A Comparison of Ground-Dwelling Arthropod Assemblages Among Different Habitats Resulting from the 1977 La Mesa Fire

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Abstract.—This study was conducted to determine whether or not post-fire habitats resulting from the 1977 La Mesa Fire support different assemblages of ground-dwelling arthropods. Four principal post-fire vegetation habitats were identified: 1) ponderosa pine forest, 2) ponderosa pine savanna, 3) Gambel oak thickets, and 4) open grasslands. Ground-dwelling arthropods were sampled from each of the four habitats during the summer of 1993. Numerically important arthropod groups found in the samples included spiders, harvestmen, bristletails, crickets, fungus beetles, rove beetles, ground beetles, and darkling beetles. Total arthropod abundances were significantly different among the four habitats, and changed through the summer. Total species diversity differed little among the habitats. Each arthropod group was significantly more abundant in one or two habitat types, and the different arthropod groups had dissimilar abundance patterns among the habitats. These findings are consistent with other studies of post-fire patterns of ground-dwelling arthropod assemblages, and have important implications for differences in decomposition and nutrient cycling rates among habitats, and food resource availability to vertebrate animal predators in those habitats.

INTRODUCTION

The effects of fires on forest arthropods are not well known, especially in the mid-elevation ponderosa pine forests of the Southwest (Wright & Baily 1982). Most studies of arthropod responses to forest fires elsewhere have focused on relatively short-term post-fire recovery or recolonization. Such studies have found that some ground-dwelling soil and litter arthropods may survive fires, depending on burn intensity (Buck 1979, Majer 1984, Abbott 1984), while others recolonize intensely burned areas from surrounding unburned or less intensely burned forest (Touyama et al. 1989, Buck 1979). Recovery of soil and litter inhabiting arthropods after forest fires is generally about five years (Wright & Baily 1982). Actual recovery times will vary with forest type, and the intensity and extent of fires.

Post-fire ground-dwelling arthropod assemblages in forest ecosystems exhibit consistent patterns of various arthropod species and taxonomic groups occurring in different post-fire habitats (Majer 1984, Touyama et al. 1979, Harris & Whitcomb 1974, Richardson & Holliday 1982, Dindal & Metz 1977). Such variation in relative abundances of different arthropod taxa may result from dissimilar recolonization rates (Touyama et al. 1989, Abbott 1984), or from preferences for different habitats resulting from post-fire vegetation recovery (Richardson & Holliday 1982, Dindal & Metz 1977).

In June of 1977 the La Mesa Fire burned approximately 15,000 acres of ponderosa pine forest in the Jemez Mountains of north-central New Mexico (Foxx 1981a). Studies on vegetation (Potter & Foxx 1984), birds (Wauer & Johnson 1984) and small mammals (Guthrie 1984) have shown that the La

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Mesa Fire had significant effects on the resident flora and fauna. Pippin and Nichols (This Volume) sampled arthropods in burned and unburned areas immediately after, and up to one year after the fire. They found reductions in diversity and abundance of arthropods immediately after the fire, and some increases within one year. The greatest reductions in arthropods were in severely burned locations. Nothing is known about the long-term effects of the La Mesa Fire on invertebrates.

Invertebrates are important components of forest ecosystems (Mattson 1977), yet little is known about the taxonomic composition and ecology of invertebrates of ponderosa pine forests of the Southwest. Existing literature on forest insects focuses on plant-feeding insects associated with dominant tree species (Furniss & Carolin 1977). Relatively little is known about ground-dwelling arthropods in coniferous forests.

The goals of this research project were to sample ground-dwelling macro-arthropods from major post-fire habitats resulting from the 1977 La Mesa Fire to: 1) determine the taxonomic composition of ground-dwelling arthropods in the La Mesa Fire area, 2) determine whether or not total arthropod abundance and species diversity differed among post-fire habitats, and 3) to identify which taxonomic and trophic groups were numerically dominant in the different post-fire habitats.

METHODS

This research project was conducted in the north-central portion of the La Mesa Fire, on Apache Mesa and Escobas Mesa, near Ponderosa Campground (Figures 1 & 2). The sampling was performed for a five-month period from late May through early November of 1993. Four vegetation types were identified as major physical habitats resulting from different fire intensities during the La Mesa Fire, and subsequent post-fire vegetation recovery. These four habitat types included 1) intact ponderosa pine forest that was exposed to low-intensity ground fire, and most of the trees survived the fire, 2) ponderosa savanna that resulted from moderately burned ponderosa forest, where some trees survived the fire, 3) Gambel oak thickets that have expanded into areas where all pine trees were killed by intense fire, and 4) open grassland areas that were also intensely burned, and all ponderosa pine trees killed.

Ground-dwelling arthropods were sampled from the four habitats by the use of pitfall traps (Southwood 1978). Pitfall traps used in this study consisted of steel cans measuring 4.5 inches deep, and 3 inches in diameter. Each can was buried in the soil with the open tops flush with the ground surface. Each open can contained one 10 oz. plastic cup, which was half-filled with propylene glycol. A 6-inch diameter, 3/8-inch thick plywood cover was placed over each trap, supported on four 3.5-inch nails, to protect the traps from weather.

Pitfall traps were placed in at least two locations in each of the four habitat types (Figure 2). Each of the site locations were selected subjectively to represent the major post-fire habitat types in the La Mesa Fire burn area. Traps were placed randomly at each location, for a total of ten traps representing each habitat type. Traps were randomly located at each site by utilizing random compass directions and random distance measures. All traps at each site were located at least 20 meters apart.

The contents of the pitfall traps were collected once every 4–8 weeks. The contents of the traps were collected by removing each 10 oz. plastic cup, pouring the contents through a wire-mesh strainer, and transferring the contents to glass vials containing ethyl alcohol. Each vial was labelled with the site name, the trap number and the date of collection. The propylene glycol was placed back into each cup, with more added as needed, and each cup was then placed back into the can from which it came for continued trapping. All traps were collected within a several day time period. All of the traps were collected four times during the summer and autumn, 1) mid-July or early summer (sampling period: June, mid-July), 2)

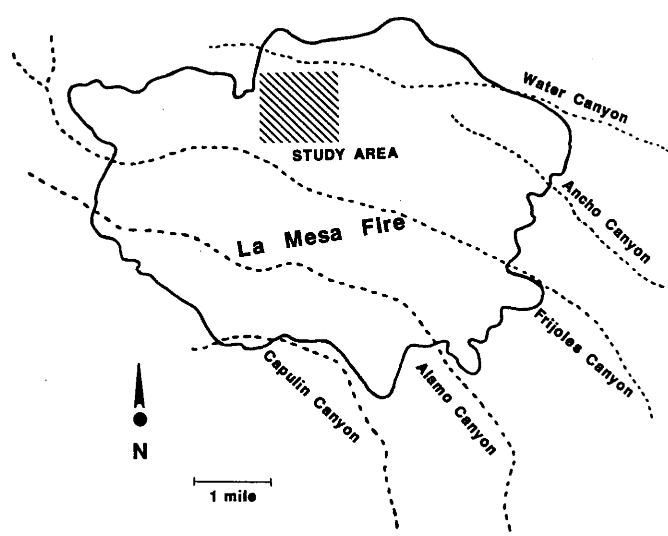


Figure 1.—Location of arthropod study area within the 1977 La Mesa Fire.

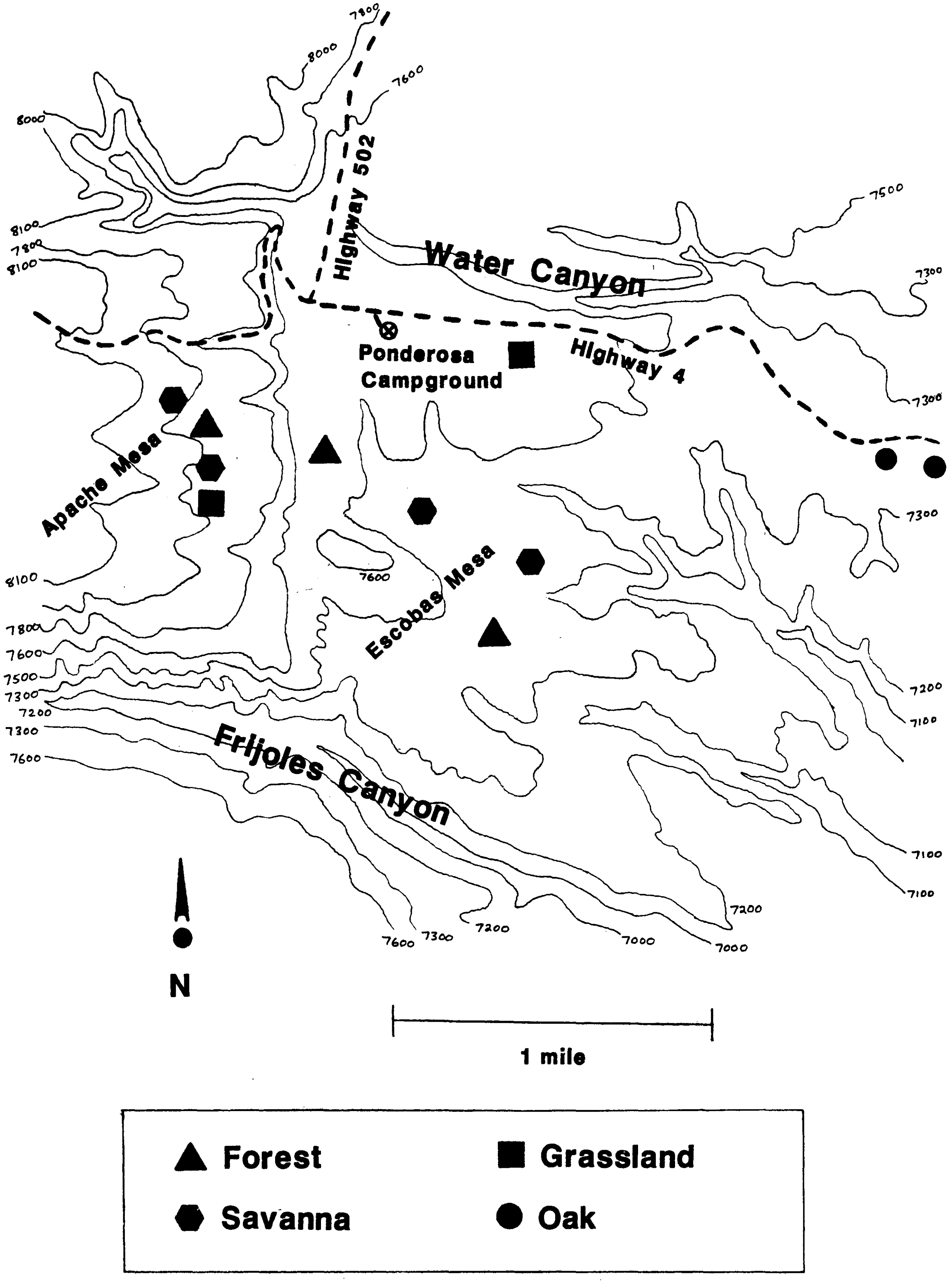


Figure 2.—Locations of arthropod pitfall trapping sites representing post-fire ponderosa pine forest, ponderosa pine savanna, Gambel oak thickets, and grassland habitats.

mid-August or mid-summer (sampling period: late July-early August), 3) early October or late summer (sampling period: late August-early October), and 4) mid-November or autumn (sampling period: mid-October-mid-November).

The labelled vials with the trap contents were taken to a laboratory at UNM where the arthropods from each vial were sorted, identified, and counted. Count data of individuals representing each species, for each date were entered onto data sheets. Only ground-dwelling or ground-surface active arthropods that are appropriately captured by pitfall traps were considered. Such target groups included ground-dwelling spiders, centipedes, millipedes, beetles, crickets, and others. Non-target, or typically non-ground-dwelling arthropods such as flies, were not recorded. Although ants are ground-dwelling arthropods, their populations are not adequately sampled by pitfall traps, and ants were not included in this study.

Many of the arthropods could not be identified to the species, genus, or in some cases family level at the time that samples were sorted and tabulated. Such species were assigned alpha-numeric codes as operational taxonomic units (OTU'S) or morphospecies. Each code consisted of two characters for classification to the order, family, genus, and species ranks. If the name of a particular rank was known, the first two letters of that name was used for that level of the code. If the name was not known, a numeric value was used, and ascending numeric values were used for additional unknown taxa of that rank. Taxonomic classification of insects to the order and family level corresponds to Arnett (1985). Taxonomic classification of non-insect arthropods to the class, order, and family levels corresponds to Borror et al. (1981).

A reference collection of voucher specimens of all species or OTU's was assembled. Those species that were not initially identified are in the process of being identified by experts of the particular taxonomic groups. OTU codes will then be changed to the actual species codes as the identifications are completed.

A data book of taxonomic codes was maintained, as well as data books for the species count data. All data read from data books were entered into a computer spreadsheet database. Various sorting routines were used to visually error-check the data within the spreadsheet.

Data analysis was performed with SAS (SAS Institute 1990) analytical software. Means of arthropod count data were generated by PROC MEANS (SAS Institute 1990) to provide graphs of mean counts for the arthropods. Univariate analysis of variance (ANOVA) was preformed on the data with PROC GLM (SAS Institute 1990) to provide tests for differences in arthropod abundances among the four habitats on different dates. The numerically important taxonomic groups of arthropods were identified and separate ANOVA tests were performed for each group. Duncan's multiple range test was used to determine which mean values from each habitat were significantly different between each other. The arthropod count data were log-transformed for the ANOVA tests.

PROC CANDISC (SAS Institute 1990) multivariate canonical discriminant analysis (Manly 1986) was used to test for differences among the habitats based on the combined variances from the major arthropod taxonomic groups, and to determine which arthropod groups were the best discriminators between the four habitats. Separate analyses were run for each of the sampling dates. The arthropod count data were log-transformed for the canonical discriminant analysis.

RESULTS

Many types of ground-dwelling arthropods were collected in the pitfall traps, including spiders, harvestmen, centipedes, millipedes, jumping bristletails, crickets, and several families of beetles. Many micro-arthropods such as mites and springtails were also common in the traps but they were not included in the analysis because they are more appropriately sampled by other techniques, and because of their small size they were difficult to identify to morphospecies or OTU's.

The arthropod groups that were most numerous and most consistently encountered in samples, were spiders, harvestmen, bristletails, crickets, fungus beetles, rove beetles, ground beetles, and darkling beetles (Table 1). Individuals of those taxonomic groups were consistently numerous in traps from most of the four habitats.

Total numbers of all ground-dwelling arthropods peaked during early to mid-summer (June to mid-July) in the two non-forest habitats, and in mid-summer (late-July through August) in the two forest habitats. There were significantly more arthropods in the oak habitat during the early summer than in the other three habitats (Figure 3). In mid-summer there were significantly fewer arthropods in the grassland habitat than in the

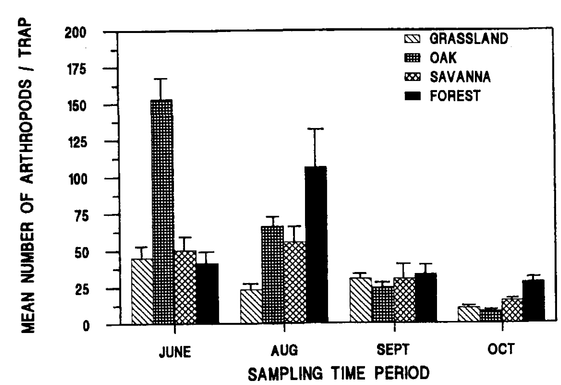
Table 1.—Major taxonomic arthropod groups sampled from pitfall traps in all four habitats.

Arthropod group	Important taxa	Trophic status
spiders (Araneae)	Clubionidae	predators
	Dictynidae	predators
	Gnaphosidae	predators
	Lycosidae	predators
	Thomisidae	predators
harvestmen (Opiliones)	two species	predators
bristletails (Microcoryphia)	*Mesomachilis leechi*	detritivores
	Machilinus aurdantidcus	detritivores
camel crickets (Gryllacrididae)	*Ceuthophilus utahensis*	detritivores
	Ceuthophilus pallidus	detritivores
	Styracosceles neomexicanus	detritivores
fungus beetles (Cryptophagidae)	several species	detritivores
rove beetles (Staphylinidae)	several species	predators
ground beetles (Carabidae)	*Synchus dubius*	predators
	Cimindis punctiger	predators
	Carabus taedatus	predators
darkling beetles (Tenebrionidae)	*Eleodes extricata*	detritivores
	Eleodes nigrinus	detritivores
	Eleodes planipennis	detritivores

other habitats. In late summer (late August-early October) there was no significant difference in arthropod abundances among the four habitats, and in autumn (mid-October-mid November), there were significantly more arthropods in the forest habitat than the others. There was an overall trend for decreasing numbers of arthropods from early summer to autumn in the non-forested habitats, with similar declines observed after mid-summer in the forest and savanna sites (Figure 3).

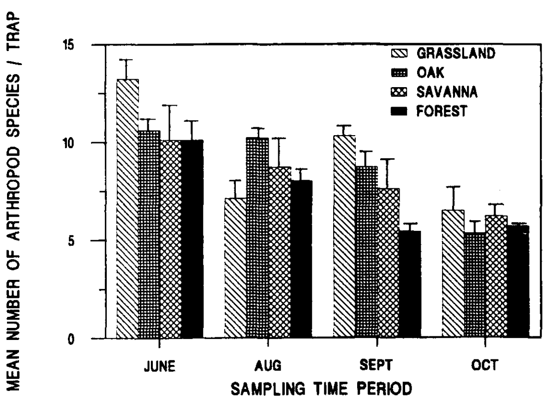
Species diversity, or total numbers of species of ground-dwelling arthropods (i.e., species richness), did not differ significantly among habitats in early summer. In mid-summer, the oak habitat had significantly more species than the grassland, but neither were significantly different from the forest or savanna (Figure 4). In late summer, the grassland and oak habitats had significantly more species than the forest, and the grassland also had significantly more species than the savanna. There was no significant difference in species diversity among habitats in autumn. There was an overall trend for decreasing species diversity from early summer to autumn (Figure 4).

Spider abundance was not significantly different among the four habitats in early summer (Figure 5). In mid-summer, spiders were significantly less abundant in the forest habitat than the oak, but neither habitat was significantly different from the savanna or grassland. In late summer, spiders were significantly less abundant in the forest habitat than the other three. In autumn, spiders were significantly more abundant in the grass habitat than



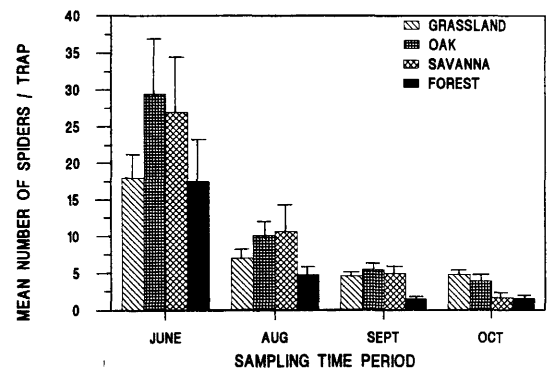
Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
All individuals	June	0.0001	Yes	O S G F
	Aug.	0.0003	Yes	F O S G
	Sept.	0.8172	No	G F S O
	Oct.	0.0001	Yes	F S G O

Figure 3.—Graph of mean numbers and standard errors of all ground-dwelling arthropods per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
All species	June	0.1670	No	G O F S
	Aug.	0.0586	No	O S F G
	Sept.	0.0092	Yes	G O S F
	Oct.	0.6149	No	G S F O

Figure 4.—Graph of mean numbers and standard errors of all arthropod species per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Spiders	June	0.3036	No	O S G F
	Aug.	0.1124	No	O S G F
	Sept.	0.0014	Yes	O G S F
	Oct.	0.0256	Yes	G O F S

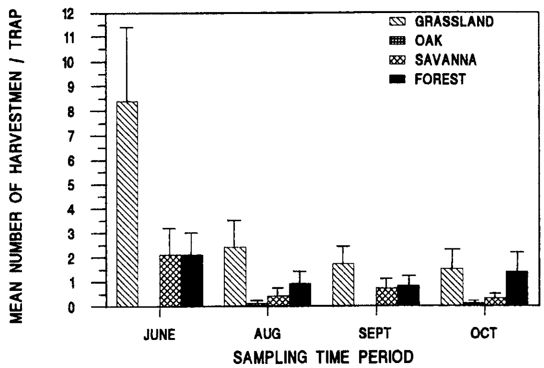
Figure 5.—Graph of mean numbers and standard errors of spiders per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

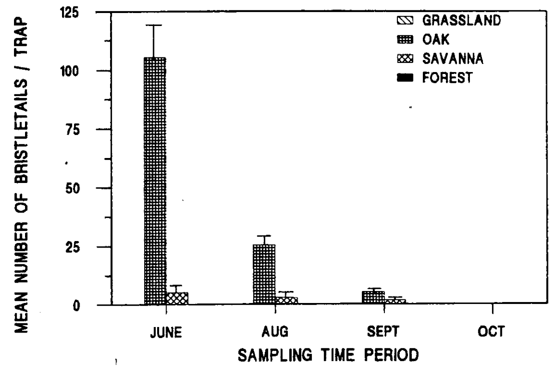
the forest or savanna. Overall spider abundance decreased from early summer to autumn (Figure 5).

Harvestmen were significantly more abundant in early summer in the grassland habitat (Figure 6). In mid-summer, harvestmen were significantly more abundant in the grassland habitat than the oak and savanna, but numbers were not significantly different between grassland and forest, or between forest, savanna, and oak. In late summer, harvestmen were significantly more abundant in the grassland than the oak habitat, but counts from both habitats were not different from forest and savanna. There were no significant differences in the abundances of harvestmen among habitats in autumn. Overall harvestmen abundance was high in the grassland in early summer but varied little thereafter, and remained relatively constant through the seasons in the other habitats (Figure 6.)

Bristletails were significantly more abundant in traps from the oak habitat in early summer, mid-summer, and late summer (Figure 7). In early and mid-summer, bristletails were significantly more abundant in the savanna sites than the grassland and forest sites where bristletail numbers were near zero throughout the sampling period. In autumn bristletail abundances were near zero, and there were no significant differences in bristletail abundance among habitats. In the oak and savanna habitats, bristletail abundances were high in early summer and declined through the seasons to near zero by autumn (Figure 7).

Cricket abundance did not differ significantly among the four habitats at any time of the season





Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Harvestmen	June	0.0039	Yes	G S F O
	Aug.	0.0412	Yes	G F S O
	Sept.	0.0382	Yes	G F S O
	Oct.	0.1214	No	G F S O

Figure 6.—Graph of mean numbers and standard errors of harvestmen per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Bristletails	June	0.0001	Yes	O S F G
	Aug.	0.0001	Yes	O S F G
	Sept.	0.0001	Yes	O S G F
	Oct.	0.1347	No	O G F S

Figure 7.—Graph of mean numbers and standard errors of bristletails per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

(Figure 8). Overall cricket abundance was greatest during mid-summer.

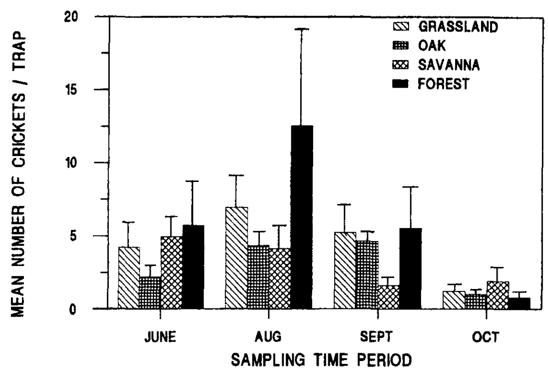
Fungus beetles were significantly more abundant in the forest and savanna habitats then the grassland or oak habitats in early summer, and mid-summer (Figure 9). In late summer, the numbers of fungus beetles did not differ significantly among the four habitats. In autumn, fungus beetles were significantly more abundant in the forest habitat than the other three. Overall fungus beetle abundance peaked during the mid-summer period (Figure 9).

Rove beetles were significantly more abundant in the forest habitat in early summer and autumn, and the forest and savanna habitats in mid-summer and late summer (Figure 10). Overall rove beetle abundance tended to increase through the seasons (Figure 10).

Ground beetles were significantly more abundant in the oak habitat in early summer and mid-summer (Figure 11). There was no significant difference in ground beetle counts among the four habitats in late summer and autumn. Overall ground beetle abundance was greatest during the mid-summer period, and declined to low levels by autumn (Figure 11).

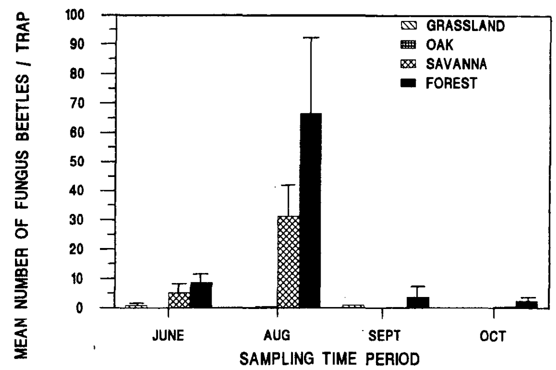
Darkling beetles were significantly more abundant in the grassland habitat in early summer, and the oak habitat in mid-summer (Figure 12). There was no significant difference in darkling beetle abundance among the four habitats in late summer or autumn. Overall darkling beetle abundance was greatest in early summer, and declined through the rest of the season (Figure 12).

Multivariate canonical discriminant analysis of differences among habitats based on abundance



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Crickets	June	0.7739	No	S F G O
	Aug.	0.8414	No	G O F S
	Sept.	0.1650	No	O G F S
	Oct.	0.8014	No	S G O F

Figure 8.—Graph of mean numbers and standard errors of crickets per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Fungus Beetles	June	0.0340	Yes	F S G O
	Aug.	0.0001	Yes	F S O G
	Sept.	0.5830	No	F G S O
	Oct.	0.0015	Yes	F S O G

Figure 9.—Graph of mean numbers and standard errors of fungus beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

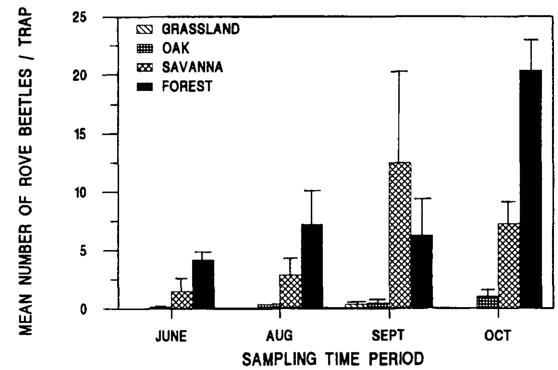
data for the major taxonomic arthropod groups resulted in overall significant differences among habitats, at all four times of the season (Table 2a-d).

Examination of standardized canonical coefficients for each of the arthropod groups revealed that bristletails, ground beetles, fungus beetles and rove beetles contributed to the discrimination of habitats in early summer and mid-summer (Table 2a-d). Bristletails, spiders, ground beetles, and crickets accounted for the discrimination of habitats in late summer, and rove beetles and fungus beetles accounted for most of the discrimination in autumn (Table 2a-d).

Graphical plots of canonical variate scores for individual traps from each habitat type based on canonical scores for the first two discriminant functions, illustrate the discrimination of the four habitats based on abundances of the major arthropod groups (Figure 13a-d). The scores for traps from forest, grassland, and oak habitats were very different from each other at each sample period. Scores for savanna traps tended to be intermediate between those of the other three habitats, although they were most similar to the forest habitat (Figure 13a-d).

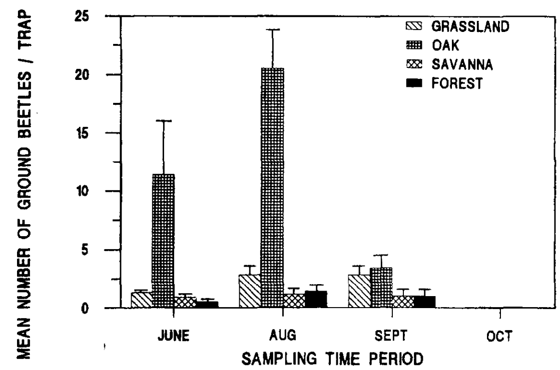
DISCUSSION

Results of this study reveal that there were significant differences in overall abundances of ground-dwelling arthropods among the four habitat types, and differences in the abundances of the major taxonomic arthropod groups among the four habitats. Significantly higher numbers of all arthro-



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Rove Beetles	June	0.0001	Yes	F S O G
	Aug.	0.0047	Yes	F S O G
	Sept.	0.0456	Yes	S F G O
	Oct.	0.0001	Yes	F S O G

Figure 10.—Graph of mean numbers and standard errors of rove beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Ground Beetles	June	0.0001	Yes	O G S F
	Aug.	0.0001	Yes	O G F S
	Sept.	0.1048	No	G O S F
	Oct.	0.6017	No	S O F G

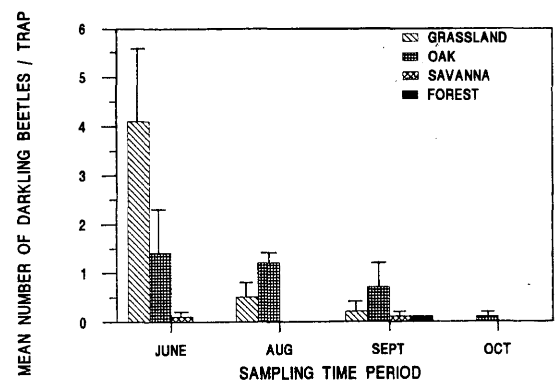
Figure 11.—Graph of mean numbers and standard errors of ground beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

pod individuals in the oak habitat in early summer, forest, oak, and savanna in mid-summer, and forest in autumn may be attributed to high numbers of particular major taxonomic groups in those habitats at those times of the season. During those time periods, the oak habitat was dominated by bristletails, spiders, and ground beetles, and the forest and savanna habitats were dominated by fungus beetles, and rove beetles. Harvestmen and darkling beetles were most abundant in grassland habitats, but since the numbers of those arthropods were low relative to the other arthropod groups the grassland sites had consistently low overall arthropod abundances.

Total arthropod species diversity did not change much among the four habitats, even though abundances of various arthropod groups did. Such results indicate that the different groups contributed differentially to the total numbers of species in each habitat. Thus, species composition changed between the habitats, but overall species richness or diversity did not.

Seasonal trends in total arthropod abundance reflected the seasonal trends in the abundances of the individual major taxonomic groups. Bristletails, spiders, harvestmen, and darkling beetles were all most abundant in early summer, with declining populations through the season to autumn. Such a pattern probably reflects the life-history patterns of these arthropods. Bristletails, spiders, and harvestmen all reproduce once a year, with juveniles present in the spring and early summer, maturing to adults by mid-summer. Adults and juveniles of these arthropods occur in the same habitats. Many juvenile bristletails, spiders, and harvestmen were present in the early summer. Mortality among juveniles over time may account for the seasonal decline in these arthropods. In contrast, darkling beetles have distinct larval and adult stages, where the larvae live in the soil and are not caught in pitfall traps, and adults are active on the ground surface, and are caught in pitfall traps. All darkling beetles captured were adults. The seasonal pattern in darkling beetle abundance indicates that adult activity is greatest in the early summer for the three dominant species of *Eleodes*.

Crickets, fungus beetles, and ground beetles were most abundant in the middle of the summer. Perhaps the activity of these insects is synchronous with the summer rainy season. Rove beetles were most abundant late in the summer. Most of the species of rove beetles found in the traps were very small, indicating that they probably feed on micro-



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high x̄ -> low x̄
Darkling Beetles	June	0.0007	Yes	G O S F
	Aug.	0.0001	Yes	O G F S
	Sept.	0.4662	No	O G S F
	Oct.	0.4635	No	O G F S

Figure 12.—Graph of mean numbers and standard errors of darkling beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

Table 2.—Results of canonical discriminant function analysis for arthropod taxonomic group data among four habitats.

a. Sample Period: June (early summer)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0001	0.0632
Eigenvalue:	14.99	5.99	0.56
Cumulative variance:	69%	97%	100%
Standardized Canonical Coefficients			
Darkling Beetles	0.39	0.50	0.86
Ground Beetles	0.91	0.69	0.89
Fungus Beetles	0.06	–1.08	0.12
Rove Beetles	–0.13	–1.60	1.20
Spiders	0.12	0.08	–0.96
Crickets	–0.18	0.23	–0.59
Harvestmen	0.29	0.91	0.67
Bristletails	3.11	–1.46	0.25
b. Sample Period: August (mid–summer)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0003	0.4119
Eigenvalue:	13.59	1.98	0.22
Cumulative variance:	86%	99%	100%
Standardized Canonical Coefficients			
Darkling Beetles	0.31	–0.42	0.25
Ground Beetles	1.26	–0.27	0.78
Fungus Beetles	0.44	1.16	–0.09
Rove Beetles	0.25	0.74	0.54
Spiders	–0.29	0.07	–0.78
Crickets	0.20	–0.12	0.07
Harvestmen	–0.55	–0.21	–0.08
Bristletails	2.61	0.91	–0.54
c. Sample Period: September (late summer)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0527	0.2410
Eigenvalue:	2.89	0.76	0.36
Cumulative variance:	72%	91%	100%
Standardized Canonical Coefficients			
Darkling Beetles	0.15	0.01	–0.01
Ground Beetles	0.07	1.16	–0.19
Fungus Beetles	–0.24	0.15	–0.20
Rove Beetles	–0.27	–0.76	0.63
Spiders	0.67	0.67	0.55
Crickets	0.16	–1.02	–0.60
Harvestmen	–0.44	0.41	0.14
Bristletails	1.16	–0.64	0.11
d. Sample Period: October (autumn)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0383	0.2941
Eigenvalue:	12.27	0.96	0.32
Cumulative variance:	90%	98%	100%
Standardized Canonical Coefficients			
Darkling Beetles	–0.90	–0.12	0.70
Ground Beetles	0.17	–0.36	0.26
Fungus Beetles	0.44	1.06	0.56
Rove Beetles	2.76	–1.11	0.32
Spiders	0.62	0.05	0.65
Crickets	–0.07	–0.60	–0.18
Harvestmen	0.43	1.30	0.25
Bristletails	–0.16	–0.49	0.88

arthropods such as springtails and mites. Springtail and mite populations probably increase following summer rains, providing increased food resources for rove beetles late in the season.

The relatively high numbers of bristletails, spiders, and ground beetles in the oak habitat indicates that some features of the environmental characteristics of those habitats are more favorable to these three arthropod groups. An important feature of the oak habitats that is different from the other three habitats is the oak leaf litter that covers the ground in the Gambel oak thickets. This oak leaf litter apparently provides a favorable food resource for bristletails in the early summer. The large numbers of bristletails in the oak leaf litter may in turn

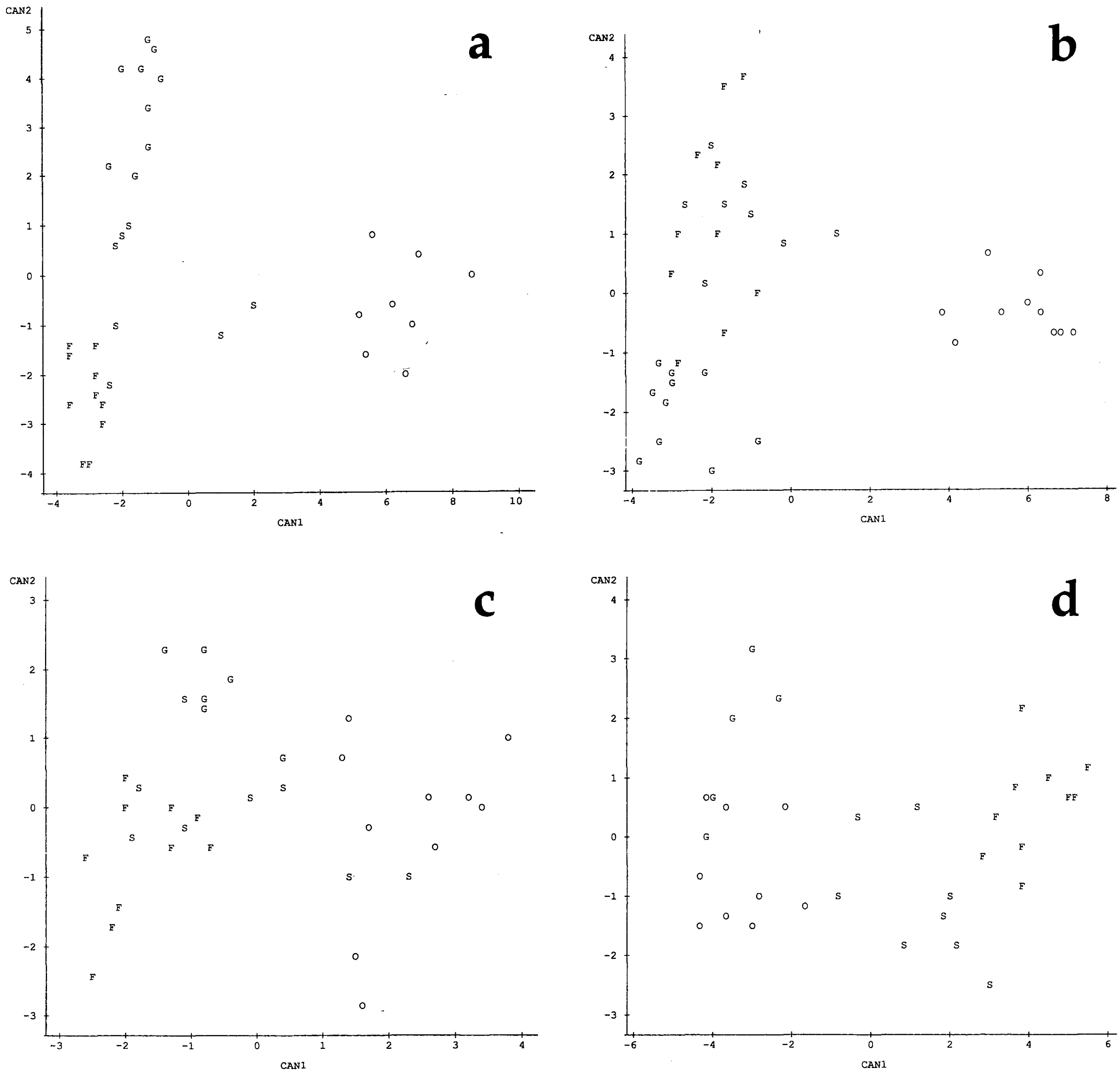


Figure 13a-d.—Plots of canonical variate scores for traps from each habitat from each of the sampling dates (a. June=early summer, b. Aug.=mid-summer, c. Sept.=late summer, and d. Oct.=autumn).

support large populations of predators such as spiders and ground beetles.

Fungus beetles and rove beetles are typically abundant in forest litter. The relatively high numbers of fungus and rove beetles from the forest and savanna habitats in this study is consistent with known habitat preferences for these beetles.

Darkling beetles and harvestmen were most abundant in the open grassland habitats. The most common species of darkling beetle, *Eleodes extricatus*, is usually found in open piñon-juniper woodlands, as are the harvestmen. The open vegetation canopy of the grassland areas may provide a habitat similar to the open piñon-juniper habitats found at elevations slightly below the La Mesa Fire area. Such open canopy habitats are apparently preferred by these arthropods.

Results from this study demonstrate that different burn intensities from the La Mesa Fire did change the composition of ground-dwelling arthropods occurring in four post-fire vegetational habitat types. These findings are consistent with other studies of post-fire responses of ground-dwelling arthropods in forest ecosystems (Harris & Whitcomb 1974, Abbott 1984, Majer 1984, Touyama et al. 1989). Pippin and Nichols (This Volume) found immediate reductions in arthropod diversity and abundances apparently caused by mortality from the La Mesa Fire. In contrast, this study was conducted 16 years after the La Mesa Fire, and the differences found in arthropod assemblages between post-fire habitats are probably due to arthropod preferences for different habitats resulting from differences in post-fire vegetation, not post-fire recolonization of areas where the pre-fire arthropod fauna was destroyed or altered by the fire. Other studies of arthropod response to forest fires have found that several years after fires, different species or groups of arthropods are found in different post fire habitats as a result of habitat selection (Harris & Whitcomb 1974, Dindal & Metz 1977).

Implications of these findings at the La Mesa Fire are pertinent to ecosystem processes where arthropods probably regulate rates of decomposition of ground-level vegetation litter. Detritivores such as bristletails, crickets, and darkling beetles probably have major roles in nutrient cycling in forest ecosystems, and predators such as spiders and ground beetles may have important roles regulating populations of detritivores. Different taxonomic groups of detritivores and predators in the four habitats reveals that the trophic structure varies between each habitat, and thus the decomposition processes and rates are also likely to differ. For example, Springett (1979) found that post-fire effects on detritivore arthropods led to changes in litter decomposition rates. Any future studies on decomposition and nutrient cycling in post-burn habitats of the La Mesa Fire should be concerned with differences in arthropod trophic groups.

Different assemblages of ground-dwelling arthropods with dissimilar seasonal abundance patterns in the four post-fire habitats reveal that food resources to higher level vertebrate predators are not the same among the four habitats. Ground-level foraging animals such as small mammals, birds, and reptiles and amphibians, will encounter different prey items and prey abundances among the four post-fire habitats. Changes in arthropod prey composition will probably have important implications to the foraging strategies, and perhaps species composition of vertebrate predators in different post-fire habitats in the La Mesa Fire area.

Ground-dwelling arthropods are important components of forest ecosystems as regulators of nutrient cycling, and as food resources for higher trophic level consumers (Mattson 1977). Future studies of forest ecosystem processes or biological community dynamics in the La Mesa Fire area should address the roles and attributes of these animals relative to the study questions.

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