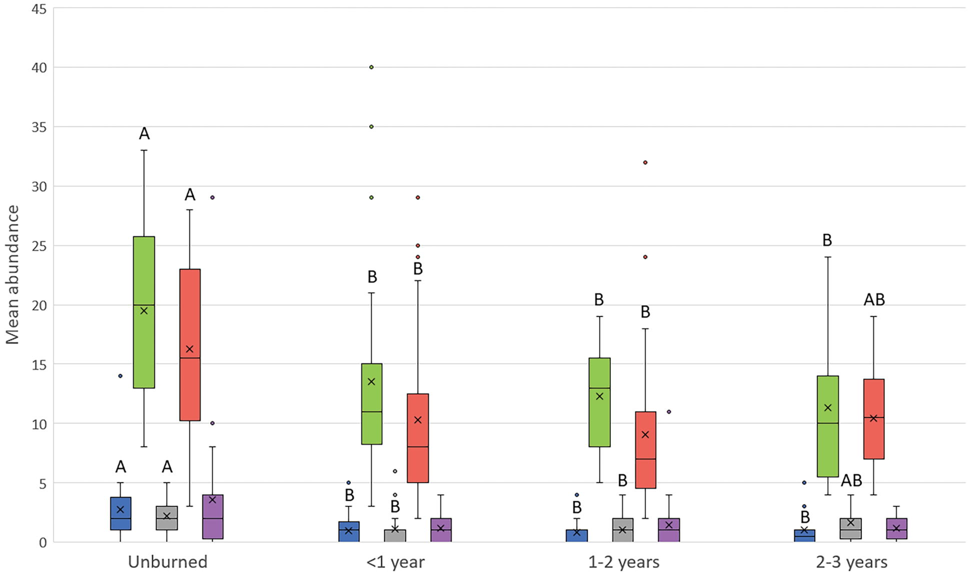

Fig. 4. Mean abundance of the five most abundant guilds captured during the study. Guilds are in this order under each treatment: Ambushers (AMB), Ground-dwellers (GRO), Other hunters 1 (OT1), Sheet-web weavers (SHE), and Space-web weavers (SPA). Different letters represent significantly different values at $\alpha = 0.05$ within a guild.

functionality. This assessment is supported by the observations that neither abundance (Fig. 1) nor species assemblage composition (Fig. 2A) returned to unburned levels at 2–3 yr postburn.

As suggested by the guild assemblage analysis, there was great variation in how certain spider families and guilds responded to fire. Most families and guilds of spiders decreased in abundance postfire and none increased. Vickers and Culin (2014) reported similar statistics from a study in a piedmont forest in South Carolina, in that all of their collected families decreased in abundance postfire. Similarly, Haddad et al. (2015) found that most ground-dwelling families decreased in abundance after fire in a South African grassland, although a few did increase. This contrasts with Larrivée et al. (2005) and Polchaninova (2015), who both found that ground spider capture rate increased after fire in a Canadian boreal forest and Ukrainian steppe, respectively. Some of the guilds (and families within them) that decreased in abundance in response to fire included the Ambushers (AMB; Thomisidae), Ground-dwellers [GRO; Corinnidae, Gnaphosidae, *Cicurina* (Hahniidae), Liocranidae, Lycosidae, and Phrurolithidae], Other hunters 1 (OT1; Anyphaenidae, Cheiracanthiidae, Ctenidae, Miturgidae, Philodromidae, and Salticidae), and Sheet-web weavers (SHE; Agelenidae, Pisauridae, Linyphiidae, Cybaeidae, and non-*Cicurina* Hahniidae). The Ambushers (AMB) and Other hunters 1 are largely dependent on low-lying vegetation to hunt their prey, whereas the Sheet-web weavers (SHE) use both low-lying vegetation and leaf litter to build their flattened webs to sit and wait for prey (Foelix 2010, Cardoso et al. 2011). Ground-dwellers (GRO) also showed a marked decrease postfire, probably because they are also commonly found in the leaf litter (Ubick et al. 2017). The reduction in habitat complexity due to fire (Hatley and MacMahon 1980, Phillips et al. 2003) probably negatively affected thomisids (AMB) and Sheet-web weavers in finding appropriate feeding habitat, whereas a reduction in leaf litter (Prieto-Benítez and Méndez 2011, Polchaninova 2015) and the patchiness of fire (Paquin and Coderre 1997) probably caused the drops in leaf litter dwellers such as Ground-dwellers and Sheet-web weavers. Though, interestingly, Sheet-web weavers and Other hunters 1 started to recover in abundance in the 2- to 3-yr treatment, perhaps showing a sign of resilience (Fig. 4). This recovery is likely due to the return of low-lying vegetation, which gives a better architectural environment for the web-building Sheet-web weavers (Post and Riechert 1977, Robinson 1981, Halley et al. 1996) and hunting habitat for the Other hunters (Cardoso et al. 2011).

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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