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GROUND-DWELLING ARTHROPOD ASSOCIATION WITH COARSE WOODY DEBRIS FOLLOWING LONG-TERM DORMANT SEASON PRESCRIBED BURNING IN THE LONGLEAF PINE FLATWOODS OF NORTH FLORIDA

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ABSTRACT

A 5-year study of long-term (40 years) study plots was conducted on the Osceola National Forest in northern Florida to determine how dormant-season fire frequency (annual, biennial, quadrennial, or unburned) affects ground-dwelling macroarthropod use of coarse woody debris in longleaf pine (*Pinus palustris* Mill.) forests. Pitfall traps were used to sample arthropods near logs or metal drift fences of equal length. Samples were identified to genus or the lowest practical taxonomic level. Overall, significantly more arthropods and more arthropod biomass were captured near drift fences than near logs. Similarity of arthropods captured near logs or drift fences ranged from 64.4% in annually burned plots to 69.2% in quadrennially burned plots, with no significant differences noted. Likewise, Shannon diversity, evenness, richness, and number of rare genera were the same for traps regardless of the trap location. Interaction between fires and trap location were observed in 31 of 932 arthropod taxa. Of those, 10 taxa had significantly higher numbers captured in traps near logs in some burn treatments but there was no consistent pattern between log use and fire frequency. In most cases, more were captured in log pitfalls in frequently burned plots but that was not the case for at least 4 taxa. Where interactions between trap location and fire frequency were not significant, arthropods in an additional 101 taxa were captured in higher numbers at 1 trap location or the other. Of those, 73 were captured in higher numbers in pitfalls near drift fences and 28 were captured in higher numbers near logs. Results showed no increase in log usage by general or more mobile ground-dwelling arthropods as more frequent burning reduced the herbaceous and woody under story. However, logs were clearly important to a wide variety of arthropods regardless of burn frequency.

Key Words: prescribed burning, coarse woody debris, habitat heterogeneity

RESUMEN

Una investigación de 5 años usando parcelas de estudio de largo plazo (40 años) fue realizado en el Bosque Nacional de Osceola en el norte del estado de la Florida para determinar como la frecuencia de los incendios en la estación latente (anual, bienal, cuadrienal o no quemada) afecta el uso de los escombros leñosos en bosques del pino, *Pinus palustris* Mill. por los macroartropodos que viven en el suelo. Se usaron trampas de caída para muestrear los artrópodos cerca de troncos o de postes metálicos de retensión de una misma longitud. Las muestras fueron identificadas al nivel de género o al nivel taxonómico más práctico. Sobretodo, se capturaron significativamente mas artrópodos con un mayor cantidad de biomasa cerca de los postes metálicos que cerca de los troncos. La similitud de los artrópodos capturados cerca de los troncos y los postes metálicos varia de 64.4% en las parécelas quemadas anualmente a 69.2% en las parcelas quemadas cuadrienales (cada 4 años) sin diferencias significativas anotadas. Asimismo, la diversidad Shannon, la igualdad, riqueza y el número de géneros raros fueron los mismos en las trampas a pesar de la ubicación de la trampa. Se observaron la interacción entre los incendios y la ubicación de las trampas en 31 de los 932 taxa de artrópodos. De estos, 10 taxa tuvieron un mayor número capturados en trampas cerca de los troncos en algunos de los tratamientos quemados pero no hubo un patrón consistente entre el uso de los troncos y la frecuencia de los incendios. En la mayoría de los casos, se capturaron más en las trampas de caída puestas cerca de los troncos en las parcelas quemadas frecuentemente pero esto no fue el caso en por lo menos 4 taxa. Donde las interacciones entre la ubicación de la trampa y la frecuencia del incendio no fueron significativas, los artrópodos en 101 taxa adicionales fueron capturados en números más altos en la 1 ubicación de trampa o la otra. De estos, 73 fueron capturados en números mas altos en trampas de caída cerca de los postes metálicos y 28 fueron capturados en números mas altos cerca de los troncos. Los resultados mostraron ningún aumento en el uso de los troncos por los artrópodos generales o los más móviles que viven en el suelo mientras que la quemada mas fre-

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cuente redujo la vegetación herbácea y leñosa en las plantas bajeras. Sin embargo, los troncos fueron claramente importantes a una amplia variedad de artrópodos a pesar de la frecuencia de la quema.

Large dead wood in terrestrial forest habitats is an important resource for a number of arthropods and other animals that use it for food, oviposition sites, protection from environmental extremes, and foraging habitat (Elton 1966; Harmon et al. 1986; Grove 2002). Within this habitat saproxylic arthropod communities vary with species of tree, stage of decomposition, types of fungal colonists, and location (aquatic to xeric) of dead wood in the landscape (Harmon et al. 1986; Speight 1989; Økland et al. 1996; Grove 2002). In addition to direct contribution to forest diversity, saproxylic arthropods are an important part of the food web supporting a variety of predators and parasites (Harmon et al. 1986). Considerable research on coarse woody debris and its function in forests has been done in North America but most of the emphasis has been in the Pacific Northwest and Canada (Harmon et al. 1986; Woldendorp et al. 2002). Within North America there is a large body of literature on the Scolytinae (Curculionidae: Coleoptera) and their associates but relatively little work on other saproxylic species or those that occur in later stages of decay (Savely 1939; Howden & Vogt 1951; Hammond et al. 2001, 2004), and less is known about how dead wood affects the distribution of arthropods that may be associated with it but not totally dependent on it (Irmler et al. 1996; Marra & Edmonds 1998; Andrew et al. 2000; Buddle 2001). Despite the growing interest in this topic, interactions between woody debris and arthropod communities in the Southeastern United States have received little attention (McMinn & Crossley 1996) and this is particularly true for longleaf pine (*Pinus palustris*) forests.

Longleaf pine once occupied about 30 million hectares in the Southeastern region of North America (Frost 1993). Today <1.3 million hectares remain as small, isolated parcels (Outcalt & Sheffield 1996) resulting in longleaf pine and associated communities being classified as the third most endangered ecosystem in the United States (Noss et al. 1995). Conservation and restoration of these communities is a priority for forest management and conservation groups throughout the region (Van Lear et al. 2005).

Prior to European arrival in North America, longleaf pine communities were maintained by frequent fires (1-3 year intervals) started by lightning or Native Americans (Landers 1991) but this is no longer the norm. An unanticipated result of reduced fire frequency is the increased accumulation of fuels which foster fires that are significantly more likely to damage both the environment and stand improvements, and pose a much greater threat to human health and safety (Oultcalt & Wade 2004). A number of remedies are available and, although prescribed burning is the only alternative that addresses the full suite of ecosystem components, other alternatives are commonly chosen to achieve short-term results (Van Lear et al. 2005). Even when fire is used, these remaining longleaf pine communities are often not managed under the appropriate fire regime (Brose & Wade 2002).

A number of studies and reviews have looked at effects of fire on arthropods but no clear general trends have emerged (Rice 1932; Heyward & Tissot 1936; Pearse 1943; Buffington 1967; Ahlgren 1974; Hurst 1971; Warren et al. 1987; Muona & Rutanen 1994; Buddle et al. 2000; Niwa & Peck 2002; Hanula & Wade 2003). However, despite the lack of a general trend, fire has a significant effect on many epigaeic arthropods and this is particularly true for the longleaf pine flatwoods ecosystem where it reduces diversity, community similarity and populations of many taxa (Hanula & Wade 2003). In addition to direct mortality, fire alters the forest habitat and community structure resulting in either positive or negative effects on a given species. For example, by reducing predators (spiders, centipedes, ground beetles, etc.) some species may experience population increases or, conversely, reductions in prey may reduce predator populations. Fire may also reduce food for detritivores (e.g., termites) and cover for other species. By removing refuges such as litter or low growing shrubs, fire may increase susceptibility to predation, temperature extremes or desiccation.

Elton (1966) recognized the importance of woody debris as a source of forest diversity and he noted that as wood decomposes it is increasingly colonized by generalists that do not require specific tree species or even depend on woody debris as their sole habitat. For example, Irmler et al. (1996) found that the increasing variety of wood-dwelling species as dead wood aged was due largely to immigration of litter dwelling species to dead wood and to species using dead wood for overwintering. Likewise, Cárcamo & Parkinson (1999) reported that decomposed coarse woody debris was a major factor in shaping ground beetle assemblages, and Evans et al. (2003) and Jabin et al. (2004) reported that proximity to logs was an important factor in shaping litter-dwelling invertebrate communities. These studies demonstrate the role dead wood can play in shaping epigaeic arthropod communities, which can in turn affect a variety of ecological processes (Evans et al. 2003; Jabin et al. 2004).

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While planning a study on the long-term effects of frequent dormant-season burning on epigaeic arthropods (Hanula & Wade 2003) we hypothesized that the presence of coarse woody debris would be more important to these arthropods on annually burned plots where much of the leaf litter, understory vegetation and structure is sparse and has little time to recover between burns. To address this hypothesis, we conducted a study over a 5-year period to examine whether the presence of woody debris influenced pitfall trap captures under varying burn frequencies in a longleaf pine forest. In addition, we measured the amount of coarse woody debris and other habitat variables to determine how long-term frequent burning interacted with these variables to shape the epigaeic arthropod community.

Materials and Methods

Study Site and Prescribed Burn Treatments

The study was conducted in the Osceola National Forest in Baker County, Florida. Study plots were established in 1958 to examine effects of burning frequency on fuel reduction for wildfire prevention. At that time the overstory trees were 45-year-old longleaf pines that were 20 m tall and 29 cm diameter (DBH) with a few slash pine (*P. elliottii*) of similar size. The presence of remnant "boxed" longleaf pine trees from past turpentine operations suggest that the area was never cleared for agriculture. The understory consists of typical flatwoods vegetation dominated by saw palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), *Vaccinium* sp. and wiregrass (*Aristida beyrichiana*). The study was a randomized complete block design consisting of 24, 0.8-ha plots arranged in 6 blocks of 4 treatments. Initial treatments were winter burns applied every 2, 4 or 6 years and unburned controls. However, in 1964 the 6-year interval treatment was replaced with annual winter burns. The entire site was burned in 1958 to initialize the study area, and treatments have been applied as scheduled since then between Dec and early Mar. Fire intensity varied from year to year depending on weather conditions, dead fine-fuel moisture content (which typically ranged from 7-20%), and firing techniques. Our study, superimposed on this long-term winter burn study, started in fall, 1994 just before the application of annual burns in the winter of 1994-1995. The study continued for the full cycle of burn treatments (annual, biennial, and quadrennial) ending after the quadrennial plots were again burned the winter of 1999-2000. Control plots had been unburned for 42 years at the close of our study.

We sampled the naturally occurring large dead wood on the plots in Dec 2003, three years after the study. Small dead wood was not affected by fire frequency on our plots (Hanula & Wade 2003), so it is unlikely that large dead wood was, and there was no evidence of increased tree mortality following our study so the delay in measuring this attribute did not result in significant changes in dead wood volumes between the time insects and dead wood were sampled. We estimated large dead wood volume by measuring the end diameters of all down woody debris in five 10-m wide transects which resulted in sampling approximately 50% of the plot surface. In addition, we conducted a 100% survey of standing dead wood. We used Huber's equation (volume = $m \times l$; where, m = mid-point cross-sectional area and l = length) to estimate volume of dead wood (Avery 1975). The mid-point diameter of downed wood was estimated by taking the average of the end diameters. The mid-point diameter of standing dead wood was estimated using taper equations for coastal plain longleaf pine (Clark et al. 1991).

Pre-burn live and dead plant biomass (dried) was estimated on each plot from eight 1-m^2 subplots. Details of sampling procedures for live and dead plant material can be found in Hanula & Wade (2003). Sampling methods were adapted from Shea et al. (1996). Two clusters of 8 transect lines were established in each plot. We ran 15 m long transects from the center of each cluster in the 4 cardinal directions and 4 additional 15-m long transects were established at 90° from the ends of the original transects. Sampling frames (1 m^2) were placed on the ground 4 m from the starting point of each transect. All stems <1.9 cm basal diameter were collected by category from each sample point, bagged, oven-dried at 42°C for a minimum of 48 h, and weighed. Plant biomass was separated into 11 categories consisting of (1) live palmetto, (2) dead palmetto, (3) live gallberry, (4) live pine needles (seedlings), (5) live grasses and forbs, (6) litter layer (O1 or L layer), (7) humus (O2 and O3 or F and H layers), (8) pine cones, (9) 0-0.6 cm dead branches, (10) 0.6-2.5 cm dead branches, and (11) other dead woody material.

Arthropod Sampling

We hypothesized that logs could function in two ways to increase trap captures of arthropods: (1) they could be a preferred habitat resulting in concentrations of arthropods around them, or (2) they could act as drift fences concentrating and directing arthropods normally wandering across the forest floor into traps near them. To determine if large dead wood was a preferred habitat or acted as a drift fence, we placed 3-m long logs of longleaf pine (20-25 cm diameter) in the center of each plot and installed pitfall traps along them immediately after felling. Four pitfall traps constructed from 480-mL capacity plastic cups (Hanula & Franzreb 1998) were installed near the log at plot center (2 on each side 0.5 m from each end)

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as close to the log as possible. To decrease the chances of an arthropod bypassing the pitfall by moving between the log and the pitfall we inserted wedge-shaped pieces of aluminum sheet metal into the space so that the metal sheeting created a barrier from the point where the log contacted the ground to the edge of the pitfall. A second set of 4 pitfall traps was installed along a 3-m long aluminum sheet metal drift fence (15 cm high). The drift fence was located 10 m from the center log. Traps were constructed and placed in the same manner as the log pitfalls except that the edge of each trap was in direct contact with the drift fence. Beginning in Jan 1995, pitfall traps were opened for month-long periods 6 times per year and covered with ceramic tiles during months when not in use to prevent arthropods from falling in. Arthropods collected in this way were placed in 70% ethyl alcohol, sorted to morphologically similar groups, and identified to genus or the lowest taxonomic level possible by using a reference collection and appropriate taxonomic keys. Biomass estimates were obtained by oven drying (40°C for 72 h) and weighing at least 20-30 specimens of each taxon. The average weight of these specimens was multiplied by the number of individuals within a sample to estimate sample biomass.

Statistical Analyses

Horn's simplification of Morisita's index of similarity was used to compare arthropod communities captured in the 2 types of traps (Horn 1966). We used richness and the Shannon diversity index to measure arthropod community diversity. Evenness was calculated to give further information about the arthropod communities among burn treatments. Calculations were based on the cumulative totals of each arthropod for each plot for the entire study period.

Because 2 trap locations were designated within each plot, the study was analyzed as a split-plot design. Analyses of variance were conducted with the SAS GLM procedure (SAS 1985) to test for interactions of burn frequency and trap location, and trap location effects. Model effects were burn treatment, trap location, block, treatment × block interaction, and burn treatment × trap location interaction. Analyses were conducted for taxa in which 30 or more individuals were caught during the entire study. Digweed et al. (1995) found evidence of depletion of certain Carabidae when traps were 10 m apart, so we also plotted annual captures of some common families and species to determine if there was any depletion effect from trapping 4 years at the same location or from drift fence pitfalls being 10 m from the pitfalls near logs.

In order to examine arthropod community responses, we used non-metric multidimensional

TABLE 1. PEARSON'S CORRELATION COEFFICIENTS AMONG ENVIRONMENTAL VARIABLES OF STUDY PLOTS IN A LONGLEAF PINE FOREST IN NORTH FLORIDA UNDERGOING DIFFERENT BURN FREQUENCIES. COEFFICIENTS MARKED WITH AN ASTERISK ARE SIGNIFICANT ($N = 24$, $P < 0.05$). THE ABBREVIATIONS STAND FOR THE FOLLOWING: FIRE FREQUENCY (FRQ), LITTER (LIT), HUMUS (HUM) SMALL DEAD WOOD (SWD), TOTAL DEAD PLANT MATERIAL (DEAD), LIVE GALLBERRY (GALL), LIVE PALMETTO (PALM), LIVE GRASSES (GRASS), TOTAL LIVE PLANT BIOMASS (LIVE), DOWN COARSE WOODY DEBRIS (DCWD) AND STANDING COARSE WOODY DEBRIS (SCWD).

FRQ	LIT	HUM	SWD	DEAD	GALL	PALM	GRASS	LIVE	DCWD	SCWD
FRQ	0.84*	0.90*	-0.08	0.93*	-0.14	0.86*	-0.54*	0.85*	-0.36	0.15
	LIT	0.85*	-0.15	0.86*	-0.23	0.82*	-0.51*	0.76*	-0.26	0.02
		HUM	-0.13	0.96*	0.01	0.88*	-0.60*	0.88*	-0.45*	0.11
			SWD	0.02	0.06	-0.20	0.02	-0.18	0.15	-0.15
				DEAD	-0.12	0.90*	-0.63*	0.88*	-0.42	0.14
					GALL	0.19	0.19	0.04	-0.16	0.05
						PALM	-0.62*	0.96*	-0.37	0.30
							GRASS	-0.66*	0.52*	-0.10
								LIVE	-0.44*	0.30
									DCWD	-0.12
										SCWD

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TABLE 2. COMPARISON OF SEVERAL MEASURES OF ABUNDANCE AND DIVERSITY OF ARTHROPODS CAPTURED IN PITFALL TRAPS NEAR LONGLEAF PINE LOGS OR DRIFT FENCES OF EQUAL LENGTH IN STUDY PLOTS IN A LONGLEAF PINE FOREST IN NORTH FLORIDA UNDERGOING DIFFERENT CONTROLLED BURN FREQUENCIES FROM 1994 TO 2000.

	Trap Location		
Variable	Drift fence (Mean ± SE)	Log (Mean ± SE)	P > F
Number of arthropods	3950.1 ± 192.9	2859.1 ± 101.8	<0.0001
Biomass (g dry wt/plot)	38.9 ± 3.5	27.4 ± 2.6	<0.0001
Shannon Diversity (H')	3.61 ± 0.06	3.54 ± 0.06	0.086
Evenness (J)	0.67 ± 0.01	0.66 ± 0.01	0.21
Richness (genera/plot)	216.8 ± 3.46	212.1 ± 3.41	0.25

Analyses of variance were conducted by the SAS GLM procedure (SAS 1985).

scaling analysis (NMDS) of trends in arthropod abundance in the study plots. We chose NMDS because there appeared to be an "arch effect" in a preliminary canonical correspondence analysis and because this method is more robust to variability in underlying patterns in morphospecies responses than are eigenvalue-based ordination techniques (Clarke 1993; Gaiser et al. 1998). Morphospecies that had less than 10 individuals were excluded resulting in a total of 184 morphospecies in the analysis. To examine responses of the arthropod community to environmental variables, we analyzed the relationship between the NMDS scores and environmental variables using vector analysis (Gaiser et al. 1998). Vector analysis, a form of indirect gradient analysis, is a regression of the environmental variables on the NMDS scores with the results displayed as vectors overlaid on a plot of NMDS scores. Because we were interested in coarse woody debris effects on arthropod community structure, and because fire frequency had such a strong effect on several variables, we excluded those environmental measures that were highly correlated to fire frequency (Table 1). We included fire frequency, gallberry biomass, small woody debris, downed coarse woody debris, and standing woody debris as the environmental variables in the vector analysis.

RESULTS

We caught significantly more total arthropods and a greater biomass of arthropods in pitfall traps near drift fences than in those near logs (Table 2). The similarity of what was caught in the 2 types of traps ranged from 64.4% (SE = 3.6) in the annually burned plots to 69.2% (SE = 1.4%) in the quadrennially burned plots, but there were no significant differences in similarity among burn treatments. Likewise, Shannon diversity, evenness, richness, and numbers of rare species were not significantly different for traps regardless of adjacent barrier.

We observed significant ($P < 0.05$) interactions between fire and trap location in 31 taxa (Table 3). Of those, 10 taxa had higher numbers captured in traps nears logs in some burn treatments (Fig. 1). However, there was no consistent pattern, i.e., in some cases frequent burning resulted in more of a given taxa near logs while infrequent or no burning had the same result for other taxa. In only a few cases did frequent burning result in concentrations of arthropods near logs, despite much lower leaf litter, less live herbaceous vegetation biomass, and reduced plant structure on those plots compared to unburned or quadrennially burned plots (Hanula & Wade 2003). Total volumes of coarse woody debris among burn treatments were not significantly different and ranged from a mean of 8.0 m^3/ha (SE = 1.01) for unburned control plots to 9.1 m^3/ha (SE = 1.73) on annually burned plots.

The Monte Carlo test results of the NMDS indicated a two-dimensional solution was optimal (final stress 11.73, $P = 0.0323$). The first 2 axes of the NMDS ordination explained 91.4% of the original variance, with the first axis explaining 69.6% and the second axis explaining an additional 21.8% (Fig. 2). The vector analysis indicated that fire frequency was correlated with both axes, more so with Axis 1 ($R^2 = 0.678$, $P < 0.05$) than Axis 2 ($R^2 = 0.574$, $P < 0.05$). DCWD was also significantly correlated to Axis 1 ($R^2 = 0.197$, $P < 0.05$) but not Axis 2. Other environmental variables were not correlated at $\alpha = 0.05$.

We captured over 932 genera in 5 years of trapping of which 297 were captured in sufficient numbers for analysis. Of those, 101 arthropod taxa were captured in significantly higher numbers in one trap type or the other (Table 3). When examining this many individual taxa, one is certain to encounter some significant results simply by chance. However, the 101 taxa represent 34% of the total number of arthropod taxa with 30 or more individuals. At $\alpha = 0.05$ one would only expect 5% to have been captured in statistically higher numbers by chance. Seventy three different arthropods were captured in significantly ($P < 0.05$) higher numbers in pitfalls

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TABLE 3. MEAN (±SE) NUMBER OF INDIVIDUALS OF ARTHROPOD TAXONOMIC GROUPS CAPTURED IN SIGNIFICANTLY ($P < 0.05$) HIGHER NUMBERS IN PITFALL TRAPS NEAR EITHER DRIFT FENCES OR LOGS PLACED IN STUDY PLOTS IN A LONGLEAF PINE FOREST IN NORTH FLORIDA UNDERGOING DIFFERENT CONTROLLED BURN FREQUENCIES, 1994-2000. ANALYSES OF VARIANCE WERE CONDUCTED BY SAS GLM PROCEDURE (SAS 1985).

			Drift Fence		Log		
Order	Family	Genus or Lowest Taxa	Mean	SE	Mean	SE	$P > F$
Scorpiones	Buthidae	*Centruroides*	11.9	1.5	2.8	0.6	<0.0001
Araneae	Ctenizidae	*Ummidia*	7.0	1.0	3.4	0.6	0.0003
	Zoridae	*Zora*[a]	1.8	0.6	0.4	0.2	—
	Gnaphosidae	*Callilepis*	9.6	1.9	4.9	1.3	0.004
		Drassyllus	10.3	2.5	7.2	1.7	0.04
		Herpyllus[a] *	0.9	0.2	5.7	1.2	—
		Sergiolus	1.5	0.4	0.4	0.2	0.04
	Theridiidae	*Dipoena*	1.7	0.6	0.3	0.1	0.02
	Linyphiidae		68.3	7.6	36.7	3.4	<0.0001
		Ceratinops[a]	1.8	0.4	0.3	0.4	—
		Erigone[a]	17.4	4.5	6.0	1.3	—
		Meioneta	21.9	2.6	3.8	0.6	<0.0001
	Tetragnathidae	*Pachygnatha*[a]	1.3	0.3	0.3	0.1	—
	Thomisidae	*Ozyptila*[a]	11.3	3.4	7.5	2.9	—
	Corrinidae	*Scotinella*[a] *	0.5	0.2	2.3	1.2	—
	Agelenidae	*Cicurina*[a]	3.3	1.1	0.8	0.3	—
	Hahnidae		48.0	9.1	24.1	4.0	0.0001
		Hahnia	13.8	2.3	8.0	1.9	0.01
		Neoantistea[a]	34.2	8.5	16.1	3.5	—
	Lycosidae		423.8	46.5	287.1	26.2	<0.0001
		Allocosa[a]	1.7	0.6	0.8	0.2	—
		Hogna	51.5	7.2	28.3	6.4	0.0006
		Immatures[a]	112.2	23.2	32.0	7.9	—
		Pardosa	16.2	4.1	5.0	0.8	0.02
		*Pirata**	60.2	7.1	86.6	7.3	0.0005
		Schizocosa	46.8	9.3	36.6	7.1	0.05
		Sosippus	19.9	2.1	12.3	2.3	0.04
		Varacosa	104.0	9.5	77.8	8.2	0.005
	Salticidae	*Corythalia**	4.1	0.7	8.3	0.9	0.0002
		Habronattus	1.2	0.4	0.2	0.1	0.02
		Phlegra	1.0	0.3	0.2	0.1	0.003
		Sitticus[a]	2.8	0.7	0.8	0.2	—
Opiliones	Gagrellidae	*Leiobunum*	21.7	1.9	6.6	1.5	<0.0001
	Phalangiidae[a]		32.1	4.6	26.9	3.4	—
Isopoda[a]			7.3	1.8	5.0	1.3	—
Spirobolida	Spirobolidae	*Narceus*	2.5	0.4	0.6	0.2	<0.0001
Lithobiomorpha	Lithobiidae		18.4	1.5	12.9	1.2	0.001
Orthoptera	Tettigoniidae	*Atlanticus*	1.8	0.3	0.4	0.2	0.002
	Acrididae		4.5	0.70	2.5	0.49	0.02
		Conocephalinae[a]	0.9	0.22	0.3	0.95	—
	Gryllacrididae	*Ceuthophilus*	11.2	3.3	3.9	1.1	0.005
	Gryllidae		304.4	23.7	126.2	11.6	<0.0001
		Anaxipha[a]	6.9	1.1	3.9	1.5	—
		Cycloptilum	4.4	0.6	0.9	0.2	<0.0001
		Gryllinae[a] *	2.1	1.1	14.7	1.7	—
		Gryllus	21.7	1.7	13.6	1.4	<0.0001
		Miogryllus[a]	24.7	3.4	9.3	1.4	—
		Mogoplistinae[a]*	1.9	0.5	3.1	0.5	—
		Orocharis	2.8	0.5	1.5	0.4	0.02

Asterisks (*) denote groups that were captured in higher numbers near logs.
Taxa followed by an "a" had a significant interaction of trap location with burn frequency.

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TABLE 3. (CONTINUED) MEAN (±SE) NUMBER OF INDIVIDUALS OF ARTHROPOD TAXONOMIC GROUPS CAPTURED IN SIGNIFICANTLY ($P < 0.05$) HIGHER NUMBERS IN PITFALL TRAPS NEAR EITHER DRIFT FENCES OR LOGS PLACED IN STUDY PLOTS IN A LONGLEAF PINE FOREST IN NORTH FLORIDA UNDERGOING DIFFERENT CONTROLLED BURN FREQUENCIES, 1994-2000. ANALYSES OF VARIANCE WERE CONDUCTED BY SAS GLM PROCEDURE (SAS 1985).

			Drift Fence		Log		
Order	Family	Genus or Lowest Taxa	Mean	SE	Mean	SE	$P > F$
		Pictonemobius	218.7	18.7	77.6	9.1	<0.0001
Blattaria	Blattellidae	*Cariblatta*	10.3	1.4	5.6	1.1	0.01
Isoptera	Rhinotermitidae	*Reticulitermes*	3.4	0.6	1.9	0.4	0.05
Hemiptera	Reduviidae	*Repipta* *	0.1	0.06	0.4	0.1	0.04
Homoptera *			25.0	2.5	32.1	2.5	0.04
	Cicadellidae		4.7	0.7	2.8	0.6	0.01
	Delphacidae[a] *		0.9	0.3	2.3	0.5	—
	Cixiidae*		5.3	1.0	12.9	1.4	<0.0001
		Oilarus[a] *	2.0	0.5	3.6	0.8	—
	Achilidae*		2.9	0.6	9.2	1.5	0.0003
		Catonia[a] *	0.2	0.1	1.9	0.3	—
	Aphididae		6.0	0.9	0.3	0.1	<0.0001
Coleoptera	Carabidae		88.2	8.3	42.6	3.3	<0.0001
		Larvae[a]	2.4	0.6	0.7	0.1	—
		Anisodactylus	2.7	0.5	0.6	0.1	0.0009
		Cyclotrachelus	38.0	4.6	14.0	1.9	<0.0001
		Megacephala [a]	2.3	1.1	0.3	0.1	—
		Pasimachus	5.9	1.8	3.1	1.1	0.002
		Piemus *	0.08	0.06	1.7	0.4	0.0003
		Pterostichini *	0.2	0.1	2.3	0.5	0.0002
		Pterostichus	11.8	2.6	5.8	1.3	0.006
		Scaritini	1.8	0.7	0.4	0.2	0.02
	Dytiscidae	*Hydaticus*	1.2	0.3	0.3	0.1	0.01
	Scydmaenidae		5.6	1.7	3.7	1.5	0.0001
	Staphylinidae	*Larvae*[a]	24.9	2.3	3.6	0.6	—
		*Aleochariinae**	0.8	0.8	2.9	0.9	0.008
		*Osoriinae**	0.08	0.08	2.5	0.5	0.0002
		Oxyteninae	3.5	1.1	0.6	0.2	0.007
		*Steninae**	0.13	0.07	4.0	0.9	0.0005
	Scarabaeidae		190.8	38.1	91.1	18.9	0.003
		*Aphodius**	0.0	0.0	2.4	0.8	0.01
		Bolbocerus	4.2	0.7	1.5	0.4	0.003
		Canthon	66.6	17.4	23.4	8.8	<0.0001
		Onthophagus	104.9	21.6	54.5	12.9	0.03
		Trox	3.6	1.2	0.7	0.2	0.02
	Elateridae	*larvae**	1.63	0.3	4.8	0.7	0.0001
	Lycidae	*Plateros**	0.3	0.1	1.0	0.2	0.01
	Cantharidae	*Larvae*[a]	3.7	0.9	0.2	0.2	—
	Endomychidae	*Epipocus*[a]*	0.04	0.01	1.4	0.4	—
	Melandryidae*		0.3	0.3	2.2	0.6	0.003
		*Eustrophinus**	0.1	0.06	1.7	0.5	0.003
	Tenebrionidae*		26.1	2.8	36.7	3.6	0.04
		Helops	5.9	2.2	0.4	0.1	0.01
		*Platydema**	1.8	0.6	20.0	2.9	<0.0001
	Cerambycidae*		0.6	0.2	2.1	0.4	0.003
		*Prionus**	0.54	0.2	1.2	0.2	0.02
	Chrysomelidae	*Myochrous*	2.0	0.4	0.7	0.2	0.006
	Curculionidae		20.2	2.0	10.2	1.1	<0.0001
		Hylobius	10.5	1.2	4.8	0.7	0.0005
		*Ips**	0.04	0.04	2.3	0.71	0.007

Asterisks (*) denote groups that were captured in higher numbers near logs.
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			Drift Fence		Log		
Order	Family	Genus or Lowest Taxa	Mean	SE	Mean	SE	$P > F$
		Sphenophorus	4.1	0.6	1.5	0.4	<0.0001
Mecoptera	Panorpidae	*Panorpa*	6.9	1.5	3.7	0.9	0.009
Diptera	Tipulidae*		0.4	0.1	4.3	0.5	<0.0001
	Mycetophilidae	*Unidentified*[a]*	0.9	0.2	5.2	0.8	—
		Orfelia [a]	5.7	1.3	0.5	0.1	—
	Sciaridae		205.5	30.2	86.0	19.5	<0.0001
		*Bradysia**	0.3	0.1	2.6	1.0	0.04
		Corynoptera[a]	198.3	30.5	77.8	19.3	—
		Epidapus	5.2	1.0	0.6	0.3	<0.0001
		*Pseudosciara**	0.6	0.2	2.2	0.6	0.01
		Sciara[a]*	0.08	0.06	2.0	0.8	—
	Culicidae		6.5	1.0	1.8	0.4	0.0003
		Culex	6.1	0.9	1.2	0.3	0.0001
	Chironomidae*		0.6	0.2	2.8	0.9	0.03
	Empididae		1.1	0.2	3.8	1.2	0.04
		*Drapetis**	0.5	0.1	1.3	0.2	0.004
	Dolichopodidae*		11.4	1.3	25.3	1.7	<0.0001
		*Medetera**	6.8	1.0	19.8	1.8	<0.0001
	Phoridae	*Megaselia*	108.5	16.5	59.6	14.5	0.03
	Sphaeroceridae	*Leptocera*	14.5	4.6	3.7	1.0	0.03
Lepidoptera	Arctiidae	*larvae*	9.0	1.1	6.0	0.8	0.02
	Noctuidae	*larvae*	3.3	0.5	5.6	0.7	0.0009
Hymenoptera	Diapriidae		6.6	1.0	1.5	0.3	<0.0001
	Mutillidae		7.0	0.9	2.8	0.4	<0.0001
		Dasymutilla	2.7	0.5	0.5	0.2	0.0003
		Timulla	3.6	0.5	1.6	0.3	0.001
	Pompilidae	*Priocnemella*	1.8	0.3	0.5	0.1	0.0003
	Formicidae		978.7	75.3	764.4	37.5	0.02
		Formica	24.1	5.0	13.5	2.9	0.007
		Leptothorax	3.8	1.3	0.3	0.2	0.007
		Monomorium	4.5	1.7	0.9	0.5	0.04
		Odontomachus	364.8	33.8	339.0	33.9	0.05
		Pheidole	353.4	35.3	263.3	33.4	0.02

Asterisks (*) denote groups that were captured in higher numbers near logs.
Taxa followed by an "a" had a significant interaction of trap location with burn frequency.

near drift fences while 28 different arthropods were captured in higher numbers near logs. We plotted the numbers captured by year to see if there was evidence of depletion from pitfall trapping for a long period of time or competition between traps. Fig. 3 shows 6 examples of those plots. Four years of trapping did not affect the abundance of arthropods in the vicinity of our traps nor did we see evidence of declining trap captures in one trap type as the other increased.

DISCUSSION

Prescribed burning over a 40-year period significantly changed the understory vegetation and litter layer of the study plots (Hanula & Wade 2003; Glitzenstein et al. 2003). Despite reduced litter and less shrub cover on annually burned plots, we saw no increased use of logs as habitat by ground dwelling arthropods. Andrew et al. (2000) reported similar results for ants although they suggested that a few rare species may benefit from the presence of logs in areas where frequent low intensity fires are commonly used. We found community similarity, diversity, and richness were the same for the 2 trap locations regardless of the frequency of winter burning. Likewise, we saw no increase in overall arthropod abundance or biomass near logs but instead we captured more in traps near metal drift fences.

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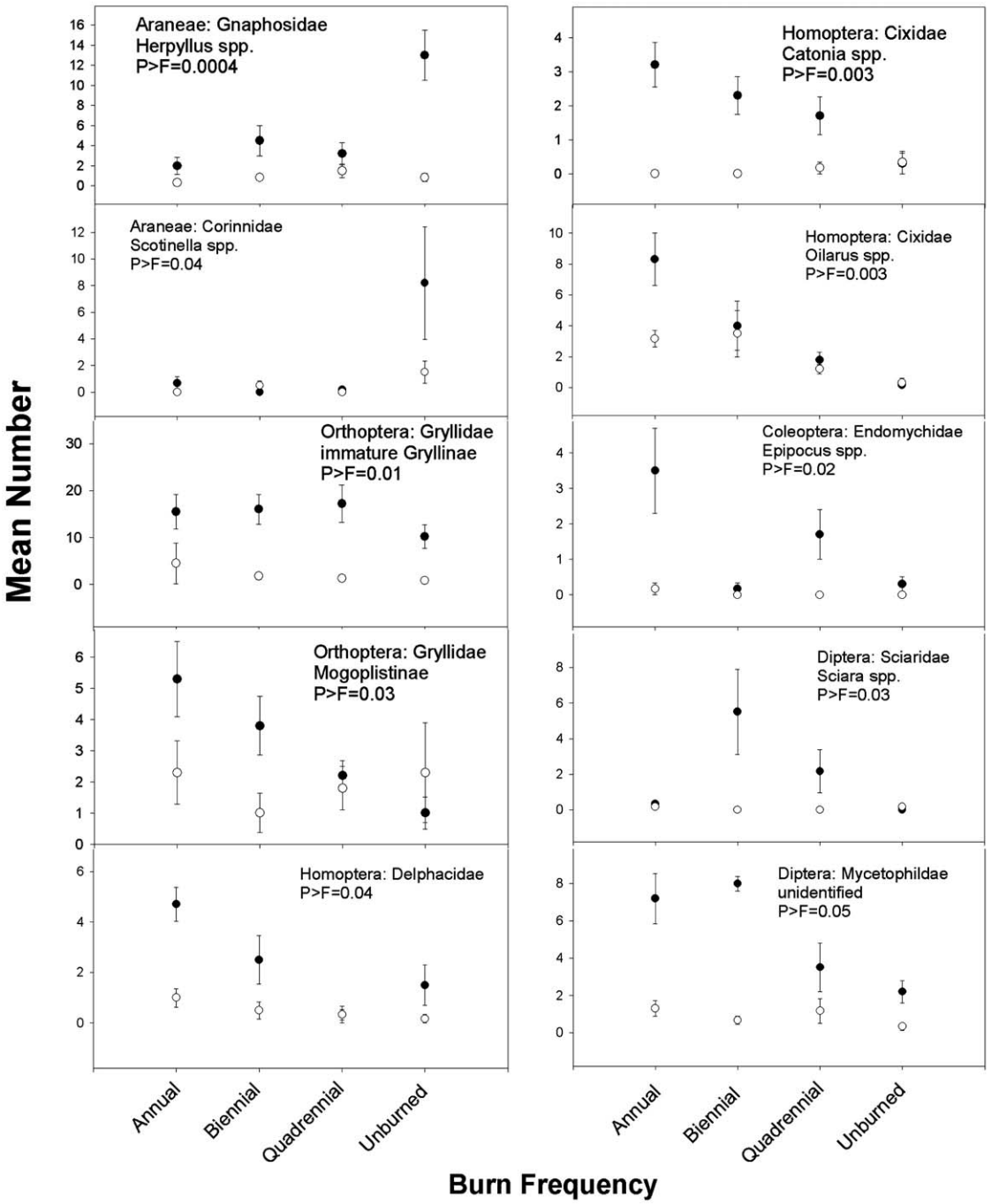


Fig. 1. Mean number (±SE) of individual arthropod taxa collected in pitfall traps near logs (●) or drift fences (○) between 1994 and 2000. Trapping occurred in study plots in a north Florida longleaf pine forest, undergoing different controlled burn frequencies. Graphs are for taxa in which fire frequency significantly affected trap captures and captures near logs were greater than those in traps near metal drift fences. Probabilities ($P > F$) are for the trap location × fire frequency interaction term in analyses of variance (Proc GLM, SAS 1987).

Habitat heterogeneity and structural diversity are considered important factors in determining community richness and diversity (Hutchinson 1959; Southwood et al. 1979; Tilman & Pacala

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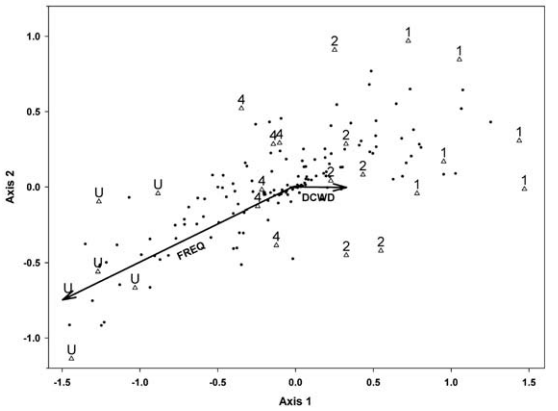


Fig. 2. NMDS biplot of fire frequency (FREQ) and downed coarse woody debris (DCWD) from study plots in a north Florida longleaf pine forest, 1994-2000. The points represent individual species scores. The open triangles the plots scores and the labels above represent their fire frequency in years, with U indicating the unburned plots. The angle and length of the vectors indicate the direction and strength of the relationship of the respective variable with the species and plot scores.

1993; Wright et al. 1993). However, in our study added logs did not result in greater overall abundance or diversity in their vicinity, despite annual burning on some plots, which greatly simplified the structure of the habitat for arthropods (Hanula & Wade 2003).

Arthropod community structure was driven by fire frequency and reported by Hanula & Wade (2003). The first axis of the NMDS ordination that explained almost 70% of the variance was highly correlated to fire return interval (R^2 = 0.678). Downed coarse woody debris did have some impact on overall insect community structure but the effect was much weaker than fire frequency (R^2 = 0.197). Possibly, the small differences in the volume of woody debris on the plots were insufficient to affect the arthropod community or the study time frame was too short (5 years). The results of Gunnarsson et al. (2004) suggest that the former may be the case. They found that diversity and abundance of ground-active beetles were related to the size of slash piles left after harvesting. Thus, larger amounts of dead wood in a given location may result in greater diversity of ground-dwelling arthropods in the vicinity. Gunnarsson et al. (2004) also point out that pitfall traps measure arthropod activity and not necessarily abundance. In contrast, Jabin et al. (2004) examined soil arthropods in litter samples near logs and distant from them in forests that contained about the same volume of dead wood as our study area. They found that CWD was an important structural component to a variety of saprophagous species regardless of season of sampling, while for other groups abundance near CWD was affected by timing of collection. Studies are underway to determine if large volume inputs of woody debris over an extensive area affect ground-dwelling arthropods and other organisms (McCay et al. 2002).

The higher numbers of arthropods captured near drift fences, and the higher number of taxa captured more frequently in traps along drift fences, suggest that the drift fences were more efficient at directing arthropods into pitfall traps than logs. Hansen & New (2005) found that pitfalls with barriers were more efficient at capturing beetles than those without. Our data suggest that traps near metal drift fences were more efficient than those near logs despite our efforts to prevent that. However, Sanzone (1995) also caught more arthropods overall and higher numbers of most arthropod orders in pitfalls away from logs. Sanzone's order level identifications make it difficult to compare her results to our study, but greater trap efficiency was not a factor in that study because pitfalls away from logs did not have drift fences. Our data, when considered together with Sanzone (1995), suggest that many common ground-dwelling arthropods negotiate around logs in ways that allowed them to avoid being trapped. Originally we hypothesized that many arthropods would prefer the moist, shaded habitat near logs. Again, our data and Sanzone's (1995) suggest this is not generally the case for most ground-dwelling arthropods. Although we captured 36 taxa more frequently near logs, most were known saproxylic species. For example, bark beetles (Curculionidae: Scolytinae), woodborers (Cerambycidae), and click beetle larvae (Elateridae) were captured more frequently near logs and all either directly feed in large dead wood or are commonly found in it. Likewise, *Medetera* spp. flies (Dolichopodidae) captured more frequently near logs are known predators of bark beetles (Goyer et al. 1980) and many crane flies (Tipulidae) and fungus gnats (Mycetophilidae) are saproxylic (McAlpine et al. 1981). Beetles in the Endomychidae, Melandryidae, and Euglenidae captured more frequently near logs are also known to be associated with fungi and rotten logs (Borror et al. 1989). Although the majority of ground beetles (Carabidae) were captured more frequently along metal drift fences, members of the genus *Piemus* and unidentified members of the tribe Pterostichini were captured more often near logs. Thiele (1977) points out that preferences for certain levels of humidity among the Carabidae is one of the most important factors governing their choice of habitats. Despite Thiele's (1977) conclusion that most forest carabid species preferred darkness and moist conditions, we found only a few were common near logs. In contrast, most rove beetles (Staphylinidae) were captured in greater numbers in traps near

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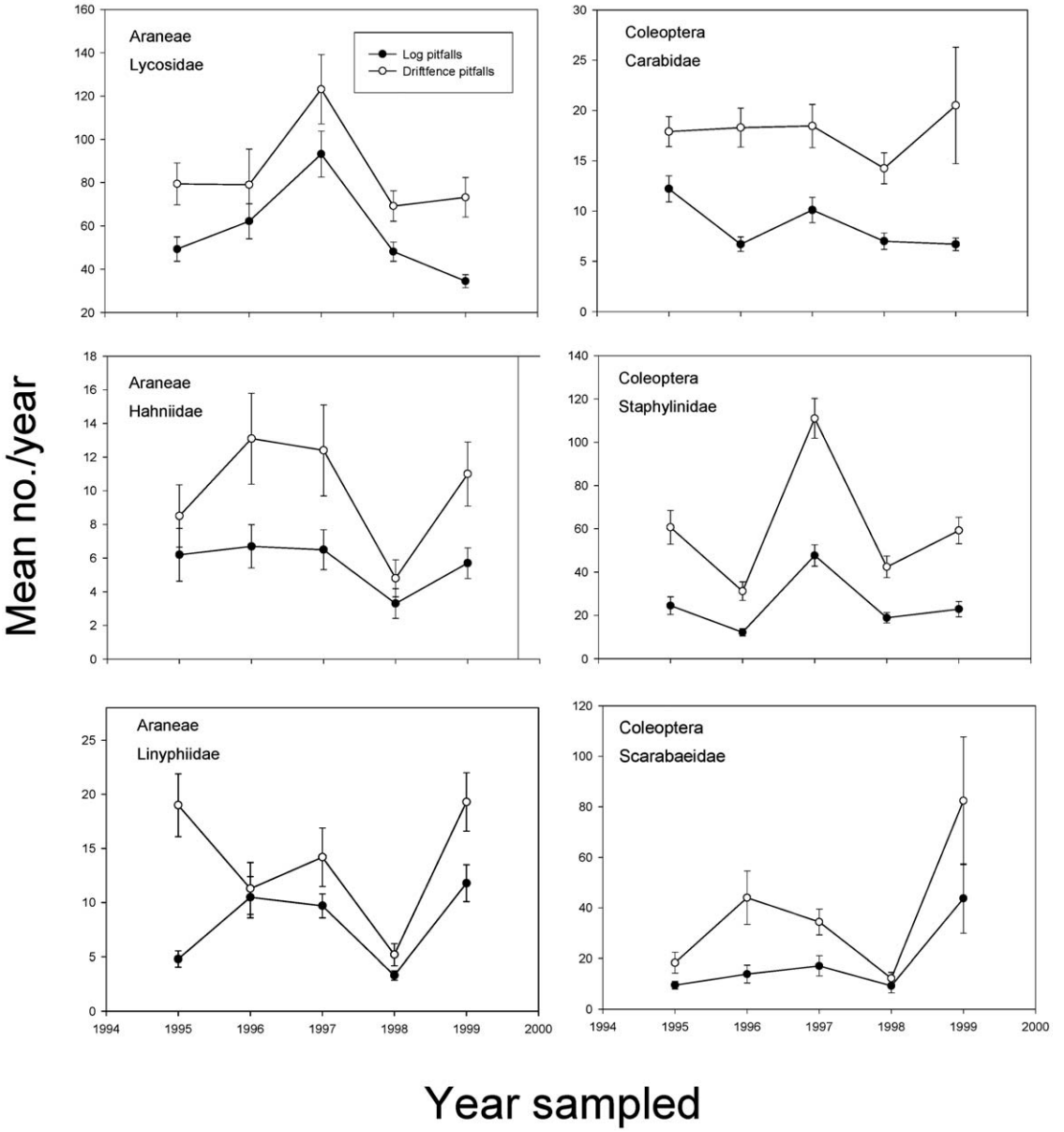


Fig. 3. Mean number (±SE) of individual arthropod taxa collected between 1994 and 2000 in pitfall traps in study plots in a north Florida longleaf pine forest. Graphs are examples of the variation in trap captures over time shown to demonstrate that pitfall trapping over a 5-year period did not deplete arthropod numbers.

logs. Although staphylinids have diverse habits, they are frequently found near decaying material or beneath logs, stones or other debris. These results support those of Jabin et al. (2004) who also found staphylinids were more abundant close to logs. Overall, our data are similar to those of Evans et al. (2003) who found that some invertebrate groups increased in abundance in litter samples close to logs while others decreased. They speculated that logs might influence abundance of various arthropods in several ways including increased predation near logs, changes in the litter composition near logs as they decompose, and alteration of the C:N ratio of the fermentation layer near logs. Clearly arthropods are a diverse group and, as Thiele's (1977) extensive studies of carabids show, even within a single family they have highly varied habitat requirements.

Throughout the world dead wood is a critical habitat to a number of saproxylic species that are

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important for maintaining overall forest diversity (Elton 1966; McMinn & Crossley 1996; Braccia & Batzer 2001; Grove 2002; Grove & Hanula 2006). Experience in European forests demonstrates that without it a number of saproxylic species could go extinct or be reduced to critically low levels (Berg et al. 1994). We found that relatively few non-saproxylic macroarthropods were captured more frequently near logs even on plots where forest structure was greatly simplified by annual burning. Arthropod community structure might have been affected by the overall volume of logs on frequently burned plots but the effect was weak in comparison to the impact of fire frequency. Detailed studies are needed to clearly understand how deadwood contributes to the habitat needs of those species or groups found associated with it in longleaf pine communities.

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REFERENCES CITED

AHLGREN, I. F. 1974. The effects of fire on soil organisms, pp. 47-71 *In* T. T. Kozlowski and C. E. Ahlgren [eds.], Fire and Ecosystems. Academic Press, New York.

ANDREW, N., ROGERSON, L., AND YORK, A. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. Austral. Ecol. 25: 99-107.

AVERY, T. E. 1975. Natural Resources Measurements. McGraw-Hill Book Co., New York.

BERG, Å, EHNSTRÖM, B., GUSTAFSSON, L., HALLINGBÄCK, T., JONSELL, M., AND WESLIEN, J. 1994. Threatened plant, animal and fungus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8: 718-731.

BORROR, D. J., TRIPLEHORN, C. A., AND JOHNSON, N. F. 1989. An Introduction to the Study of Insects. Harcourt Brace College Publishers, New York.

BRACCIA, A., AND BATZER, D. P. 2001. Invertebrates associated with woody debris in a southeastern U. S. forested floodplain. Wetlands 21: 18-31.

BROSE, P. H., AND WADE, D. D. 2002. Potential fire behavior in pine flatwood forests following three different fuel reduction techniques. For. Ecol. and Manage. 163: 71-83.

BUDDLE, C. M., SPENCE, J. R., AND LANGOR, D. W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23: 424-436.

BUDDLE, C. M. 2001. Spiders (Araneae) associated with downed woody material in deciduous forests in central Alberta, Canada. Agric. and For. Entomol. 3: 241-251.

BUFFINGTON, J. D. 1967. Soil arthropod populations of the New Jersey Pine Barrens as affected by fire. Ann. Entomol. Soc. America 60: 530-535.

CARCAMO, H. A., AND PARKINSON, D. 1999. Distribution of ground beetle assemblages (Coleoptera: Carabidae) around sour gas processing plants in Western Canada. Pedobiologia 43: 160-173.

CLARK, I. A., SOUTER, R. A., AND SCHLAEGEL, B. E. 1991. Stem profile equations for southern tree species. Res. Paper SE-282, Southeastern Forest Experiment Station, Asheville, N.C.

CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18: 117-143.

DIGWEED, S. C., CAMERON, R. C., CÁRCAMO, H. A., AND SPENCE, J. R. 1995. Digging out the "digging-in effect" of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiologia 39: 561-576.

ELTON, C. S. 1966. The Pattern of Animal Communities. John Wiley and Sons, New York.

EVANS, A., CLINTON, P. W, ALLEN, R. B., AND FRAMPTON, C. M. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. For. Ecol. Manag. 184: 251-262.

FROST, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Tall Timbers Fire Ecol. Conf. 18: 17-44.

GAISER, E. E., PHILLIPI, T. E., AND TAYLOR, B. E. 1998. Distribution of diatoms among intermittent ponds on the Atlantic Coastal Plain: development of a model to predict drought periodicity from surface sediment assemblages. J. Paleolimn. 20: 71-90.

GLITZENSTEIN, J. S., STRENG, D. R., AND WADE, D. D. 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Nat. Areas J. 23: 22-37.

GOYER, R. A., LENHARD, G. J., NEBEKER, T. E., AND JARRARD, L. D. 1980. How to identify common insect associates of the southern pine beetle. Agricul. Handb. No. 563, USDA Forest Service, Combined Forest Pest Research and Development Program, Pineville, La.

GROVE, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Sys. 33: 1-23.

GROVE, S. J., AND HANULA, J. L. (Eds.) 2006. Insect Biodiversity and Dead Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

GUNNARSSON, B., NITTÉRUS, K., AND WIRDENÄS, P. 2004. Effects of logging residue removal on ground-active beetles in temperate forests. For. Ecol. Manage. 201: 229-239.

HAMMOND H. E. J., LANGOR, D. W., AND SPENCE, J. R. 2001. Early colonization of Populus wood by saproxylic beetles (Coleoptera). Can. J. For. Res. 31: 1175-1183.

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HAMMOND H. E. J., LANGOR, D. W., AND SPENCE, J. R. 2004. Saproxylic beetles (Coleoptera) using Populus in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Can. J. For. Res. 34: 1-19.

HANULA, J. L., AND WADE, D. D. 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. For. Ecol. Manage. 175: 163-184.

HANULA, J. L., AND FRANZREB, K. 1998. Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. For. Ecol. and Manag. 102: 89-102.

HANSEN, J. E., AND NEW, T. R. 2005. Use of barrier pitfall traps to enhance inventory surveys of epigaeic Coleoptera. J. Insect Conserv. 9: 131-136.

HARMON, M. E., FRANKLIN, J. F., SWANSON, F. J., SOLLINS, P., GREGORY, S. V., LATTIN, J. D., ANDERSON, N. H., CLINE, S. P., AUMEN, N. G., SEDELL, J. R., LIENKAEMPER, JR., G. W., CROMACK, K., AND CUMMINS, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133-302.

HEYWARD, F., AND TISSOT, A. N. 1936. Some changes in the soil fauna associated with forest fires in the longleaf pine region. Ecol. 17: 659-666.

HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. American Nat. 100: 419-424.

HOWDEN, H. F., AND VOGT, G. B. 1951. Insect communities of standing dead pine (*Pinus virginiana* Mill.). Ann. Entomol. Soc. America 44: 581-595.

HURST, G. E. 1971. The effects of controlled burning on arthropod density and biomass in relation to bobwhite quail brood habitat on a right-of-way. Proc. Tall Timbers Conf. on Ecol. Animal Control and Habitat Manage. 2: 173-183.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Nat. 93: 145-159.

IRMLER, U., HELLER, K., AND WARNING, J. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134-148.

JABIN, M., MOHR, D., KAPPES, H., AND TOPP, W. 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak-beech forest. For. Ecol. Manage. 194: 61-69.

LANDERS, J. L. 1991. Disturbance influences on pine traits in southeastern United States. Proc. Tall Timbers Fire Ecol. Conf. 17: 61-98.

MARRA, J. L., AND EDMONDS, R. L. 1998. Effects of coarse woody debris and soil depth on the density and diversity of soil invertebrates on clearcut and forested sites on the Olympic Penninsula, Washington. Envir. Entomol. 27: 1111-1124.

MCALPINE, J. F., PETERSON, B. V., SHEWELL, G. E., TESKEY, H. J., VOCKEROTH, J. R., AND WOOD, D. M. 1981. Manual of Neartic Diptera, Vol. 1. Research Branch Agriculture Canada, Hull, Quebec.

MCCAY, T. S., HANULA, J. L., LOEB, S. C., LOHR, S. M., MCMINN, J. W., AND WRIGHT-MILEY, B. D. 2002. The role of coarse woody debris in southeastern pine forests: preliminary results from a large-scale experiment, *In* W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle [eds.], Proc. Symposium on the Ecol. and Management of Dead Wood in Western Forests. Gen. Tech. Rep. PSW-GTR-181. Pacific Southwest Exp. Sta., Albany, Ca.

MCMINN, J. W. AND CROSSLEY, D. A., JR. 1996. Biodiversity and coarse woody debris in southern forests: effects on biodiversity. Gen. Tech. Rep. SE-94, USDA Forest Service, Southern Res. Sta., Asheville, N. C.

MUONA, J., AND RUTANEN, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Zoologici Fennici 31: 109-121

NIWA, C. G., AND PECK, R. W. 2002. Influence of prescribed fire on the carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in southwestern Oregon. Environ. Entomol. 31: 785-796

NOSS, R. F., LAROE, E. T., AND SCOTT, J. M. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. USDI National Biological Survey, Biological Report 28.

ØKLAND, B., BAKKE, A., HÅGVAR, S., AND KVAMME, T. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in northern Norway. Biodiv. Conserv. 5: 75-100.

OUTCALT, K. W., AND SHEFFIELD, R. M. 1996. The longleaf pine forest: trends and current conditions. U.S. Forest Service Resource Bull. SRS-RB-9, Southern Res. Sta., Asheville, NC.

OUTCALT, K. W., AND WADE, D. D. 2004. Fuel management reduces mortality from wildfire. South. J. Appl. For. 28: 28-34.

PEARSE, A. S. 1943. Effects of burning-over and raking-off litter on certain soil animals in the Duke Forest. American Midl. Nat. 43: 406-424.

RICE, L. A. 1932. The effect of fire on the prairie animal communities. Ecol. 13: 392-401.

SANZONE, D. M. 1995. Macroarthropods Associated with Coarse Woody Debris: Factors Influencing Abundance and Diversity Patterns. M. S. Thesis, University of Georgia, Athens.

SHEA, R. W., SHEA, B. W., KAUFFMAN, J. B., WARD, D. E., HASKINS, C. I., AND SCHOLES, M. C. 1996. Fuel biomass and combustion factors associated with fires in savanna ecosystems of South Africa and Zambia. J. Geophysical Res. 101D: 23551-23568.

SAS. 1985. SAS guide for personal computers. Version 6 ed., SAS Institute, Cary, NC.

SAVELY, H. E., JR. 1939. Ecological relations of certain animals in dead pine and oak logs. Ecol. Monographs 9: 321-385.

SOUTHWOOD, T. R. E., BROWN, V. K., AND READER, P. M. 1979. The relationship of plant and insect diversities in succession. Biol. J. Linn. Soc. 12: 327-348.

SPEIGHT, M. C. D. 1989. Saproxylic Invertebrates and their Conservation. Strasbourg, Fr: Counc. Eur. 79 pp.

THIELE, H.-U. 1977. Carabid Beetles in their Environment: A Study on Habitat Selection by Adaptations in Physiology and Behavior. Springer-Verlag, New York.

TILMAN, D., AND PACALA, S. 1993. The maintenance of species richness in plant communities, pp 13-25 *In* R. E. Ricklefs and D. Schluter [eds.], Species Diversity in Ecological Communities: Historical and Geographical Perspectives., University of Chicago Press, Chicago, IL.

VAN LEAR, D. H., CARROLL, W. D., KAPELUCK, P. R., AND JOHNSON, R. 2005. History and restoration of the

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longleaf pine-grassland ecosystem: implications for species at risk. For. Ecol. and Manage. 211: 150-165.
WARREN, S. D., SCIFRES, C. J., AND TEEL, P. D. 1987. Response of grassland arthropods to burning: a review. Agric. Ecosys. and Environ. 19: 105-130.
WOLDENDORP, G., KEENAN, R. J., AND RYAN, M. F. 2002. Coarse woody debris in Australian forest ecosystems. Bureau of Rural Sciences, Canberra, Australia.
WRIGHT, D. H., CURRIE, D. J., AND MAUER, B. A. 1993. Energy supply and patterns of species richness on local and regional scales, pp. 66-74 *In* R. E. Ricklefs and D. Schluter [eds.], Species Diversity in Ecological Communities: Historical and Geographical Perspectives., University of Chicago Press, Chicago, Il.

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