Short-Term Effects of Prescribed Burning on Ant (Hymenoptera: Formicidae) Assemblages in Ozark Forests

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ABSTRACT Prescribed fire is a valuable and effective tool in forest management, and understanding the effects of fire on animal communities is increasingly important for monitoring and conservation. We quantified the short-term responses of leaf litter ants to fire in Ozark oak-dominated forests of Arkansas. We repeatedly surveyed litter ants in replicate burned and unburned sites via Berlese extraction, baiting, and hand collecting 30–170 d postfire. We collected 6,301 ants representing 59 species. Cumulative ant species richness was lower in burned forests than in unburned forests. However, differences in average richness and abundance between treatments were inconsistent over time; lower ant abundance and species richness in burned sites occurred only during the first few months postburn. Ant species composition was very similar between treatments, although some species typically associated within mesic and lowland habitats were found only in unburned forests. We conclude that litter ant communities in Ozark forests, as in other regions, are relatively resilient to the effects of prescribed burning.

KEY WORDS abundance, Arkansas, community, disturbance, fire

Fire is an important source of disturbance in many terrestrial biomes, and is a key determinant of plant and animal community structure in fire-prone forests worldwide (Sousa 1984, Anderson 1990, Abrams 1992). Forest insect communities are particularly sensitive to fire (e.g., Baker 1972; York 1994, 1999; Ratchford et al. 2005; Verble and Stephen 2009; but see Buffington 1967). Even mild fires moving through a forest should have pronounced short-term effects on insect community structure (i.e., widespread reduction in abundance and species richness because of catastrophic heat exposure; Ahlgren and Ahlgren 1960, Panzer and Schwartz 2000, Swengel 2001, Hanula and Wade 2003). However, many taxa inhabiting fire-prone landscapes possess traits promoting escape or resistance of the lethal effects of fire (e.g., Linsley 1943, Wikars 1997), and some may benefit from frequent fires over long time scales (e.g., Andersen 1991, Moretti and Barbalat 2003, Moretti et al. 2004). Here, we examine the effects of prescribed fire on leaf litter ant communities in Ozark oak-dominated forests.

Given their propensity for nesting in protected microhabitats such as soil, hollow limbs, and damp dead wood, it is likely that forest ants are particularly well insulated from the immediate effects of fire. Indeed, fire sometimes has minimal effects on ant assemblages (Coleman and Rieske 2006, Pryke and Samways 2012), and fire may increase ant abundance and diversity under some circumstances (Miller 1979, Wilkinson et al. 2005). Whereas ant communities change in response to fire frequency and seasonality over long time scales (Andersen 1991, New and Hanula 1998, Castaño–Meneses and Palacios–Vargas 2003, Hanula and Wade 2003, Stephens and Wagner 2006), we know relatively little about the short-term effects of fire on ant community parameters such as species richness and composition. Ants are a particularly good focal group for such studies because they are diverse, widespread, and ecologically relevant (Hölldobler and Wilson 1990, Lach et al. 2010), and are potential indicators of disturbance (MacKay 1993, Andrew et al. 2000, Stephens and Wagner 2006, Sorvari and Hakkarainen 2007). Moreover, forest ants in Arkansas are relatively poorly known (Warren and Rouse 1969).

The principal goal of this study was to examine the short-term effects of prescribed burning on ant community structure in Ozark forests of Arkansas. Given that fires modify abiotic conditions and the availability of resources important to insects, such as nest sites, cover, and food (Ahlgren and Ahlgren 1960), we predicted that ant species richness and abundance would be significantly reduced in recently burned areas relative to adjacent unburned sites.

Materials and Methods

Study Area. The Ozark Mountain Ecoregion extends from Missouri to Arkansas and Oklahoma at elevations of 75–750 m above sea level. Typical Ozark

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forest vegetation includes second-growth hardwood and mixed pine stands on poor shallow soils and xeric slopes (Read 1952). Fire (both natural and managed) has been shaping Ozark forests for centuries (Van Lear 2004). Historically, low to moderate intensity fires disturbed these temperate zone oak-hickory forests at frequent intervals (mean interval = 7 yr; Whelan 1995, Foti 2004). Currently, Ozark fire managers burn large contiguous areas (200–2,800 ha) of forests each year to reduce fuel accumulations, release nutrients, control insects, and increase native species abundance (Russell et al. 1999).

Sampling Protocol. Five replicate study sites were established in Ozark oak-hickory forest. Each replicate site included a large (>50 ha) burned treatment area and a similar adjacent unburned treatment area. All burns used in this study occurred during the 2010 prescribed fire season (February–April). We defined unburned areas as stands that had not burned since 1980. Each site was characterized by its tree species composition, tree density (number of trees per hectare), tree size (diameter at breast height [DBH]), and composite fire characteristics (proportion of trees with char, proportion of trees with char at 1.5 m on the bole). Tree density was estimated by counting the number of trees >10 cm DBH and converting the result to trees per hectare.

Ants were sampled at each site between 10:00–16:00 hours in fair weather using three standard techniques: 1) tuna baits placed on the litter and on tree trunks; 2) hand collecting for 40 min; and 3) extraction from litter using Berlese funnels (Southwood 1978). Baits consisting of ≈5 g of canned tuna (in water) mixed with honey were placed in ten distinct locations on the surface of the leaf litter and on 20 tree trunks ≈1.5 m above the ground. Baits were examined multiple times (ca. every 10 min) over a 60 min period. Hand collecting consisted of targeted visual searches for ants on the surface of litter, on exposed rocks or soil, within small twigs, and on tree trunks.

Samples for Berlese extraction were collected from ten 0.5×0.5 m (0.25 m^2) quadrats located haphazardly within each site. Litter depth was measured to the nearest 1 cm in each quadrat center before sample collection by inserting a metal wire vertically through the litter down to mineral soil. We collected all leaf litter within each quadrat and separated the coarse material from the fine leaf fragments and arthropods in a 1 cm mesh litter sifter (Bestelmeyer et al. 2000). The siftate was transported to the laboratory in cloth bags and transferred to a Berlese funnel (30.5 cm diameter, 25 watt bulb, 24 h) to extract the ants. Ant sampling began 30–60 d postfire depending on the site, and was repeated monthly for 4 mo (April through July 2010). We took care to collect samples from different locations within a site on different dates.

Collected ants were stored in 95% ethanol and identified to species or morphospecies using published keys. Problematic specimens were confirmed by taxonomists, and voucher specimens were deposited in the Watson Museum of Entomology at the University of Arkansas at Little Rock.

Data Analysis. Statistical analyses used data only from Berlese extractions because baiting and hand collecting yielded no additional species. We used a hierarchical experimental design replicated in space and over time, with individual Berlese collections treated as independent samples nested within sites, and sites nested within treatments ($n = 400$ samples: 2 treatments × 5 replicate sites × 10 Berlese samples per treatment × 4 sample dates). All data were checked for normality (Shapiro–Wilk), and log-transformed when necessary to correct variance heterogeneity (Sokal and Rohlf 1995).

We used a nested analysis of covariance (ANCOVA) to test the effects of treatment (burned/unburned) and sites nested within treatments on ant abundance and species richness, with days since fire as a covariate. We used this approach rather than a repeated-measures analysis because the time interval between the burn and the first sample differed by as much as 30 d among sites because of logistical constraints. Forest stand characteristics were compared among sites with a multivariate analysis of variance (MANOVA) and multiple contrasts to determine if sites differed in habitat structure and composition. All analyses were conducted with SAS software (SAS Institute 2008).

Cumulative ant species richness was additionally compared between treatments using rarefaction-based species accumulation curves generated by the program EstimateS (Colwell 2009). Such curves illustrate how the number of species captured compares to the number of species that are likely present at a site, based on the number of new species added per sample.

Results

We collected 6,301 ants representing 59 species over the 4 mo sampling period (Table 1). Our Berlese samples contained an average of 13.5 ants (range = 0–182) and 2.2 ant species (range = 0–11). Rarefaction curves showed that the sampling design captured >80% of the species that are likely present in the region (Fig. 1), and that cumulative species richness was greater in the unburned treatment (Fig. 2).

The number of ant species found in a sample increased with ant abundance ($R^2 = 0.32$; $F_{1,398} = 188.9$; $P < 0.0001$), and average species richness and abundance showed similar declining trends over the course of the study (Figs. 3 and 4). The ANCOVA yielded significant time*treatment(site) interactions for both ant abundance and ant species richness ($F_{8,381} > 4.7$; $P < 0.0001$ in both cases), indicating that differences between the treatments were inconsistent over time since burn. Specifically, the biologically important effects of fire on ant communities are limited to a relatively short postfire time interval (i.e., <60 d), which is evident when means are plotted for data pooled by time categories (Figs. 3 and 4).

The species composition of ants collected in this study was typical for the region (see MacGown 2011).

Table 1. Ants collected in the study

Subfamily	Species	% burned	% unburned
Amblyoponinae	*Stigmatomma pallipes*	<1	<1
Dolichoderinae	*Forelius pruinosus*	<1	<1
	Tapinoma sessile	<1	<1
	Linepithema humile	<1	<1
Formicinae	*Camponotus americanus*	<1	<1
	C. castaneus	<1	<1
	C. decipiens	0	<1
	C. nearcticus	<1	<1
	C. pennsylvanicus	<1	<1
	Formica pallidefulva	<1	<1
	F. subsericea	<1	<1
	Lasius alienus	<1	<1
	L. interjectus	<1	0
	L. neoniger	0	<1
	Nylanderia parvula	16.8	10.8
	Paratrechina longicornis	<1	<1
	Prenolepis impairs	2.1	2.3
Myrmicinae	*Aphaenogaster carolinensis*	0	<1
	A. fulva	<1	1.4
	A. rudis	1.2	1.8
	A. texana	4.2	2.5
	A. treatae	<1	0
	Crematogaster ashmeadi	1.3	1.0
	C. lineolata	2.2	2.3
	C. sp. 1	<1	<1
	Monomorium minimum	<1	<1
	M. sp. 1	0	<1
	Myrmecina americana	<1	<1
	Myrmica pinetorum	<1	<1
	M. punctiventris	<1	<1
	Pheidole dentigula	<1	<1
	P. diversipilosa	<1	<1
	P. lamia	<1	<1
	P. tysoni	<1	<1
	Solenopsis molesta	10.8	6.2
	Stenamma brevicorne	<1	<1
	S. diecki	<1	<1
	Strumigenys bimarginata	<1	<1
	S. clypeata	0	<1
	S. dietrichi	<1	0
	S. louisianae	<1	<1
	S. ohioensis	<1	<1
	S. ornata	<1	<1
	S. pergandei	<1	0
	S. rostrata	<1	<1
	S. sp. 1	0	<1
	Temnothorax ambiguous	<1	0
	T. curvispinosus	<1	<1
	T. pergandei	<1	<1
	T. schaumii	<1	<1
	Tetramorium caespitum	<1	<1
	T. sp. 1	<1	<1
	Wasmannia auropunctata	<1	<1
Ponerinae	*Hypoponera opaciceps*	<1	<1
	H. opacior	<1	<1
	Ponera exotica	4	3.5
	P. pennsylvanica	3	4.5
Proceratinae	*Discothyrea testaceae*	0	<1
	Proceratium sp. 1	<1	<1

% = percent of total collection represented by each species.

Most species were broadly distributed among treatments and were collected in both burned and unburned sites. Burned and unburned forests shared 43 species among a total of 51 species collected in each. *Discothyrea testaceae* Roger, a relatively uncommon species, was found exclusively in unburned forests. Likewise, mesic and low elevation species such as *Aphaenogaster carolinensis* Wheeler, *Strumigenys clypeata* Roger, and *Stenamma* spp. were found only in samples from unburned forests.

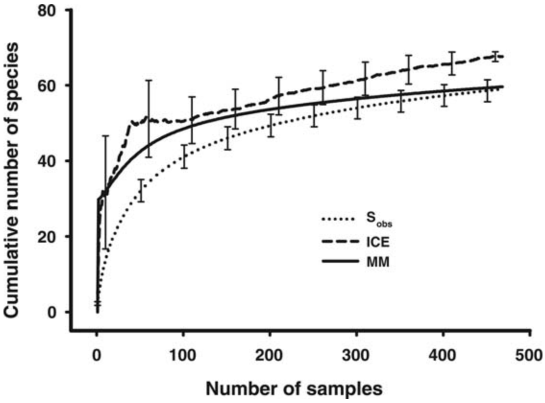

Fig. 1. Species accumulation curves for ants collected in the study. S_{obs} (Mao Tau), Incidence-based (ICE Mean), and Michaelis–Menten (MMMeans) were used as estimators of overall species richness. Bars represent ±1 SD.

Average leaf litter depth differed among treatments and sites, with burned forests consistently having less litter than unburned forests; however, average litter depth at a site on a given date did not explain variation in ant abundance ($R^2 = 0.03$; $F_{1,37} = 1.14$; $P = 0.29$) or ant species richness ($R^2 = 0.01$; $F_{1,37} = 0.42$; $P = 0.52$). Composite site and stand characteristics (proportion of trees with char, proportion of trees with char at 1.5 m on the bole, DBH) did not differ among sites ($F_{27,507} = 1.09$, $P = 0.35$; Table 2).

Discussion

Here we show that prescribed fire reduces ant abundance and species richness in Ozark forests, but that such effects are of relatively short duration; ant community parameters were similar in burned and unburned sites within a few months postburn. Whereas some studies report strong negative effects of

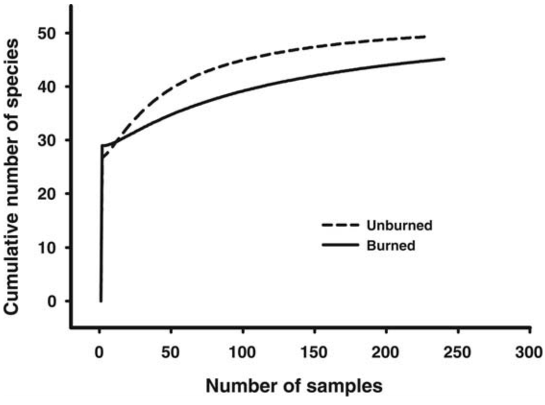

Fig. 2. Michaelis–Menten species accumulation curves by treatment.

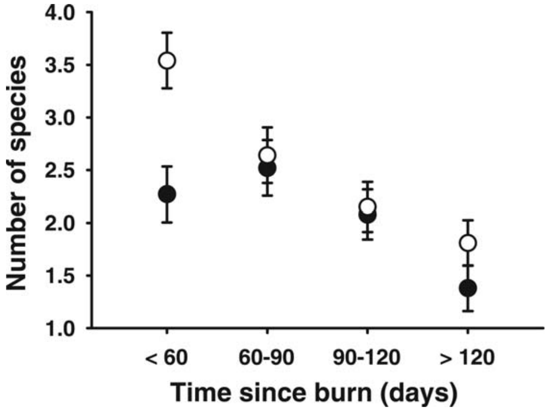

Fig. 3. Average (±SE) ant species richness in burned (filled circles) and unburned (open circles) treatments over time since burn. Data were pooled into discrete time intervals for clarity of presentation and not for statistical analyses; ANCOVA results for the unpooled data revealed an interaction between treatment effects over time (see text).

fire on ants and other insects (Andrew et al. 2000), results of this and other comparative studies indicate that litter and ground-dwelling ants are relatively resilient to the effects of fire (e.g., Parr et al. 2004, Pryke and Samways 2012). Resiliency (i.e., the time required for recovery to prefire community structure) is highly variable among insect taxa (Pryke and Samways 2012), and depends on fire conditions, habitat structure, and various other factors. Recovery times may be quite short (i.e., weeks or months; Buffington 1967) or protracted (a decade or longer; Moretti et al. 2006), although 1–5 yr appears to be typical (York 1994, Hanula and Wade 2003, Stephens and Wagner 2006). Ozark ants fall on the short end of this spectrum, indicating that fire effects on ants are not as catastrophic as we predicted.

The high resiliency of Ozark litter ants to fire suggests that the observed reduction in ant abundance and species richness immediately postfire is at least partly driven by behavioral changes rather than loss of nesting habitat. Ant activity on burned sites was conspicuously lower in the weeks after the fire, suggesting that burned habitats are suboptimal for foraging (Farji–Brener et al. 2002), perhaps because of lack of food or cover, or ash toxicity (e.g., Edwards and Schwartz 1981). Fires reduce leaf litter depth to near zero and increase light in the understory (Rieske et al. 2002, Kay et al. 2007), thus soil- and litter-dwelling ants are more highly exposed while foraging after a fire, potentially leading to higher desiccation rates or increased predation by ant-specialist foragers (e.g., Torgensen 1995).

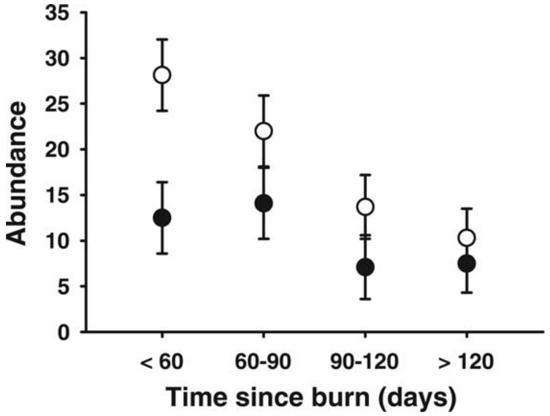

Fig. 4. Average (±SE) ant abundance in burned (filled circles) and unburned (open circles) treatments over time since burn. Data were pooled for clarity as described in Fig. 3.

We suspect that the gradual decline in ant abundance and species richness over the course of this study resulted from the unusually high average summer temperatures and drought that occurred during the study period (National Weather Service 2011). No studies have examined seasonal patterns of ant activity specifically in the Ozarks; however, temperature extremes can strongly affect ant activity (e.g., Hölldobler and Wilson 1990, Bestelmeyer 2000), and it is likely that ant activity consistently declines with the onset of hotter and drier summer conditions in the region.

Although the structure of ant communities was very similar between burned and unburned forests, the minor differences in species composition we observed are consistent with results of other studies showing that fire influences local species distributions (York 1994, Parr et al. 2004, Moretti et al. 2006, Stephens and Wagner 2006). Similarly, the presence of certain mesic and low elevation species only in our unburned sites may be because of the cooler, more humid conditions in unburned forests relative to burned forests (Swift et al. 1993).

The timing of prescribed burns has potentially important implications for the maintenance (or control) of insect populations. Insects active in the early spring are likely to be destroyed during prescribed burning (e.g., Schaber and Entz 1988), thus delaying burning until the dormant season may be necessary for conservation of threatened taxa (Panzer 2002). Among Ozark ants, *Stenamma* spp. are perhaps the most likely to be sensitive to the timing of fires. Temperate *Stenamma* spp. are twig-nesters that prefer cooler, humid conditions (Backus and Herbers 2009), and tend to be active in Arkansas only in the early spring (R. M. Verble, personal observation). Given that most oak-hickory forests burn in early spring in Arkansas, it is likely that prescribed burning facilitates local extinctions of *Stenamma* spp., although this remains to be tested.

In summary, we show that ant communities are significantly altered by prescribed fire in Ozark oak forests, but recover from the effects of fire relatively rapidly. The addition of preburn data collection would strengthen our conclusions; however, this was not possible because of uncertainty in fire schedules (i.e., prescribed burn managers cannot guarantee that a site will burn on a specific day or week). Regardless, the temporal and spatial replication used in this study support the conclusion that the results are represen-

Table 2. Characteristics of forest sites used in the study

Plot	N Lat.	W Long.	Burn Month	DBH	Composition	Char1	Char2	Trees per ha
Baker	35.976	92.842	n/a	23.8	Oak-hickory	0	0	375
Baker Burn	35.975	92.842	Feb.	25.4	Oak-hickory	18	11	425
Clarksville	35.654	93.417	n/a	26.1	Oak-hickory	0	0	450
Clarksville Burn	35.613	93.418	Feb.	28.6	Oak-pine	16	5	475
Erbie	36.096	92.253	n/a	28.6	Oak-maple	0	0	550
Erbie Burn	36.095	92.225	Mar.	27.2	Oak-hickory	0	0	550
Hobbs	36.295	93.975	n/a	24.9	Oak-hickory	0	0	475
Hobbs Burn	36.291	93.417	Mar.	25.4	Oak-hickory	18	6	425
Sorghum	35.261	93.509	n/a	24.9	Oak-pine	0	0	375
Sorghum Burn	35.261	93.505	Mar.	21.7	Oak-pine	13	5	375

DBH is the avg diam at breast ht (cm) for trees >10 cm within the study area. *Composition* is a qualitative determination of the two most abundant tree genera at a site. *Char1* is the percent of trees >10 cm DBH that have char postfire. *Char2* is the percent of trees charred at or above 1.5 m on the trunk.

tative of patterns occurring in the region during the burn season. Information about Ozark ant ecology is very limited, and our results provide a foundation for future experimental studies focusing on the mechanisms by which ants respond to fire. Appropriate extensions of this work could include quantification of ant recolonization on burned sites, and investigations of behavioral or physiological mechanisms of heat tolerance or fire avoidance in ants. This and related projects ultimately will provide a biological framework for appropriately managing fire in the Ozarks in the face of changing climatic conditions (e.g., Dale et al. 2001).

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References Cited

Abrams, M. D. 1992. Fire and the development of oak forests. Bioscience 42: 346–353.

Ahlgren, I. F., and C. E. Ahlgren. 1960. Ecological effects of forest fires. Bot. Rev. 26: 483–517.

Andersen, A. N. 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. Biotropica 23: 575–585.

Anderson, R. C. 1990. The historic role of fire in the North American grassland, pp. 8–18. *In* S. L. Collins and L. L. Wallace (eds.), Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman.

Andrew, N., L. Rodgerson, and A. York. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. Aust. Ecol. 25: 99–107.

Backus, V. L., and J. M. Herbers. 2009. Demography and reproduction in the cavity-dwelling ant *Stenamma diecki* (Emery) (Hymenoptera: Formicidae). Northeastern Nat. 16: 113–124.

Baker, W. L. 1972. Eastern forest insects. USDA Forest Service Miscellaneous Publication 1175.

Bestelmeyer, B. T. 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. J. Animal Ecol. 69: 998–1009.

Bestelmeyer, B. T., D. Agosti, L. E. Alonso, R. F. Brando, W. L. Brown, Jr., J.H.C. Delabie, and R. D. Silvestre. 2000. Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation, pp. 125–145. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Shultz (eds.), Ants: Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, Washington, DC.

Buffington, J. D. 1967. Soil arthropod populations of the New Jersey pine barrens as affected by fire. Ann. Entomol. Soc. Am. 60: 530–535.

Castaño–Meneses, G., and J. G. Palacios–Vargas. 2003. Effects of fire and agricultural practices on neotropical ant communities. Biodivers. Conserv. 12: 1913–1919.

Coleman, T. W., and L. K. Rieske. 2006. Arthropod responses to prescription burning at the soil-litter interface in oak-pine forests. Forest Ecol. Manag. 233: 52–60.

Colwell, R. K. 2009. EstimateS: statistical estimation of species richness and shared species from samples, version 8.2. (http://purl.oclc.org/estimates).

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. M. Wotton. 2001. Climate change and forest disturbances. Bioscience 51: 723–734.

Edwards, J. S., and L. M. Schwartz. 1981. Mount St. Helens ash: a natural insecticide. Can. J. Zool. 59: 714–715.

Farji–Brener, A. G., J. C. Corley, and J. Bettinelli. 2002. The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context. Divers. Distrib. 8: 235–243.

Foti, T. L. 2004. Upland hardwood forests and related communities of the Arkansas Ozarks in the early 19th century, pp. 21–29. *In* M. A. Spetich (ed.), Upland Oak Ecology Symposium. USDA Forest Service, Asheville, NC.

Hanula, J. L., and D. Wade. 2003. Influence of long-term dormant season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. Forest Ecol. Manag. 175: 163–184.

Hölldobler, B. and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, MA.

Kay, A. D., J. D. Schade, M. Ogdahl, E. O. Wesserle, and S. E. Hobbie. 2007. Fire effects on insect herbivores in an oak savanna: the role of light and nutrients. Ecol. Entomol. 32: 754–761.

Lach, L., C. L. Parr, and K. L. Abbott. (eds.). 2010. Ant ecology. Oxford University Press, New York, NY.

Linsley, G. E. 1943. Attraction of *Melanophila* beetles by fire and smoke. J. Econ. Entomol. 35: 341–342.

MacGown, J. A. 2011. Ants of Mississippi. (http://mississippientomologicalmuseum.org.msstate.edu/).

MacKay, W. P. 1993. Succession of ant species (Hymenoptera: Formicidae) on low-level nuclear waste sites in northern New Mexico. Sociobiology 23: 1–11.

Miller, W. E. 1979. Fire as an insect management tool. Entomol. Soc. Am. Bull. 25: 137–140.

Moretti, M., P. Duelli, and M. K. Obrist. 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149: 312–327.

Moretti, M., and S. Barbalat. 2003. The effects of wildfires on wood-eating beetles in deciduous forests on the southern slope of the Swiss Alps. Forest Ecol. Manag. 187: 85–103.

Moretti, M., M. K. Obrist, and P. Duelli. 2004. Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the southern Alps. Ecography 27: 173–186.

National Weather Service. 2011. Little Rock yearly climate summary (2010). (http://www.srh.weather.gov/lzk/?n=2010.htm).

New, K. C., and J. L. Hanula. 1998. Effects of time elapsed after prescribed burning in longleaf pine stands on potential prey of the red-cockaded woodpecker. Southern J. Appl. For. 22: 175–183.

Panzer, R., and M. Schwartz. 2000. Effects of management burning on prairie insect species richness within a system of small highly fragmented reserves. Biol. Conserv. 96: 363–369.

Panzer, R. 2002. Compatibility of prescribed burning with conservation of insects in small, isolated prairie reserves. Conserv. Biol. 16: 1296–1307.

Parr, C. L., H. G. Robertson, H. C. Biggs, and S. L. Chown. 2004. Response of African savanna ants to long-term fire regimes. J. Appl. Ecol. 41: 630–642.

Pryke, J. S., and M. J. Samways. 2012. Differential resilience of invertebrates to fire. Aust. Ecol. 37: 460–469.

Ratchford, J. S., S. E. Wittman, E. S. Jules, A. M. Ellison, N. Gotelli, and N. J. Sanders. 2005. The effects of fire, local environment and time on ant assemblages in fens and forests. Divers. Distrib. 11: 487–497.

Read, R. A. 1952. Tree species occurrence as influenced by geology and soil on an Ozark north slope. Ecology 33: 239–246.

Rieske, L. K., H. H. Housman, and M. A. Arthur. 2002. Effects of prescribed fire on canopy foliar chemistry and suitability for an insect herbivore. Forest Ecol. Manag. 160: 177–187.

Russell, K. R., D. H. Van Lear, and D. C. Guynn. 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Soc. Bull. 27: 374–384.

SAS Institute. 2008. SAS OnlineDoc. SAS Institute, Cary, NC.

Schaber, B. D., and T. Entz. 1988. Effect of spring burning on insects in seed alfalfa. J. Econ. Entomol. 81: 668–671.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. W. H. Freeman and Company. San Francisco, CA.

Sorvari, J., and H. Hakkarainen. 2007. Wood ants are wood ants: deforestation causes population declines in the polydomous wood ant *Formica aquilonia.* Ecol. Entomol. 32: 707–711.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. 15: 353–391.

Southwood, T.R.E. 1978. Ecological methods, with particular reference to the study of insect populations. Chapman & Hall, New York, NY.

Stephens, S. S., and M. R. Wagner. 2006. Using ground foraging ant (Hymenoptera: Formicidae) functional groups as bioindicators of forest health in northern Arizona ponderosa pine forests. Environ. Entomol. 35: 937–949.

Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation methods of open habitat. Biodivers. Conserv. 10: 1141–1169.

Swift, L. W., K. J. Elliott, R. D. Ottmar, and R. E. Vihnanek. 1993. Site preparation burning to improve southern Appalachian pine-hardwood stands: fire characteristics and soil erosion, moisture, and temperature. Can. J. Forest Res. 23: 2242–2254.

Torgensen, T. R. 1995. Down logs as habitat for forest-dwelling ants: the primary prey of pileated woodpeckers in northeastern Oregon. Northwest Sci. 69: 294–303.

Van Lear, D. H. 2004. Upland oak ecology and management, pp. 65–71. *In* M. A. Spetich (ed.), Upland Oak Ecology Symposium. USDA Forest Service, Asheville, NC.

Verble, R. M., and F. M. Stephen. 2009. Occurrence of carpenter ants in Ozark forests in relation to prescribed fire and stand variables. Southern J. Appl. Forestry 33: 42–45.

Warren, L. O., and E. P. Rouse. 1969. The ants of Arkansas. University of Arkansas Agricultural Experiment Station Bulletin, Fayetteville, AR.

Whelan, R. J. 1995. The ecology of fire. Cambridge University Press. New York, NY.

Wikars, L.-O. 1997. Effects of forest fire and the ecology of fire-adapted insects. Doctoral thesis. Uppsala University, Sweden.

Wilkinson, E. B., E. G. Lebrum, M. L. Spencer, C. Whitby, and C. Kleine. 2005. Short-term effects of fire on Sky Island ant communities. USDA Bulletin RMRS-P-36.

York, A. 1994. The long-term effects of fire on forest ant communities: management implications for the conservation of biodiversity. Mem. Queesland Mus. 36: 231–239.

York, A. 1999. Long term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. J. Insect Conserv. 3: 191–199.

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