

Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems

James L. Hanula^{*}, Dale D. Wade

USDA Forest Service, Forestry Sciences Laboratory, 320 Green Street, Athens, GA 30602-2044, USA

Received 27 December 2001; accepted 13 April 2002

Abstract

Frequent dormant-season prescribed burns were applied at 1-, 2- and 4-year intervals to longleaf pine stands, *Pinus palustris*, for over 40 years on the Osceola National Forest in Baker County, Florida. Control plots were unburned for the same period of time. Pitfall traps were operated from November 1994 to October 1999 to measure the short- and long-term effects of prescribed burning frequency on the relative abundance and diversity of ground-dwelling macroarthropods. We also measured dead and live plant biomass to determine how long-term frequent fires affected the structure of the forest floor. The average total dead plus live plant biomass was significantly higher on plots where fire had been excluded. Annual and biennial burning resulted in about the same amount of total plant biomass (dead and live plant material combined) which was significantly less than the quadrennially burned plots. Shannon diversity (H') and evenness of ground-dwelling arthropods were reduced by burning. Annually burned plots had the lowest diversity and evenness while biennially and quadrennially burned plots also were significantly lower than unburned control plots. Dormant-season burning did not increase the number of rare genera regardless of frequency. Percent similarity of arthropod communities was highest for comparisons between plots that had been burned (60–68%) and lowest for the comparison of annually burned plots to unburned controls (37%). Examination of diversity and similarity through time showed that changes were due to short-term effects caused by the application of fire and not long-term changes in the ground-dwelling arthropod community. Burning significantly reduced the numbers of predators regardless of fire frequency and resulted in an increased number of detritivores. A total of 42 genera were reduced by prescribed burning; 32 genera were captured in greater numbers on annually burned plots, and 11 genera had higher numbers in one or both of the intermediate burn frequencies (biennial or quadrennial). Twenty-six genera were captured in equal numbers on quadrennially and annually burned plots, but in significantly lower numbers than on unburned plots, demonstrating that 4 years was insufficient time for their populations to recover from mild dormant-season fires. Arthropod response to burning appeared to be species specific so attempts to generalize how arthropods will respond based on a few species or groups should be avoided. The slow recovery rate of so many species suggests that management oriented toward conservation of biodiversity in longleaf pine flatwoods should include areas of fire exclusion.

© 2002 Published by Elsevier Science B.V.

Keywords: *Pinus palustris*; Prescribed-burning; Fire; Arthropods; Insects

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) forests once occupied more than 24 million hectares in the southern

^{*} Corresponding author. Tel.: +1-706-559-4253;
fax: +1-706-559-4287.
E-mail address: jhanula@fs.fed.us (J.L. Hanula).

United States. Today, less than 1.3 million hectares remain as small isolated parcels (Outcalt and Sheffield, 1996). Of those, less than 1 million retain the longleaf pine/grassland association that was described by William Bartram during the late 1700s (Beach, 1993). The reasons for the decline of longleaf pine are complex; they include such events as the introduction of feral hogs that dig up seedlings, and widespread harvesting and replacement of longleaf pine stands with faster growing species (Frost, 1995). The reduction in longleaf pine habitats has been associated with the listing of at least 30 endangered or threatened species and in reductions of 187 vascular plant populations to very low levels (Hardin and White, 1989; Walker, 1993; Glitzenstein et al., 2001). Because of the decline in both quantity and quality, longleaf habitat has become a priority for restoration and conservation by The Nature Conservancy, the USDA Conservation Reserve Program, and numerous other public and private land management organizations.

Although most agree that increasing longleaf pine abundance in the landscape and restoration of existing degraded longleaf pine communities is a desirable goal, how to achieve that goal is unclear. Before European arrival to North America, longleaf pine communities most likely were maintained by fires ignited by the frequent thunderstorms in the region and by native Americans (Landers, 1991). Since severe wildfires have undesirable side effects and habitat fragmentation prevents low intensity wildfires from burning large areas, prescribed burning is considered the most logical alternative for restoring and maintaining longleaf communities.

Longleaf pine communities probably burned during the growing-season (Frost, 1990; Landers, 1991), and growing-season fires are recommended for longleaf pine community maintenance and restoration (Frost, 1990). However, burning large areas during the growing-season at recommended fire frequencies of 1–4 years is difficult because fewer windows of opportunity, when wind and fuel conditions are within guidelines, are available compared to the dormant-season. In addition, restrictions on smoke and volatile emissions from prescribed burning may prevent significant increases in the number of hectares burned during the summer. Therefore, dormant-season prescribed burning is likely to remain an important management tool

for longleaf pine communities (Brockway and Lewis, 1997).

Despite the emphasis on prescribed burning for longleaf pine restoration, and its widespread use in restoration and management of other communities, little is known about the response of arthropods to burning in this ecosystem or how repeated burning over many years affects the arthropod community. Klein (1988) estimated that 90% of the terrestrial arthropod fauna spend at least part of their life cycle in the soil or surface litter. Frequently, arthropods use the soil for a winter refuge. Since arthropods move more slowly or not at all in the winter, depending on their stage of development, dormant-season burning may have a significant affect on arthropod communities. In some cases, dormant-season burning is an effective control measure for insect pests (Miller, 1979).

The effects of natural or prescribed fire on arthropods are not clear, and depend upon a variety of factors including species studied, their stage of development at time of the fire, and their responses to a variety of habitat and community alterations caused by fire (Ahlgren, 1974; Warren et al., 1987; Siemann et al., 1997; and references therein). For example, some ant species increase following fires (Buffington, 1967; Hansen, 1986; Anderson et al., 1989; Andersen, 1991; Neumann and Tolhurst, 1991; Moya-Raygoza, 1995) while others are reduced (Pearse, 1943; Buffington, 1967; Gillon, 1972; Andersen and Yen, 1985; Andersen, 1991; Neumann and Tolhurst, 1991; Kalisz and Powell, 2000). Responses of other arthropod groups to fire also vary.

The objectives of our study were to determine how frequent, long-term dormant-season burning altered ground-dwelling arthropod community diversity, richness and composition. We were particularly interested in determining if changes were due to long-term shifts in community structure or the short-term effects of fire application. The research was conducted on a unique long-term study area that has been treated with dormant-season fire for over 40 years. In addition to measuring the arthropod community response, we also measured dead and live plant biomass on the plots to determine how fire affected the structure of the forest floor community.

2. Methods and materials

2.1. Study site, design and treatments

The study was conducted on the Osceola National Forest in Baker County, Florida. The plots were established in 1958 to examine the effects of burning frequency on fuel reduction for wildfire prevention. At that time, the overstory trees were 45-year-old longleaf pine with a few slash pine (*P. elliottii* Engelm.) and dominant trees were 20 m tall and 29 cm diameter. The presence of remnant longleaf pine trees with evidence of past turpentine operations suggests that the area had never been cleared for agriculture. The understory consists of typical flatwoods vegetation dominated by saw palmetto (*Serenoa repens*). Other common plants included gallberry (*Ilex glabra*), blueberries (*Vaccinium* spp.), huckleberries (*Gaylussacia* spp.) and wiregrass (*Aristida beyrichiana*).

The study was a randomized complete block design consisting of 24, 0.8 ha plots arranged in six replications of four 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. Our study began in fall, 1994 with treatments consisting of annual, biennial and quadrennial winter burns and unburned controls. The plots had been burned for 35 years at the beginning of our study and burning continued throughout the 5-year-study period (November 1994–October 1999). Burning was conducted in the winter (January or February) throughout the study. Fire intensity varied from year to year depending upon weather conditions and dead fuel moisture contents which ranged from 7 to 20%.

2.2. Live and dead plant biomass

Pre-burn live and dead plant biomass was estimated on each plot from eight 1 m² subplots. Fuels were 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. Sampling methods were adapted from Shea et al. (1996). Two clusters of eight

transect lines were established in each plot. We ran 15 m long transects from the center of each cluster in the four cardinal directions and four additional 15 m long transects were established at 90° from the ends of the original transects. Sampling frames (1 m²) 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. We sampled all of the burn plots in January 1996 prior to burning, at a time when all of the plots had the maximum amount of time possible for plant material to build up. The unburned controls were sampled in January 1999. For our analyses, we assumed that live and dead plant biomass on unburned controls changed little during our study since McKee (1991) found no difference in the organic content of the forest floor in unburned mature pine stands after 10 years of fire exclusion. We compared total live plant material, total dead plant material, live palmetto, live gallberry, live grasses/forbs, litter, humus, small dead wood (0–2.5 cm) and total fuel load among treatments.

2.3. Arthropod populations

We were interested in determining if large woody debris was an important resource for ground-dwelling arthropods on frequently burned plots. We measured this relationship by placing pitfall traps along 3 m long logs placed in the center of each plot. We established pitfall traps around the logs in the following manner. Four pitfall traps (Hanula and Franzreb, 1998) were installed; two traps were placed on each side 0.5 m in from the ends of the log and as close to it 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 four pitfall traps were installed along a 3 m long aluminum sheet metal drift fence (15 cm high) which provided a barrier similar to the logs. The drift fence was located 10 m from the center log and the traps were constructed and placed in the same manner as the log pitfalls except that the edge of the traps was in direct contact with the drift fence. Pitfall traps were opened

every other month for a 1-month-period. When not in use, trap openings were covered with ceramic tiles to prevent arthropods from entering. We found no significant interaction between fire frequency and captures of arthropods in pitfalls along logs, so we combined data from the log pitfalls with the drift fence pitfalls for this study.

Samples from pitfalls were stored in 70% ethyl alcohol, sorted based on morphological features, placed in individual vials of alcohol, labeled, and identified to genus or the lowest taxonomic level possible. Immature insects were identified to family. Each taxon also was classified as either a herbivore, predator, detritivore or omnivore to determine if burning affected trophic relationships within the longleaf pine arthropod community. 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.

2.4. Statistical analyses

Percentage similarity ($P = \sum \min(p_{1i}, p_{2i})$), where P is the percentage similarity between samples 1 and 2, p_{1i} is the percentage of species i in community sample 1, and p_{2i} is the percentage of species i in community sample 2) was used to compare arthropod communities among treatments (Wolda, 1981; Krebs, 1999). In some cases, data were transformed using the $\log_{10}(x + 1)$ transformation to reduce the importance of a few species that were caught in high numbers. Percent similarity was calculated for all possible treatment combinations. In addition, we compared each burn frequency treatment to the unburned controls for each year of the study to determine if community similarity changed when burns were applied and how quickly communities returned to pre-burn levels. We compared one half of the control plots to the other half to have a standard for comparison. Although the number of replicates was halved ($n = 3$) by this technique, it provided a method of determining a “maximum” similarity possible and allowed us to look at variation in similarity over time.

Rare species were of particular concern, so we compared richness of rare taxa (<10 captures per 5 years) to determine if frequent burning caused

increased rarity. We also calculated the quotient of similarity for rare taxa. We chose this index because it places more emphasis on the taxa found in both habitats than other similarity indices (Southwood, 1966), and it compares two communities based solely on the presence or absence of taxa, so it is not influenced by numerical abundance.

We used richness (genera per plot), the Shannon diversity index (H') and evenness (J) to compare arthropod community diversity among treatments. Shannon diversity meets the essential criteria for diversity indices (Elliott, 1990) and it emphasizes rare taxa (Krebs, 1999). Evenness, which gives an indication of how equally individuals are distributed among taxonomic groups, was calculated to further describe the arthropod communities.

Data were analyzed using a two-way analysis of variance. Dependent variables included vegetation characteristics, arthropod community characteristics, and arthropod abundance. The Ryan–Einot–Gabriel–Welsch (REGWQ) multiple range test was used to compare treatment means (SAS Institute, 1987). Data were transformed using the transformation $(x + 0.5)^{-2}$, where appropriate to stabilize variance (Bartlett, 1947) prior to analyses of abundance within arthropod groups. Results are presented as untransformed means and standard errors in tables and figures.

3. Results

3.1. Live and dead plant biomass

Visual differences among the various burn treatments were evident in the vegetation structure and dead plant material on the ground. Both dead and live plant biomass were affected by long-term dormant-season burning. The average total plant biomass (dead plus live plant material combined) was significantly higher on plots where fire had been excluded than on any of the burned plots (Table 1). Annual and biennial burning resulted in about the same amount of total plant biomass, which was significantly less than the quadrennially burned plots.

Total dead plant biomass also was significantly higher on unburned plots compared to burned plots, and quadrennial burning resulted in a greater build up

Table 1
 Mean (\pm S.E.) oven-dried weight (g) of selected dead and live plant material on plots receiving varying frequencies of dormant-season prescribed burns over a 40-year-period on the Osceola National Forest (Baker County, Florida)

Burn frequency	N	Dead plant biomass					Live plant biomass					Dead and live total	
		Litter	Humus	Branches	Total		Gallberry	Saw palmetto	Grasses	Total			
Annual	6	147 \pm 36.0 a	449 \pm 43.0 a	80 \pm 12.5 a	685 \pm 57.6 a	49 \pm 16.5 a	31 \pm 4.3 a	59 \pm 8.9 a	170 \pm 19.0 a	1000 \pm 201.5 a			
Biennial	6	138 \pm 26.8 a	760 \pm 47.9 ab	78 \pm 6.4 a	1010 \pm 80.2 ab	123 \pm 26.4 a	145 \pm 31.3 a	35 \pm 8.0 ab	346 \pm 19.5 b	1356 \pm 77.6 a			
Quadrennial	6	203 \pm 23.7 a	988.7 \pm 77.3 b	71 \pm 7.4 a	1417 \pm 62.8 b	108 \pm 19.8 a	287 \pm 51.5 b	24 \pm 5.8 b	467 \pm 36.1 c	2152 \pm 132.6 b			
No burn	6	453 \pm 48.7 b	2186 \pm 227.8 c	68 \pm 18.3 a	3293 \pm 266.9 c	71.7 \pm 26.4 a	581 \pm 41.3 c	12 \pm 4.4 b	727 \pm 24.7 d	4020 \pm 275.1 c			

Means within columns followed by the same letter are not significantly different (REGWQ multiple comparison test, $P < 0.05$).

of dead plant biomass than annual burning (Table 1). Biennial burning resulted in accumulations of dead plant material intermediate between annual and quadrennial burns. Dormant-season burning had no effect on the amount of small dead branches. Fire exclusion resulted in more than double the accumulation of litter, and these areas had more than twice as much humus on the soil surface as any of the burned plots. Burned plots were equal in the amount of litter regardless of burning frequency. However, they differed in the amount of humus on the plots. Quadrennial burning resulted in twice the accumulation of humus compared to annual burning. Biennial burning resulted in similar amounts of humus as annual and quadrennial burning.

Frequency of dormant-season burning also resulted in changes in the amount of plant biomass and the composition of the dominant plant groups (Table 1). Total plant biomass exhibited a significant negative relationship with burning frequency, i.e. as burning frequency increased total live plant biomass decreased. Only gallberry was unaffected by winter burning. Aboveground biomass of saw palmetto was nearly 12 times higher on unburned control plots than on those burned annually. Biennial burning resulted in a quarter of the biomass of saw palmetto observed in unburned plots, while quadrennial burning resulted in about half as much. Annual and biennial burning had similar amounts of saw palmetto. In contrast, grasses exhibited a reverse trend. Annually burned plots had four times as much grass biomass as unburned controls and twice as much as quadrennially burned plots. Biennial burning resulted in grass biomass intermediate between annual and quadrennial burns.

3.2. Ground-dwelling arthropods

3.2.1. Arthropod abundance and biomass

We captured over 163,000 arthropods from 31 orders, 265 families and 932 genera (Table 2). The Hymenoptera (primarily ants) made up almost 27% of the total number of individuals captured. Spiders (Araneae, 18%), millipedes (16%) in the order Polydesmida and beetles (Coleoptera, 14%) were other abundant groups. The millipedes comprised the largest biomass of any group and almost all of this was due to a single species, *Dicellarius maculatus*, which was also the single most abundant macroarthropod species on the plots. The total number of arthropods captured

per plot during the 5 years of the study was significantly higher in the annually burned plots while the biennial, quadrennial and unburned controls were approximately equal when *D. maculatus* were included in the analysis (Table 3). When *D. maculatus* were removed from the data there were no significant differences in numbers of arthropods. Likewise, burned plots had significantly more arthropod biomass than unburned plots when *D. maculatus* were included. When *D. maculatus* were removed from the analysis only the annually and biennially burned plots had more biomass than controls.

3.2.2. Diversity and community similarity

Richness and the number of rare genera varied little among plots with different burn frequencies (Fig. 1). We captured an average of almost 300 genera per plot, regardless of burn frequency, of which approximately 90 genera per plot were rarely captured. Frequent burning did not result in more rare genera. Shannon diversity was affected by burning. Annually burned plots had lower diversity than biennial, quadrennial or unburned control plots. Biennially and quadrennially burned plots had similar arthropod diversity, but their diversity was also lower than unburned plots. Evenness showed a similar pattern.

We also examined diversity and evenness among plots receiving different frequencies of dormant-season fire over time and found diversity and evenness exhibited similar trends (Table 4). In 1995, only annually burned plots were burned. Arthropod diversity and evenness were significantly lower in those plots than in the other three treatments which were similar in diversity and evenness. The following year (1996) all of the plots were burned except the controls. That year diversity and evenness were reduced on all burned plots and all were significantly lower than the controls. By the end of 1997, diversity and evenness rebounded, with only annually burned plots lower than unburned controls. In winter 1998, annually and biennially burned plots were burned, and again both exhibited reductions in diversity when compared to unburned plots. However, evenness was reduced only on the biennially burned plots. In 1999, only the plots receiving annual treatments were burned. Those plots had lower diversity and evenness than the controls as did the biennially burned plots. Diversity of unburned plots remained nearly constant throughout the study.

Table 2

Total number of families, genera and individuals, and total biomass of various orders of arthropods captured in pitfall traps on the Osceola National Forest (Baker County, Florida) from 1995 to 1999

Order	Number of families	Number of genera	Total number	Total biomass (g)
Araneae	26	139	29728	96.9
Blattaria	1	5	2994	19.5
Callipodida	1	1	67	1.9
Chordeumatida	1	1	70	0.3
Coleoptera	59	265	22360	507.8
Diptera	41	161	16409	5.6
Embiidina	1	1	1	–
Geophilomorpha	1	1	352	3.0
Hemiptera	20	57	526	3.2
Homoptera	14	42	1370	1.7
Hymenoptera	42	157	43225	55.4
Isopoda	1	1	297	1.1
Isoptera	1	1	126	0.1
Julida	1	1	15	0.3
Lepidoptera	23	25	1631	16.2
Lithobiomorpha	1	1	751	3.0
Mantoidea	1	3	4	0.1
Mecoptera	2	2	258	0.6
Microcoryphia	1	1	1	<0.1
Neuroptera	4	7	90	0.7
Opiliones	3	5	3623	30.9
Orthoptera	7	40	11206	125.2
Phasmida	1	2	16	3.2
Polydesmida	3	4	26799	628.8
Polyxenida	1	1	4	<0.1
Pseudoscorpione	1	1	55	<0.1
Psocoptera	2	2	37	<0.1
Scolopendromorpha	2	2	967	30.7
Scorpiones	1	1	353	13.2
Spirobolida	1	1	75	42.4
Thysanura	1	1	3	<0.1

Table 3

Mean (\pm S.E.) number and biomass (g oven-dried wt.) of arthropods captured per plot with and without the millipede *Dicellarius maculatus*

Burn frequency	With <i>D. maculatus</i>		Without <i>D. maculatus</i>	
	Number per plot	Biomass per plot	Number per plot	Biomass per plot
Annual	7886 \pm 648.6 a	90.7 \pm 13.72 a	5921 \pm 205.3 a	44.8 \pm 5.37 a
Biennial	6642 \pm 377.6 b	73.9 \pm 8.73 a	5510 \pm 262.3 a	47.1 \pm 5.61 a
Quadrennial	6766 \pm 424.1 b	67.8 \pm 3.30 a	5548 \pm 417.7 a	39.2 \pm 1.98 ab
No burn	5866 \pm 220.9 b	32.9 \pm 2.64 b	5718 \pm 211.3 a	29.5 \pm 1.98 b

Plots were on the Osceola National Forest (Baker County, Florida) and were burned during the dormant-season at varying frequencies over a 40-year-period. Means within columns followed by the same letter are not significantly different (REGWQ multiple comparison test, $P < 0.05$).

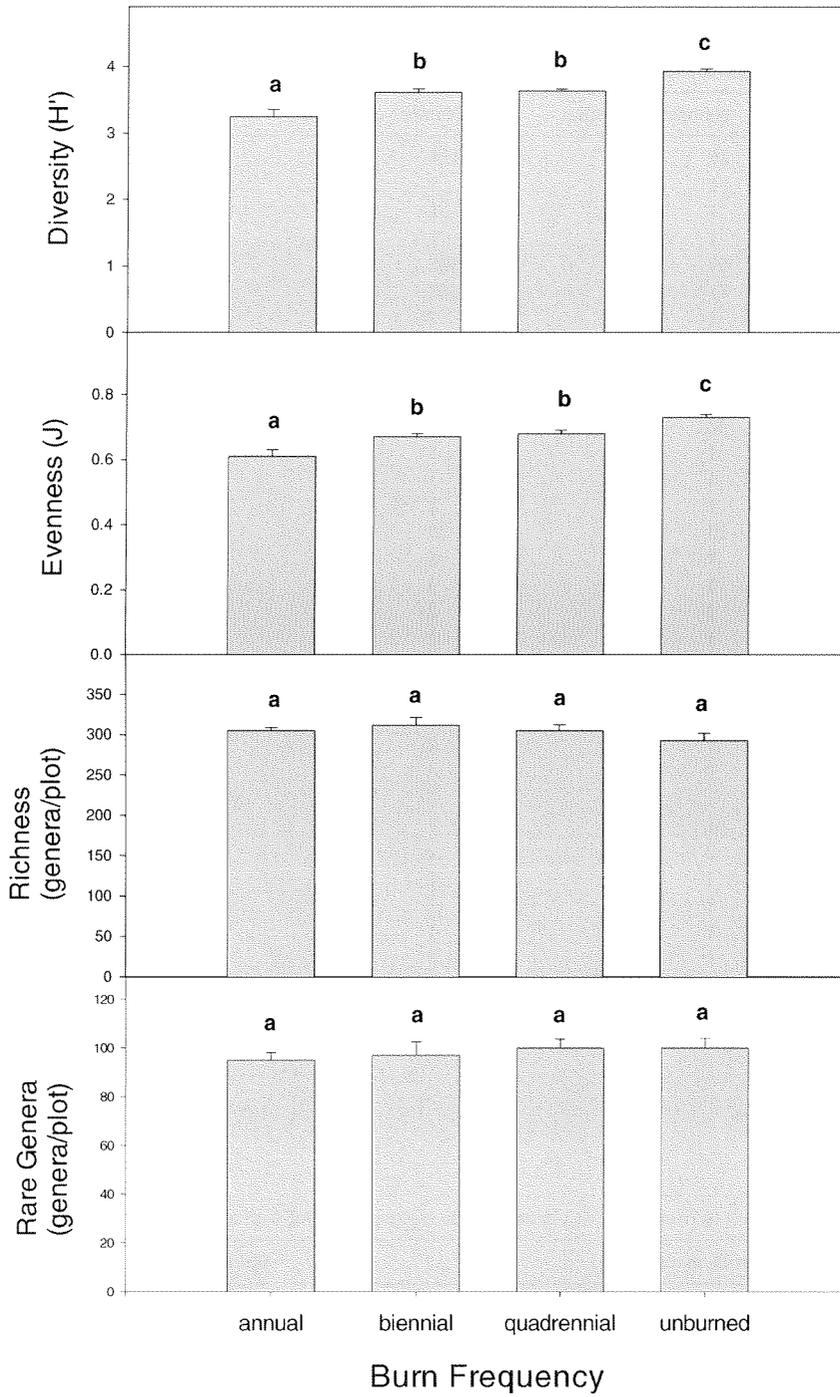


Fig. 1. Mean (\pm S.E.) number of rare genera, richness, evenness and diversity of arthropods captured in pitfall traps in plots receiving varying frequencies of dormant-season prescribed burns over a 40-year-period on the Osceola National Forest (Baker County, Florida). Columns within graphs that have the same letter above them were not significantly different (REGWQ multiple comparison test, $P < 0.05$).

Table 4
 Mean (±S.E.) diversity (H') and evenness (J) of arthropods captured in pitfall traps in plots receiving varying frequencies of dormant-season prescribed burns over a 40-year-period on the Osceola National Forest (Baker County, Florida)

Burn frequency	1995 ^a		1996 ^b		1997 ^c		1998 ^d		1999 ^e	
	H'	J								
Annual	3.0 ± 0.14 a	0.67 ± 0.04 a	2.5 ± 0.04 a	0.56 ± 0.28 a	3.2 ± 0.06 a	0.56 ± 0.10 a	2.9 ± 0.02 a	0.70 ± 0.10 a	2.9 ± 0.02 ab	0.61 ± 0.10 a
Biennial	3.4 ± 0.10 b	0.76 ± 0.02 b	2.9 ± 0.10 a	0.64 ± 0.10 a	3.5 ± 0.03 a	0.75 ± 0.06 b	2.9 ± 0.01 b	0.69 ± 0.08 a	3.3 ± 0.03 b	0.69 ± 0.01 b
Quadrennial	3.6 ± 0.04 b	0.78 ± 0.01 b	2.6 ± 0.07 a	0.58 ± 0.07 a	3.6 ± 0.01 a	0.78 ± 0.05 b	3.3 ± 0.01 b	0.76 ± 0.09 b	3.4 ± 0.02 ab	0.72 ± 0.02 bc
Unburned	3.6 ± 0.07 b	0.81 ± 0.01 b	3.6 ± 0.06 b	0.78 ± 0.06 b	3.6 ± 0.01 b	0.78 ± 0.03 b	3.5 ± 0.01 b	0.78 ± 0.05 b	3.6 ± 0.01 a	0.76 ± 0.01 c

Means within columns followed by the same letter are not significantly different (REGWQ multiple comparison test, $P < 0.05$). Diversity was calculated using the Shannon diversity index.

^a Only the annually burned plots were burned in 1995.

^b All plots except unburned controls were burned in 1996.

^c Only the annually burned plots were burned in 1997.

^d The annual and biennial burn plots were burned in 1998.

^e Only the annually burned plots were burned in 1999.

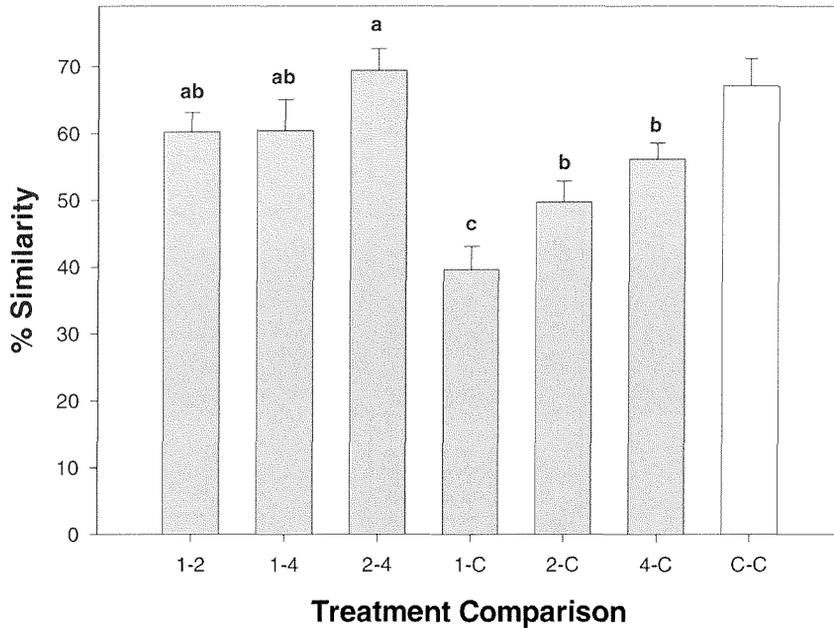


Fig. 2. Mean (\pm S.E.) percentage similarity of the ground-dwelling arthropod community in plots receiving varying frequencies of dormant-season prescribed burns (annually = 1, biennially = 2, quadrennially = 4 and not burned = C) over a 40-year-period on the Osceola National Forest (Baker County, Florida). Columns that have the same letter above them were not significantly different (REGWQ multiple comparison test, $P < 0.05$). Comparison of half of the unburned plots to the other half (C-C) is provided as an example of the maximum similarity that might occur on similarly treated plots and was not included in the statistical analysis.

Percentage similarity was highest for biennially and quadrennially burned plots, but not significantly higher than comparisons among other burn treatments (Fig. 2). Annually burned plots and plots where fire was excluded had the lowest similarity, significantly lower than all other comparisons. Similarity was 67% for comparison of half of the unburned plots to the other half. Although not included in the statistical analyses, this comparison shows how similar identically treated plots were to one another.

Like diversity, percent similarity was affected by fire in a given year. For example, in 1995, only annually treated plots were burned, and biennially and quadrennially burned plots had reached their maximum recovery period (Fig. 3a). That year annually burned plots had a 30% similarity to controls while the biennially burned plots had a 42% similarity and the quadrennially burned plots had a 44% similarity. Similarity within the two groups of control plots was 56%. In 1996, all plots were burned except the controls. Percentage similarity was reduced to 25–32% for all comparisons except unburned plots to

other unburned plots. The following year (1997), after almost 2 years of recovery, similarity of burned plots and unburned plots was about the same or slightly higher than in 1995.

To see if these trends were due to changes in abundant species, we applied a \log_{10} transformation to the data (Fig. 3b). The results showed much less fluctuation in percentage similarity over time. In particular, changes in similarities between 1995 and 1996 evident in Fig. 3a were almost completely eliminated. The transformation reduced the effect of a few species that responded positively to fire disturbance with large population increases.

Despite having approximately the same numbers of rare genera (Fig. 1), burning frequency affected the composition of the rare arthropod community. Although the quotient of similarity only considers the presence or absence of taxa, the results from this similarity index for rare taxa (Fig. 4) were much like percentage similarity for the whole community, i.e. burned plots were similar to each other regardless of burn frequency, and biennially and quadrennially

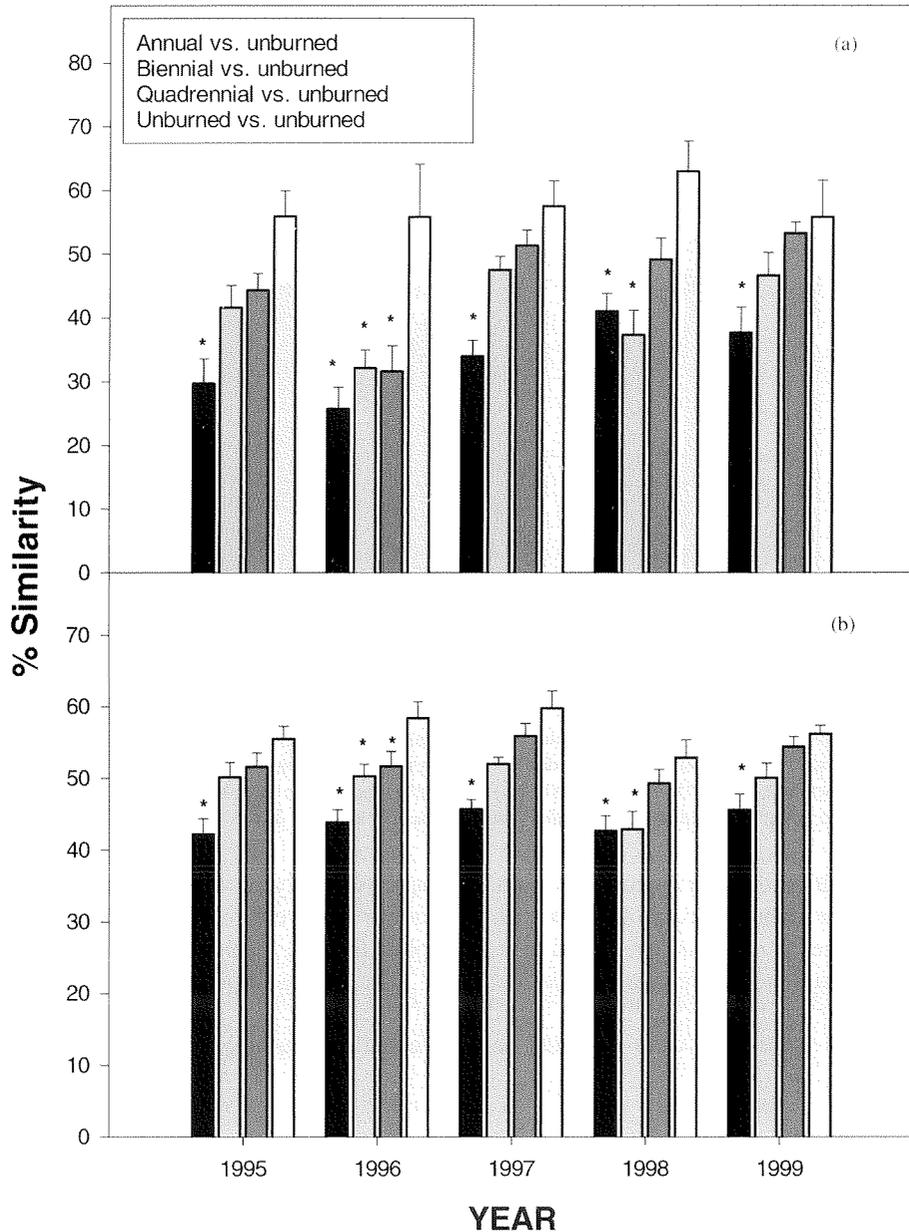


Fig. 3. Mean (\pm S.E.) percentage similarity of arthropods captured in pitfall traps in plots receiving varying frequencies of dormant-season prescribed burns over a 40-year-period on the Osceola National Forest (Baker County, Florida). Data for (a) were not transformed before calculating similarities. (b) Shows percent similarity after data were transformed to reduce the influence of a few abundant species. Asterisks above columns denote which plots were burned each year.

burned plots were more similar to the unburned plots than were the annually burned plots.

We classified each species as either a predator, herbivore, detritivore or omnivore (Table 5) to deter-

mine if prescribed burning had positive or negative effects on trophic relationships. Prescribed burning significantly reduced the numbers of predators regardless of burn frequency compared to unburned controls.

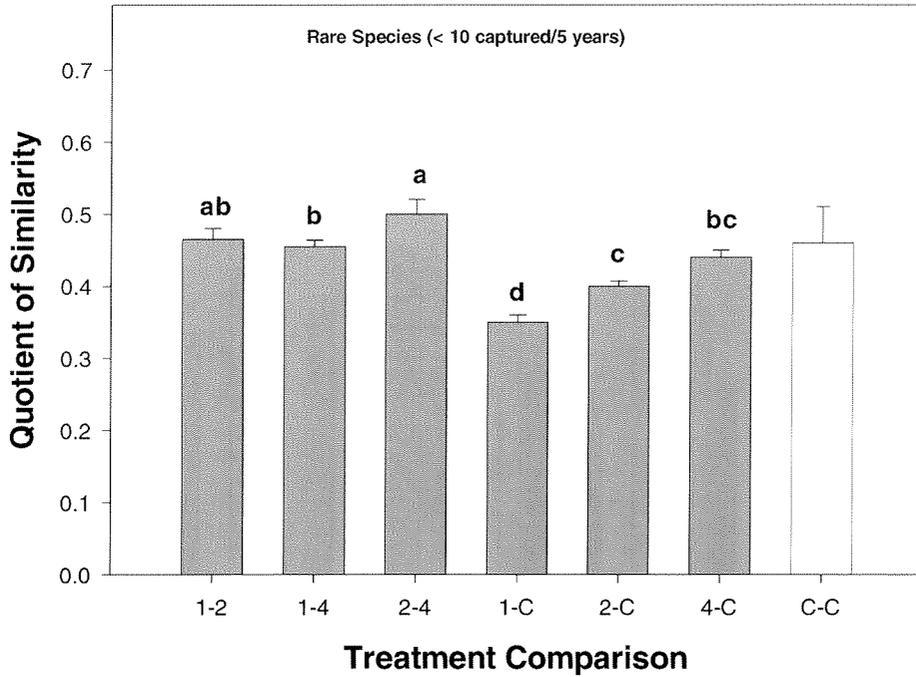


Fig. 4. Mean (±S.E.) quotient of similarity of rare genera (<10 captured/5 years) of arthropods captured in pitfall traps in plots receiving varying frequencies of dormant-season prescribed burns (annually = 1, biennially = 2, quadrennially = 4 or not burned = C) over a 40-year-period on the Osceola National Forest (Baker County, Florida). Columns that have the same letter above them were not significantly different (REGWQ multiple comparison test, $P < 0.05$). Comparison of half of the unburned plots to the other half (C–C) is provided as an example of the maximum similarity that might occur on similarly treated plots and was not included in the statistical analysis.

Conversely, more detritivores were captured on plots that were burned than on unburned controls. Even with the dominant detritivore, *D. maculatus*, removed from the analysis, we captured more detritivores in burned plots than in the unburned controls. On the other hand, omnivores and herbivores were captured in

approximately the same numbers on all plots, although omnivores were more abundant on annually burned plots than on biennially burned plots.

The average number of genera of predators, detritivores and omnivores captured per plot was unaffected by burning frequency (Table 6). However,

Table 5

Mean (±S.E.) number of arthropod feeding groups captured in pitfall traps in plots burned with varying frequencies of dormant-season prescribed burns over a 40-year-period on the Osceola National Forest (Baker County, Florida)

Burn frequency	Feeding habit					
	Predator	Detritivore		Herbivore	Omnivore	
		With <i>Dicellarius</i>	Without <i>Dicellarius</i>		With <i>Solenopsis</i>	Without <i>Solenopsis</i>
Annual	2233 ± 174.8 a	4109 ± 622.0 a	2144 ± 251.3 a	232 ± 16.0 a	1306 ± 247.0 a	661.7 ± 21.4 a
Biennial	2677 ± 162.8 a	3042 ± 236.8 b	1909 ± 99.4 a	231 ± 17.7 a	687.2 ± 129.4 b	671 ± 138.8 a
Quadrennial	2673 ± 179.0 a	2885 ± 115.6 b	1666 ± 97.8 a	187 ± 9.8 a	1022 ± 162.4 ab	1012 ± 130.8 a
No burn	3418 ± 151.3 b	1147 ± 150.5 c	998.8 ± 108.2 b	183 ± 21.4 a	1108 ± 71.9 ab	1104 ± 161.9 a

Detritivores included large numbers of *Dicellarius maculatus* and omnivores included large numbers of *Solenopsis invicta* so analyses were conducted with and without these two species. Means within columns followed by the same letter are not significantly different (REGWQ multiple comparison test, $P < 0.05$).

Table 6
Mean (\pm S.E.) richness (genera), diversity and evenness of arthropod feeding groups collected in pitfall traps on plots receiving varying frequencies of dormant-season prescribed burns over a 40-year-period on the Osceola National Forest (Baker County, Florida)

Burn frequency	Feeding habits			
	Predator	Detritovore	Herbivore	Omnivore
Richness				
Annual	130.8 \pm 3.21 a	86.8 \pm 4.14 a	52.0 \pm 1.97 a	9.3 \pm 0.76 a
Biennial	135.5 \pm 5.38 a	88.6 \pm 3.53 a	50.2 \pm 1.67 ab	11.0 \pm 0.73 a
Quadrennial	135.3 \pm 4.93 a	89.7 \pm 1.41 a	47.0 \pm 1.77 ab	9.8 \pm 0.60 a
No burn	139.2 \pm 2.60 a	77.3 \pm 2.99 a	44.0 \pm 2.92 b	9.2 \pm 0.60 a
Diversity (H')				
Annual	3.01 \pm 0.08 a	2.31 \pm 0.18 a	3.31 \pm 0.07 a	0.87 \pm 0.10 a
Biennial	2.93 \pm 0.10 a	2.53 \pm 0.06 a	3.34 \pm 0.05 a	1.09 \pm 0.10 a
Quadrennial	3.31 \pm 0.04 b	2.42 \pm 0.05 a	3.32 \pm 0.04 a	0.97 \pm 0.08 a
No burn	3.38 \pm 0.03 b	3.25 \pm 0.02 b	3.24 \pm 0.06 a	1.09 \pm 0.09 a
Evenness (J)				
Annual	0.62 \pm 0.02 a	0.52 \pm 0.04 a	0.84 \pm 0.02 a	0.39 \pm 0.04 a
Biennial	0.60 \pm 0.02 a	0.57 \pm 0.02 a	0.85 \pm 0.01 a	0.45 \pm 0.03 a
Quadrennial	0.68 \pm 0.01 b	0.54 \pm 0.01 a	0.86 \pm 0.01 a	0.43 \pm 0.04 a
No burn	0.68 \pm 0.01 b	0.75 \pm 0.02 b	0.86 \pm 0.01 a	0.49 \pm 0.03 a

Means in columns and within categories (e.g. richness) followed by the same letter are not significantly different (REGWQ multiple comparison test, $P < 0.05$).

significantly more herbivore genera were captured on annually burned plots than on control plots. Shannon diversity and evenness of predators was higher in quadrennially burned and unburned plots than in more frequently burned areas, while diversity and evenness of detritivores was higher on control plots.

3.2.3. Effects on individual taxa

Arthropods were significantly affected by dormant-season prescribed burning (Fig. 5). A total of 42 genera were reduced by prescribed burning, 32 genera were captured in greater numbers on annually burned plots than on controls and 11 genera had higher numbers in one or both of the intermediate burn frequencies (biennial or quadrennial). Graphs 1–28 (Fig. 5) are spiders. Of these, 11 genera were reduced by burning and showed no evidence of recovery, i.e. the quadrennially and annually burned plots were similar, and both had lower numbers than the controls. For example, *Agelenopsis* spp. (Fig. 5; graph 1) had an average of less than 10 individuals per plot in 5 years of trapping on the plots receiving annual, biennial, or quadrennial dormant-season burns while control plots had an average over 20 individuals per plot during the same period. Despite only being burned

once during the study, *Agelenopsis* spp. populations on the quadrennially burned plots did not differ from the annually burned plots.

Six genera of spiders were reduced by frequent burning (annual or biennial), but their populations recovered to the same levels as controls on quadrennially burned plots (Fig. 5; graphs 9, 18, 20, 22, 23, and 26) and five spider populations responded positively to frequent burning (Fig. 5; graphs 11, 14, 21, 24 and 25). Populations of these spiders were significantly higher in the annually burned plots than in the unburned controls. Two spider populations showed some evidence of recovery since more were captured on quadrennially burned plots than on annually burned ones, but quadrennially burned plots still had lower numbers than unburned controls (Fig. 5; graphs 16 and 19). Finally, three spider populations (Fig. 5; graphs 5, 10, and 13) were higher on quadrennially burned plots than on the controls or annually burned plots. These spiders appear to benefit from some disturbance, but not the levels of disturbance produced by annual and sometimes biennial prescribed burning.

The two most common genera of roaches on the plots, *Parcoblatta* and *Ishnoptera*, were affected by burning in different ways. *Parcoblatta* spp. (Fig. 5;

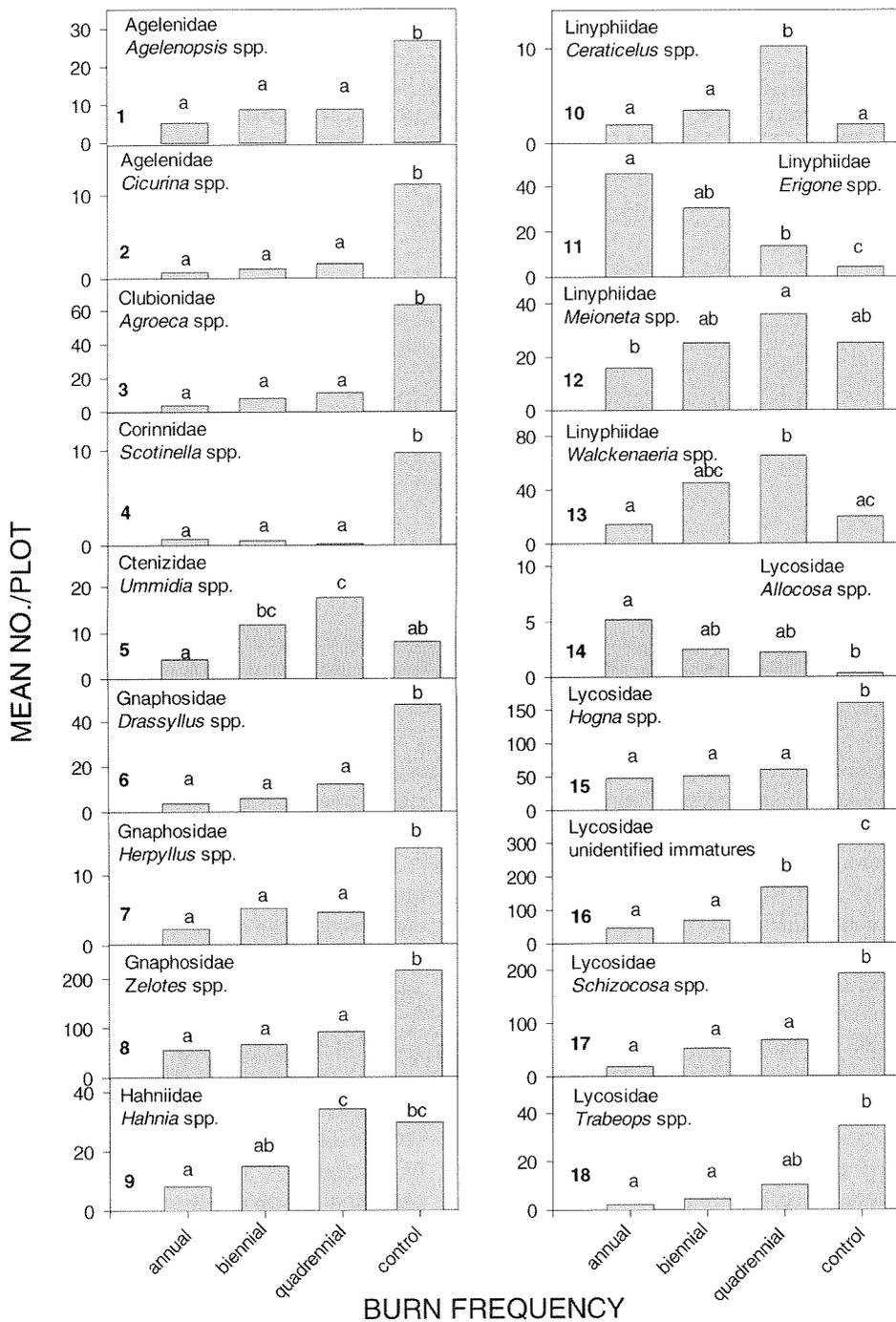


Fig. 5. Mean number of individuals within arthropod groups that were significantly affected by varying frequencies of dormant-season prescribed burns over a 40-year-period on the Osceola National Forest (Baker County, Florida). Graphs are arranged alphabetically by order, family and genus. Graphs 1–28 are spiders (Araneae), 29–30 are roaches (Blattaria), 31 is a millipede (Chordeumatida), 32–51 are beetles (Coleoptera), 52–56 are flies (Diptera), 57–60 are true bugs or plant hoppers (Heteroptera), 61–73 are ants or wasps (Hymenoptera), 74 is a sowbug (Isopoda), 75–76 are caterpillars (Lepidoptera larvae), 77 is a scorpionfly (Mecoptera), 78 is a harvestman (Opiliones), 79–85 are crickets or grasshoppers (Orthoptera), 86 is a millipede (Polydesmida) and 87 is a centipede (Scolopendromorpha). Within graphs, columns with the same letter are not significantly different (REGWQ multiple comparison test, $P < 0.05$).

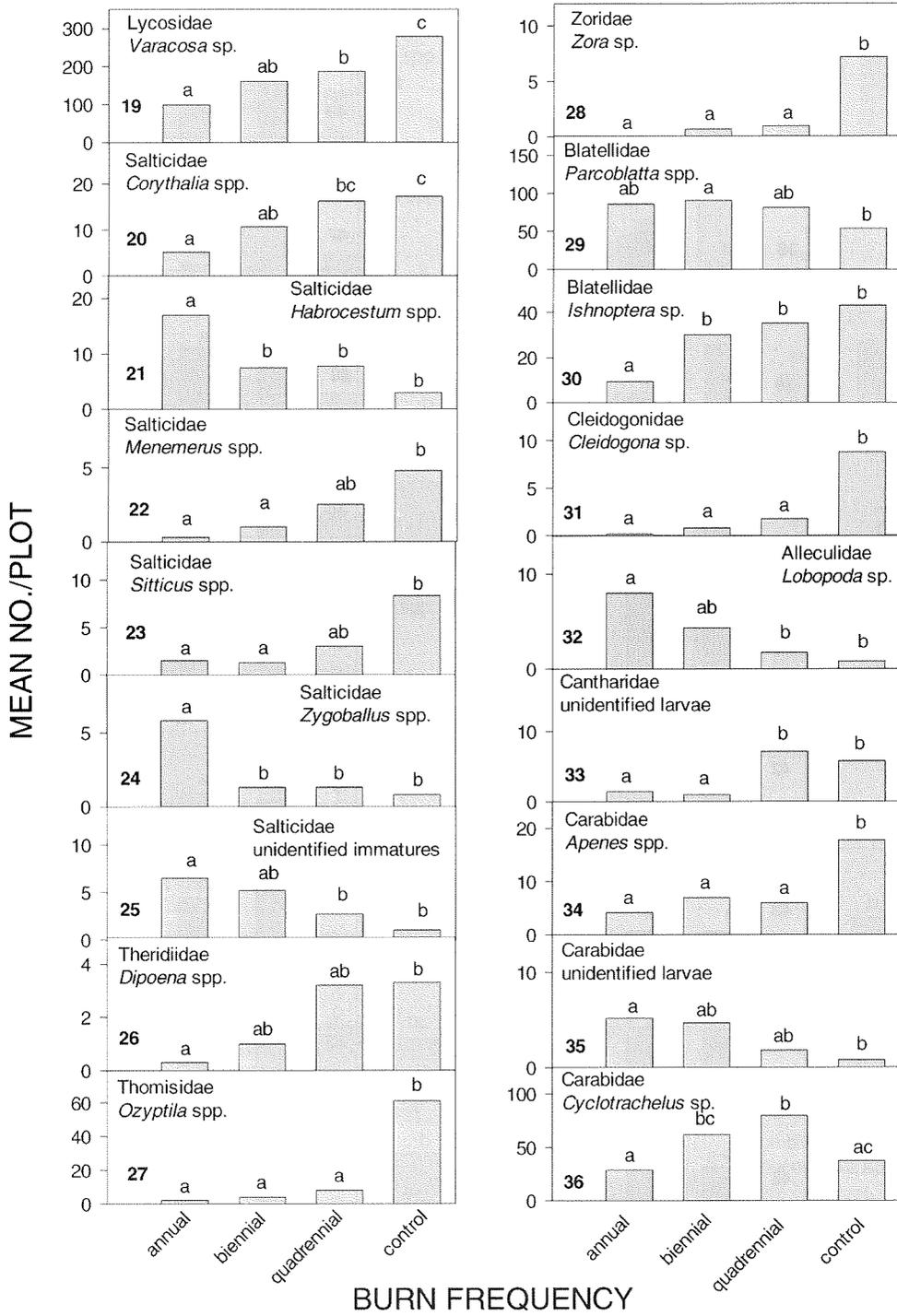


Fig. 5. (Continued).

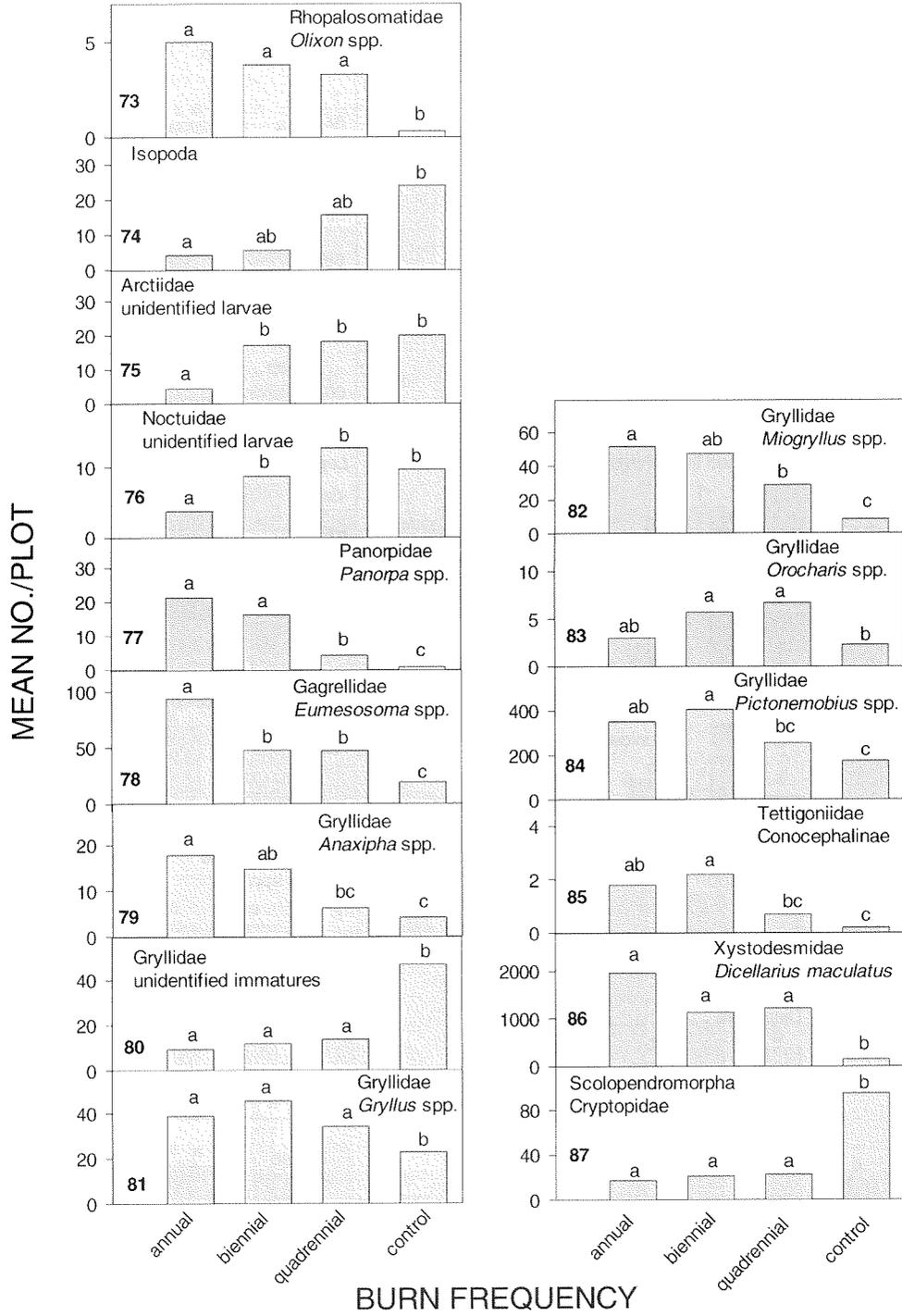


Fig. 5. (Continued).

graph 29) were captured in higher numbers on the biennially burned plots compared to the controls but, overall, dormant-season burning appeared to have little effect. In contrast, *Ishnoptera* spp. (Fig. 5; graph 30) populations were significantly reduced by annual burning while biennial and quadrennial prescribed burning had little effect.

The common millipedes (Diplopoda) also exhibited differing responses to fire. *Cleidogona* spp. (Fig. 5; graph 31) were significantly reduced by all frequencies of prescribed burning. On the other hand, *D. maculatus* (Fig. 5; graph 86) populations responded positively to all frequencies of prescribed burning.

Beetles (Coleoptera) exhibited a range of responses to prescribed burning (Fig. 5; graphs 32–51). Populations of nine genera (Fig. 5; graphs 32, 35, 39, 41, 42, 44, 45, 46 and 49) responded positively to frequent burning, i.e. more were caught on the annually burned plots and in some cases other burn frequency plots than on the control plots. Eight genera (Fig. 5; graphs 33, 34, 37, 38, 43, 47, 48 and 51) were negatively affected by frequent burning and populations of six of those (Fig. 5; graphs 34, 37, 43, 47, 48 and 51) appeared to be unable to recover in 4 years.

Most of the flies (Diptera) that were affected by dormant-season burning responded positively (Fig. 5; graphs 52–56) to some level of burning. Only populations of *Sciara* spp. (Fig. 5; graph 56) were negatively impacted by annual burning.

Of the heteropterans affected by prescribed burning, a *Cryphula* sp. seed bug, *Oliarus* spp. (Cixiidae) and immature Delphacidae were captured in higher numbers on frequently burned plots (Fig. 5; graphs 57, 59 and 60). Only immatures of the Achilidae were reduced by annual burning (Fig. 5; graph 58).

Thirteen Hymenoptera, including eight genera of ants, were affected by burning (Fig. 5; graphs 61–73). Populations of six Hymenoptera genera were reduced by annual burning including *Aphaenogaster* spp. and *Camponotus* spp. ants (Fig. 5; graphs 61, 62, 63, 64, 70 and 71). Four genera of Hymenoptera negatively affected by burning did not recover within 4 years (Fig. 5; graphs 61, 63, 70 and 71). Three genera were more abundant with frequent burning (Fig. 5; graphs 69, 72 and 73). The genus *Solenopsis* includes the red imported fire ant, *S. invicta* which responded positively to frequent disturbance. Most of the individuals

we captured were *S. invicta*. Three genera of Hymenoptera increased in abundance with intermediate levels of disturbance (Fig. 5; graphs 65, 67 and 68). These included the most common ant, *Odontomachus* sp.

Isopods (Fig. 5; graph 74) and Cryptopidae centipedes (Fig. 5; graph 87) were reduced by burning. Isopod populations were reduced only by annual burning, while centipede populations were reduced by all burn frequencies.

We identified Lepidoptera to family since the majority captured in pitfall traps were larvae. Larvae of both the Arctiidae and Noctuidae were negatively impacted by annual burning (Fig. 5; graphs 75 and 76).

Eight Orthoptera were affected by burning. Six of these were crickets (Gryllidae: Fig. 5; graphs 79–84), but not all crickets responded the same to dormant-season burning. Four were more abundant in frequently burned plots (Fig. 5; graphs 79, 81, 82 and 84) while unidentified immatures (Fig. 5; graph 80) were less abundant in burned plots, and *Orocharis* spp. were more abundant in biennially and quadrennially burned plots than controls (Fig. 5; graph 83). Other Orthopterans affected by burning were long-horned grasshoppers in the subfamily Conocephalinae which were more abundant on frequently burned plots (Fig. 5; graph 85).

Scorpionflies (*Panorpa* spp.) and the harvestman (*Eumesosoma* spp.) both increased with increasing burning frequencies (Fig. 5; graphs 77 and 78).

4. Discussion

Prescribed burning altered ground-dwelling arthropod communities. When all 5 years of data were combined we found dormant-season burning reduced diversity and evenness, regardless of frequency, below that of plots where fire had been excluded. Annual burning lowered ground-dwelling arthropod diversity below the other two fire frequency treatments. Examination of data on a yearly basis shows changes in diversity and evenness were due to frequency of fire application and not long-term changes to community diversity. Diversity of unburned control plots remained constant throughout the study, but each year fire was applied in the other plots diversity and evenness declined. Diversity returned to the same level as

controls by the end of the second year after fire. These results suggest annually burned plots had lower overall diversity because they had insufficient time to recover between burns. Fire return intervals of 2 and 4 years resulted in lower overall diversity than unburned plots, but yearly diversity trends show that this also was due primarily to reductions in diversity in years fire was applied. Changes in diversity were not the result of alterations to plots brought on by the long-term use of fire.

Dormant-season burning altered the composition of the community by reducing the numbers of predators and increasing the numbers of detritivores. Although numbers of herbivores captured were similar on all plots, herbivore richness was higher on annually burned plots. Diversity and evenness of detritivores and predators was higher on the unburned plots. Reasons for the higher number of herbivore taxa on annually burned plots are unclear. Unburned plots had a much higher overall live plant biomass, but much of this was due to a single species, saw palmetto. Annual burning increased the abundance of grasses (Table 1) and annual winter burning increases diversity of understory plant communities beneath southern pines (White et al., 1991; Brockway and Lewis, 1997), so it is possible that the greater herbivore richness was due to higher numbers and diversity of herbaceous plant species.

Detritivore diversity was highest on the unburned plots, which had almost six times as much dead plant material as the annually burned plots. However, we captured almost twice as many detritivores (Table 5; without *D. maculatus*) on burned plots. It is possible that detritivores are captured less frequently on unburned plots because the abundance of food available reduces their need to move. Another possibility was that detritus on burned plots may be higher quality. Burning usually kills but does not always consume all of the above ground portions of understory plants. Therefore, dead plant material on burned plots likely contained more nutrients, since plants were unable to recapture the nutrients before leaf death. Finally, greater predation due to higher predator numbers may have contributed to lower detritivore numbers on unburned plots.

Comparisons of overall community similarity (Fig. 2) showed that during a 5-year-period arthropod communities exposed to fire were similar to each other

regardless of fire return interval. Similarity of annually burned plots and unburned controls was lowest. As fire frequency decreased the communities became progressively more similar to the unburned plots. Comparison of similarities of burned plots and unburned controls over time (Fig. 3a) showed a pattern almost the same as diversity (Table 4), i.e. in years when fire was applied to the plots similarity of burned and unburned plots dropped, but similarity returned to pre-burn levels within 2 years. Annually-burned plots consistently had the lowest similarity to controls. Quadrennially-burned plots were as similar to unburned plots 4 years after they were burned as the comparison of half of the unburned plots to the other half in 1999. However, this was not the case in 1995 when the quadrennially-burned plots also had 4 years to recover. The results in 1999 may have been due in part to a severe drought in Florida, that began in May 1998 and extended through January 1999, that may have altered communities within unburned plots. Log transformation of numbers captured prior to calculating percentage similarity (Fig. 3b) suggests that fire had its greatest effect on the most abundant taxa and not rare ones.

Frequent fire did not increase rarity or reduce richness of ground-dwelling arthropods (Fig. 1). We further explored effects of fire frequency on the community of rare taxa with the quotient of similarity that measures only whether taxa are present without taking abundance into consideration. The pattern in comparisons among treatments was very similar to that for percentage similarity of the whole community. Comparisons among burn treatments had quotients of similarity that were approximately equal. The lowest similarity was for the comparison of annually burned plots to controls, while similarity between burn treatments and controls increased with decreasing fire frequency. Although one might expect rare individuals to be more likely to undergo local extinction as a result of fire, our results suggest that may not be the case. However, plots in this study were small with only a 2–3 m wide fire line between them so some movement of arthropods between plots was likely. Therefore, some rare individuals may have come from less frequently burned plots.

Our results and others show it is difficult to make generalizations about the effects of fire on various arthropod groups (Ahlgren, 1974; Warren et al., 1987).

Dormant-season fire did not have a broad general effect on ground-dwelling arthropods in longleaf pine. Even within orders, and in many cases families, fire affected genera differently. For example, most members of the wolf spider family, Lycosidae, were negatively impacted by burning but the genus *Allocosa* had higher numbers on the annually burned plots. Likewise, not all ground beetles (Carabidae) were reduced by burning. Some ants (Formicidae) increased dramatically in response to frequent fire while others were negatively impacted. These results are consistent with previous studies reviewed by Ahlgren (1974), Warren et al. (1987) and Siemann et al. (1997) that show arthropod response to fire is almost species-specific. Attempts to make broad generalizations about arthropod responses based on a few species or groups should be avoided.

Over 40 genera were reduced by burning and, of those, 26 were captured in equal numbers on quadrennially and annually burned plots but in significantly lower numbers than on unburned plots. Warren et al. (1987) presented a model of arthropod population response to fire divided into acute and chronic impacts. According to their model, acute impacts occur during the combustion (the fire) and “shock” phases (the period after the fire but before vegetation began to re-grow), and chronic impacts occur after vegetative regrowth starts and last until equilibrium between flora and fauna populations is attained. Our results show chronic impacts can last over 4 years for some arthropod populations in the longleaf flatwoods ecosystem. However, other species clearly benefitted from frequent burning.

Despite having a significant negative impact in many cases, repeated annual burning over 35 years rarely resulted in extirpation of a genus. In fact, plots where fire was excluded were as likely to be missing a genus that was captured on burned plots. Likewise, Panzer (1988) found little evidence that repeated burning of prairie remnants resulted in complete elimination of butterfly species or the many fire-sensitive leafhoppers (Heteroptera), moths (Lepidoptera) or Orthoptera. Winter burning had no effect on overall richness or richness of rarely collected genera. The quotient of similarity for rare genera was lowest for comparison of annually burned plots to unburned controls, but similarity between burned and unburned plots increased as fire frequency

decreased suggesting that rare genera either quickly re-colonized burned areas or they were not completely eliminated.

Like prairie remnants, longleaf pine stands that have not been heavily disturbed by previous agricultural and silvicultural practices are uncommon. We agree with Howe (1994) that varying timing (season), burning frequency and fire intensities on a given area are more likely to simulate conditions in which longleaf pine communities evolved. In addition, the slow recovery rate of so many species suggests that management oriented toward conservation of biodiversity in longleaf pine should include areas excluded from fire. However, the size or distribution of unburned areas cannot be concluded from this study. Our plots were less than 1 ha, but they apparently were large enough to provide a refuge that allowed a number of species to reach higher population levels. In addition, the unburned plots were invaluable for research, allowing us to detect effects on a number of species that otherwise would have gone unnoticed. A number of studies have shown the importance of fire in the maintenance of longleaf pine and its associated understory plant community, and we agree that prescribed burning should continue to be an integral part of longleaf pine management. However, varying fire regimes and setting aside small unburned areas replicated across a landscape would likely minimize impacts, provide refuges for a number of arthropods and a resource for future research.

Acknowledgements

We thank A. Phalo and D. Combs for technical assistance throughout this study. L. Reynolds, C. New and T. Pitts-Singer assisted in identifying arthropods. M. Williams and numerous student workers sorted samples and F. Brookshire labeled sample vials and proofed data. We thank J. Pitts for his identifications of our spiders and Hymenoptera and C. Smith for taxonomic help on other groups. Keith Lawrence and his staff on the Osceola National Forest provided assistance throughout this study. Finally, we thank the Nature Conservancy's Ecosystem Research Program and the A.W. Mellon Foundation for supporting this work.

References

- Ahlgren, I.F., 1974. The effects of fire on soil organisms. In: Kozlowski, T.T., Ahlgren, C.E. (Eds.), *Fire and Ecosystems*. Academic Press, New York, pp. 47–71.
- 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.
- Andersen, A.N., Yen, A.L., 1985. Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. *Aust. J. Ecol.* 10, 25–30.
- Anderson, R.C., Leahy, T., Dhillon, S.S., 1989. Numbers and biomass of selected insect groups on burned and unburned sand prairie. *Am. Midl. Nat.* 122, 151–162.
- Beach, V., 1993. An up and coming forest. *South Carolina Wildlife* January/February, 44–49.
- Brockway, D.G., Lewis, C.E., 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a wiregrass ecosystem. *For. Ecol. Manage.* 96, 167–183.
- Buffington, J.D., 1967. Soil arthropod populations of the New Jersey pine barrens as affected by fire. *Ann. Entomol. Soc. Am.* 60, 530–535.
- Bartlett, M.S., 1947. The use of transformations. *Biometrics* 3, 39–52.
- Elliott, C.A., 1990. Diversity indices. In: Hunter Jr., M.L., 1990. *Wildlife, Forest and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice-Hall, Englewood Cliffs, NJ, 370 pp.
- Frost, C.C., 1990. Natural diversity and status of longleaf pine communities. In: *Proceedings of the Society of American Foresters Registered Technical Conference on Forestry in the 1990s—A Changing Environment*, Pinehurst, NC, 1990.
- Frost, C.C., 1995. Presettlement fire regimes in southeastern marshes, peatlands and swamps. In: *Proceedings of the Tall Timbers Fire Ecology Conference*, Vol. 19. Tall Timbers Research Station, Tallahassee, FL, pp. 39–60.
- Gillon, Y., 1972. The effect of bush fire on the pentatomid bugs (Hemiptera) of an Ivory Coast Savanna. In: *Proceedings of the Tall Timbers Fire Ecology Conference*, Vol. 11, pp. 377–417.
- Glitzenstein, J.S., Streng, D.R., Wade, D.D., Brubaker, J., 2001. Starting new populations of longleaf pine ground-layer plants in the outer coastal plain of South Carolina, USA. *Natural Areas J.* 21, 89–110.
- Hansen, J.D., 1986. Comparison of insects from burned and unburned areas after a range fire. *Great Basin Nat.* 46, 721–727.
- Hanula, J.L., Franzreb, K.E., 1998. Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. *For. Ecol. Manage.* 102, 89–102.
- Hardin, D.E., White, D.L., 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. *Natural Areas J.* 9, 234–244.
- Howe, H.F., 1994. Managing species diversity in tallgrass prairies: assumptions and implications. *Conserv. Biol.* 8, 691–704.
- Kalisz, P.J., Powell, J.E., 2000. Effects of prescribed fire on soil invertebrates in upland forests on the Cumberland Plateau. *Natural Areas J.* 20, 236–341.
- Klein, M.J., 1988. Pest management of soil-inhabiting insects with microorganisms. *Agric. Ecosys. Environ.* 24, 337–349.
- Krebs, C.J., 1999. *Ecological Methodology*. Addison-Wesley, Menlo Park, CA, 620 pp.
- Landers, J.L., 1991. Disturbance influences on pine traits in the southeastern United States. In: *Proceedings of the Tall Timbers Fire Ecology Conference*, Vol. 17, pp. 61–98.
- McKee Jr., W.H., 1991. Long-term impacts of fire on coastal plain pine soils. In: Nodvin, S.C., Waldrop, T.A. (Eds.), *Fire and the Environment: Ecological and Cultural Perspectives*. Proceedings of an International Symposium on General Technical Report SE-69. Southeastern Forest Experiment Station, Asheville, NC.
- Miller, W.E., 1979. Fire as an insect management tool. *Bull. Entomol. Soc. Am.* 25, 137–140.
- Moya-Raygoza, G., 1995. Fire effects on insects associated with the gamagrass *Tripsacum dactylocoides* in Mexico. *Ann. Entomol. Soc. Am.* 88, 434–440.
- Neumann, F.G., Tolhurst, K., 1991. Effects of fuel reduction burning on epigeal arthropods and earthworms in dry sclerophyll eucalypts forest of west-central Victoria. *Aust. J. Ecol.* 16, 315–330.
- Outcalt, K.W., Sheffield, R.M., 1996. The longleaf pine forest: trends and current conditions. *US Forest Service Resource Bulletin SRS-RB-9*. Southern Research Station, Asheville, NC.
- Panzer, R., 1988. Managing prairie remnants for insect conservation. *Natural Areas J.* 8, 83–90.
- Pearse, A.S., 1943. Effects of burning over and raking off litter on certain soil animals in the Duke Forest. *Am. Midl. Nat.* 29, 406–424.
- SAS Institute, 1987. *SAS/STAT Guide for Personal Computers*, Version 6. SAS Institute, Cary, NC.
- Shea, R.W., Shea, B.W., Kauffman, J.B., Ward, D.E., Haskins, C.I., 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.
- Siemann, E., Haarstad, J., Tilman, D., 1997. Short-term and long-term effects of burning on oak Savanna arthropods. *Am. Midl. Nat.* 137, 349–361.
- Southwood, T.R.E., 1966. *Ecological methods with particular reference to the study of insect populations*. Methuen & Co. Ltd., London, 391 pp.
- Walker, J., 1993. Rare and vascular plant taxa associated with the longleaf pine ecosystems: patterns in taxonomy and ecology. In: *Proceedings of the Tall Timbers Fire Ecology Conference*, Vol. 18, pp. 105–125.
- Warren, S.D., Scrites, D.J., Teel, P.D., 1987. Response of grassland arthropods to burning: a review. *Agric. Ecosyst. Environ.* 19, 105–130.
- White, D.L., Waldrop, T.A., Jones, S.M., 1991. Forty years of prescribed burning on the Santee fire plots: effects on understory vegetation. In: Nodvin, S.C., Waldrop, T.A. (Eds.), *Fire and the Environment: Ecological and Cultural Perspectives*. Proceedings of an International Symposium on General Technical Report SE-69. Southeastern Forest Experiment Station, Asheville, NC.
- Wolda, H., 1981. Similarity indices, sample size and diversity. *Oecologia* 50, 296–302.