

Ground-dwelling arthropod responses to succession in a pinyon-juniper woodland

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Abstract. Stand-replacing wildfire is an infrequent but important disturbance in southwestern pinyon-juniper woodlands. A typical successional cycle in these woodlands is approximately 300 years or more after a stand-replacing fire. Arthropods, especially ground-dwelling taxa, are one of the most abundant and diverse fauna in terrestrial ecosystems and are typically responsive to microhabitat change. Little is known regarding community responses of ground-dwelling arthropods to changes in woodland successional stages from early ecosystems dominated by grasses, herbaceous plants, and fire adapted shrubs to tree-dominated old-growth ecosystems. In 2007 and 2008, within Mesa Verde National Park, Colorado, we compared the community composition of ground-dwelling arthropods between old-growth pinyon-juniper stands that were 300–400 years old and early successional areas recovering from a stand-replacing fire in 2002. The 2002 fire eliminated the dominant woody vegetation, which was replaced by increased herbaceous vegetation and bare ground. The early successional arthropod community showed a significantly higher abundance in major arthropod taxonomic groups, except spiders, compared to old-growth woodland. Old-growth species richness was greater in late August–September, 2007 and greater in early successional habitats during April–July, 2008. Spatial variability of the habitat was much greater in the recently burned early successional plots than the old-growth late successional plots. The differences in habitat were strongly correlated with arthropod community composition, suggesting that ground-dwelling arthropods are very sensitive to habitat changes. Habitat affiliation was strong, with 83% (early succession ruderal) and 91% (old-growth woodland) of the species found primarily or exclusively in one habitat. Many habitat indicator species (defined as species found in significantly greater abundance in one habitat) were found in both burned and old-growth habitats. Several species were found to be strict specialists exclusive to only one of these habitats. Collectively, the results suggest that heightened concern over loss of old-growth woodlands is warranted, given the distinct nature of the ground-dwelling arthropod community in old-growth habitats.

Key words: arachnids; arthropods; disturbance; fire; insects; Mesa Verde National Park; pinyon-juniper woodlands; spiders; succession.

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INTRODUCTION

Fire and pinyon-juniper woodlands

Fire is an important disturbance in most ecosystems and can transform landscapes for centuries (Whelan 1995). Pinyon-juniper woodland is the dominant vegetation type on the Colorado Plateau and within Mesa Verde National Park, Colorado. Disturbances such as fire, especially those that are catastrophic and stand-replacing, have significant impacts on these ecosystems. This is because the intervals between fires in semi-arid ecosystems such as pinyon-juniper woodlands tend to be long and the fires severe (Baker and Shinneman 2004, Floyd et al. 2004).

Fires have become more frequent within the area of Mesa Verde National Park over the last century. Within the last 80 years, over 80% of the park has experienced a stand-replacing fire (USFS report 2006). Within a 40-year span (1969–2009), over 400 fires were recorded within the park boundaries (Floyd et al. 2004). Of these 400 fires, roughly 90% burned less than 1 ha (small spot fires) and only 2% burned up to 4 ha (area fires). The remaining 8% accounted for roughly 80% of the park area burned during this period (large, stand replacing). Our recently-burned study sites experienced such a catastrophic stand-replacing fire in 2002 (Baker and Shinneman 2004, Floyd et al. 2004).

Studies in other tree-dominated habitats have examined the response of communities to fire disturbance and these have generally found that more intense fires result in greater habitat loss for litter and tree dwellers and habitat increase for those arthropods able to take advantage of the revegetation of these areas (Moretti et al. 2004). The Long Mesa area was severely burned, with many areas around trees observed to be scorched to the point where even the root sprouting understory vegetation would not regrow. In most of the open ground cleared by the Long Mesa Fire, grasses and herbaceous vegetation dominated the landscape.

Ground-dwelling arthropod communities

Arthropods account for over 60% of known global biodiversity and are important components in all major terrestrial ecosystems (Hammond 1990). In addition, they constitute a large

portion of the overall animal community in many habitats (Leather 2005), filling a wide range of important ecosystem niches. For a given habitat, suites of species can occupy a variety of niches within an ecosystem. Ground-dwelling arthropods directly influence soil succession and development through decomposition, maintaining soil structure, fertility, and nutrient cycling (Seastedt and Crossley 1984). Ants alone have been found to turn more soil than earthworms (Lyford and Forest 1963). Invertebrates and microorganisms are crucial to the maintenance of biodiversity because they provide the foundation for community structure through energy conversion within the food web. Invertebrates, arthropods in particular, are also important food sources for vertebrates (Hawksworth and Ritchie 1993). The diversity of trophic levels, life cycles, and development times of arthropods can provide researchers with information concerning ecosystem function (Wilson 1987).

Terrestrial arthropods can be effective indicators of environmental change (Kremen et al. 1993, Pearson 1994, Dufrene and Legendre 1997, Longcore 2003) because they are sensitive to a variety of factors such as climate, fire, disturbance, and changes in soil composition. They respond more quickly to environmental changes and human management decisions than do larger, longer-lived organisms. Small size, rapid population growth, short life cycle, and high mobility make ground-dwelling arthropods useful in detecting fine-scale spatial variation and changes over short amounts of time.

Habitat influences on arthropod communities

Disturbances, especially when leading to habitat fragmentation, can have varying effects on arthropod communities depending on trophic level (Gibb and Hochuli 2002). Ground-dwelling arthropods reproduce and mature quickly, are highly responsive to changes in microhabitat characteristics (Intachat et al. 1997, Ellis et al. 2001), and are abundant in all terrestrial habitats. The influences of fire on vascular plants, vertebrates, and ecosystem processes have been well studied (Greenberg et al. 2006, Waldrop et al. 2008, Greenberg and Waldrop 2008, McIver et al. 2008, Matthews et al. 2009). Much less is known about arthropod response to fire in forested ecosystems (but see Moretti et al. 2004) and

nothing is known about arthropod response to fire in pinyon-juniper ecosystems.

Soil composition can directly affect ground-dwelling arthropods because soil provides shelter as well as substrate for eggs and other quiescent life stages. Soils can also indirectly affect arthropods through the plants that provide ecosystem resources (Wolkovich 2010). Many species of surface-dwelling insects live in the soil during immature stages, feeding on roots (e.g., Tenebrionidae, Elateridae, and Scarabaeidae) or fungi (e.g., Sciaridae). Fine, loamy soils, which are characteristic of the pinyon-juniper woodlands of Mesa Verde, provide refuge for ants, insect larvae, spiders, and other arthropod species. Soil particle size composition may change after a fire due to increased wind and water erosion. Fire not only removes woody plant biomass, which increases near-term soil erosion, it also reduces the essential organic layers within the soil and can cause larger particles to break down under heat (Whelan 1995). The loss of the organic particles can cause hydrophobicity in the soil, which can increase surface run-off and erosion after rain (Whelan 1995).

Competing forces may affect arthropod diversity in burned vs old-growth habitats. Old-growth habitats in arid environments tend to have thicker duff and a more complex set of microhabitats that can favor a greater diversity of species. Increased tree density and cover reduces solar radiation while increasing litter and woody debris, leading to less herbaceous ground cover, greater moisture retention, and a greater diversity of microhabitats. These factors can significantly influence the amount of litter, shade, and refugia available to the insect community (Jansen 1997, Swengel and Swengel 2007). The removal of trees, litter, and fine woody debris, as well as fire effects on soil properties, are expected to open the habitat for a succession of early colonizers, generally herbivores and mobile predators (Sugg and Edwards 1998). Higher amounts of herbaceous vegetation are expected to attract and support higher densities of herbivores and omnivores (Malmström et al. 2009).

Study objectives

This study compared the community structure of ground-dwelling arthropods in early-suc-

cessional recently burned habitats and late-successional old-growth areas of Mesa Verde. We examined old-growth stands on two different mesas to investigate possible differences between treatment (fire) and control (unburned areas).

We predicted that (1) early successional burned areas would have increased herbaceous cover and late successional old-growth habitat would have a greater amount of tree cover, shrubs, litter, and woody debris. (2) Arthropod community composition and structure would reflect these habitat differences between early and late successional habitats. (3) Arthropod abundance and species richness would be greater in burned areas compared to old-growth areas due to greater concentration of resources at ground level. (4) Each habitat type would have its own separate set of indicator species associated with successional stage and they would be correlated with habitat-specific variables. We expected that arthropod abundance and species richness would be greater in burned areas due to increased herbaceous plant resources to support herbivorous and omnivorous insects, which in turn would also promote greater numbers of predator and parasite species. Based on previous studies, we expected that basic habitat variables would be highly correlated with distinct arthropod communities and predict an abundance of habitat indicator species.

METHODS

Study area plot distribution

This study was conducted in the southern portion of Mesa Verde National Park on Park and Chapin Mesas (Fig. 1). Mesa Verde National Park is located in Montezuma County, Colorado. Selected old-growth study sites were based on the location of established NPS monitoring sites and locations that had comparable burn sites nearby. The NPS plots in the unburned old-growth pinyon-juniper woodlands were selected using a Generalized Random-Tessellation Stratified design (Stevens and Olsen 2004). We excluded sites for the following reasons: (1) a slope greater than 30 degrees; (2) within 100 m of a road; (3) located on or near a historic trail, archeological site, or cut fuel break; (4) within 100 m from the edge of another site; and (5) having a record of being burned after 1934.

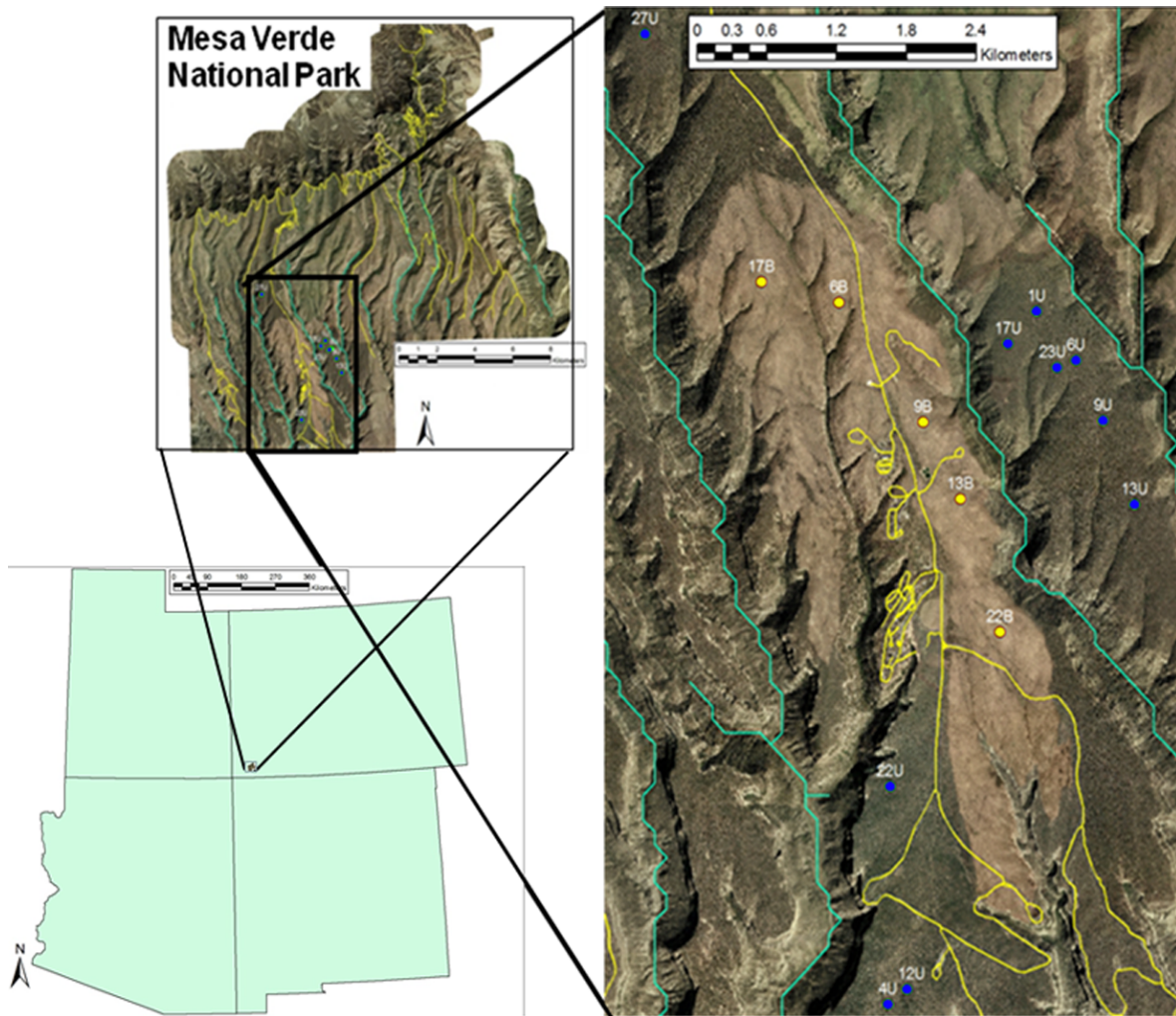


Fig. 1. Study locations within Mesa Verde National Park, Colorado. Blue circles represent old-growth plots and yellow circles represent burned plots.

Exclusion rules for burned sites were identical except for burn record data. Four old-growth and five burned sampling plots were established on Chapin Mesa, and six old-growth plots were established on Park Mesa. The old-growth sites on Chapin and Park Mesas were estimated to have been burned approximately 300 and 400 years ago, respectively (Floyd et al. 2004). The younger stands present chiefly in the southern reach of Chapin Mesa. Two of our sites were placed in this younger area.

To the degree possible, the burn-site plots were selected to be paired with the old-growth study sites established by the National Park Service. The Long Mesa Fire burned in 2002 and occurred

primarily on Chapin Mesa, while Park Mesa did not have any readily accessible locations that burned in 2002. The total area of our sampling sites was roughly 3,600 m² per site (54,000 m² total for all sites). Due to National Park Service funding directed at old-growth stands, we were able to establish five additional old-growth sites.

Weather

We collected climate data from the Western Regional Climate Center for Mesa Verde National Park (Station 055531), which is adjacent to the sites we studied, only 340 meters from the nearest trapping location. Mesa Verde National Park typically experiences two precipitation

peaks, a monsoon period from July through September and significant winter (November–April) moisture in the form of snow. Mean annual temperatures during our study (10°C, 2007; 9°C, 2008) were comparable to the mean annual temperature (9°C) taken from 1923–2008. Precipitation during the time period of the study was lower in 2007 (35.8 cm) and higher in 2008 (45.2 cm) than the long-term mean (40.3 cm) measured during winter and monsoon months.

Plot design and pitfall installation

In each of the 15 sites selected for this study we established a 2,500 m² grid of 25 potential pitfall trap locations. Of the 25 possible trap locations, only 20 locations contained traps. This allowed for flexibility in the event that a location contained a rock or other obstacle that would prevent placing a trap. This resulted in pitfall traps typically being located 10 m from adjacent traps within a five-by-five grid (Fig. 2).

Pitfall traps are one of the oldest and most widely used ground-dwelling arthropod collection methods. This sampling technique has been shown to obtain satisfactory abundance estimates for all ground-dwelling arthropods except

ants (Thomas and Sleeper 1977). We used 32 × 200 mm lipped borosilicate test tubes. This size is small enough to remain relatively unobtrusive in the ground, yet large enough to catch even the largest arthropod known to be found in these habitats. To protect the glass tubes we inserted them into 34 × 210 mm SDR 35 PVC pipe. PVC covers aided in reducing evaporation and harmful ingestion of killing agent by non-target animals. They also offered protection from rain, dilution, and any other weather effects, and lessened the effects of disturbance and potential debris from passing animals. Propylene glycol was used as the killing agent and preservative.

Sampling regime

The arthropods for this project were collected on a three-week rotation beginning in July 2007 and ending in July 2008 with a break in collecting between September 2007 and May 2008. This resulted in five sample collection events across the two years. This allowed us to account for some phenological changes in community structure throughout the summer season. Because traps were widely dispersed, 10 m apart, we did not expect to significantly impact the population of any species we monitored. After the traps were collected, all specimens were removed from the propylene glycol and stored in 70% ethanol.

Habitat characterization

To test our first hypothesis concerning habitat differentiation accounting for arthropod community structure we measured 47 habitat variables among 4 categories (ground cover, soil coarseness, woody debris, and canopy classes) for each of the 15 sites. We selected 5 out of the 20 pitfall trap subplots within each site to measure habitat variables. Habitat variables were grouped into four categories that also represented four methods of assessment; stand structure, ground cover, dead and down woody debris, and soil particle size composition.

To evaluate stand structure, we measured all the pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) trees within a 100-m² subplot surrounding a pitfall trap. To measure our 100-m² subplots, we used four ropes, each 5 m long, and a compass, stretching each rope away from the trap in each cardinal direction and flagging the corners of the plot. Each tree within

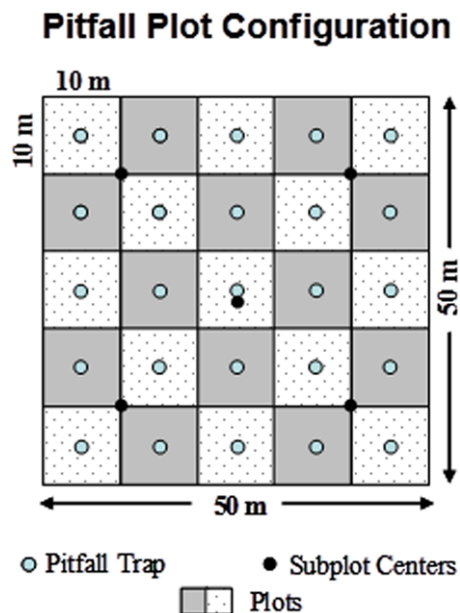


Fig. 2. Diagram showing the pitfall plot configuration. Soil samples were taken from subplot centers. The squares surrounding the pitfall traps represent the area in which habitat variables were measured.

each subplot was measured for basal trunk diameter (BTD), height (both height from ground to crown and total canopy height), and estimated canopy area.

Ground cover was differentiated into eight categories; rock, bare ground, litter, grasses, herbaceous vegetation, shrubs, cryptobiotic crusts and mosses, and woody debris. We sight-estimated the percentage of each cover category in each quadrant of a 10-m² area around its respective pitfall trap with the same premeasured ropes used to evaluate stand structure.

This study used the plane-intercept method (Kershaw 1973, Brown 1974, Grieg-Smith 1983) to make an estimate of fallen woody debris in each plot. This estimate allowed for the examination of habitat complexity. Within each 100-m² plot, a 10-m line was placed in a north to south direction. Each dead twig, branch, or log that touched the line or crossed it was measured for total length and mid-length diameter. Mid-length diameter was assumed to be equivalent to the average of the smallest and largest diameters (end points) of the wood in question. A modified Brown (1974) fuel load classification by diameter (cm) of woody debris was used to estimate downed woody debris. The following diameter classes were used for quantifying dead and down woody material: <0.64 cm, 0.64–2.54 cm, 2.54–7.62 cm, and >7.62 cm.

Each trapping plot was assessed at four areas between pitfall traps for soil particle composition (Fig. 2). At each sampling area, roughly 200 cm³ of soil was removed with a soil auger, ground with a plastic pestle for two minutes to eliminate clumps, sifted in a set of sieves to determine particle categories, and then each particle category was weighed. Categories were based on the sieves, with our set containing six diameter sizes; #5 (1.14 cm), #10 (0.80 cm), #35 (0.43 cm), #60 (0.33 cm), #120 (0.23 cm), and #230 (0.17 cm). To accurately test soil samples with differing initial volumes, the results were converted into percentages that made statistical analysis possible.

Arthropod sample processing

All specimens collected during this study were taken to the Colorado Plateau Museum of Arthropod Biodiversity (CPMAB) for processing. Each sample was first rough-sorted to remove any litter or sediment from the sample. All

specimens were transferred into 70% ethanol as soon as possible upon return to the museum to preserve the specimens for identification and curation. Each sample was then final sorted to determine the number of individuals and morphospecies within. Specimens identified as new morphospecies were removed from their respective samples and either pinned (if a large adult insect), pointed (if a small adult insect), or placed in ethanol (if a very small, fragile, or immature insect or non-insect) and added to the reference collection, which was housed in the Colorado Plateau Museum of Arthropod Biodiversity at Northern Arizona University (NAU).

Our focus was on surface-dwelling arthropods with occurrences greater than one (i.e., non-singletons). Each morphospecies identified was considered for its natural role as either a ground-dwelling, surface-dwelling, or non-surface species based on the known ecological role of the species. Surface-dwelling arthropods were defined to be those arthropods that spend a significant portion of their life-cycle on or near the ground and influence the ground-dwelling community directly. Of the more than five hundred total morphospecies identified during the sorting, 270 were determined to belong to the surface-dwelling community (Appendix A). Significant groups of arthropods that are considered to be surface-dwelling include the spiders, grasshoppers, true bugs, parasitic wasps, booklice, moth larvae observed to live on or near the ground, and fungus gnats known to feed on ground-based spores. Excluded species were mostly flying tourists, tree-dwellers, or singletons (single occurrence over the entire study).

Data analysis

Data was analyzed using PASW (Version 18.0 2009, formerly SPSS 2007), PC-Ord (Version 5.1 2006; McCune and Grace 2002, McCune and Mefford 2006), and Primer (Version 6.1.10 2007; Primer-E 2007). These programs allowed us to perform repeated-measures analysis, habitat and arthropod correlations, ordinations, species accumulation curves, and indicator species analysis. We collected over 72,000 individual arthropods categorized into over 500 species and morphospecies. We included all of Coleoptera, Araneae, Orthoptera, and Formicidae as well as species from the orders Hemiptera,

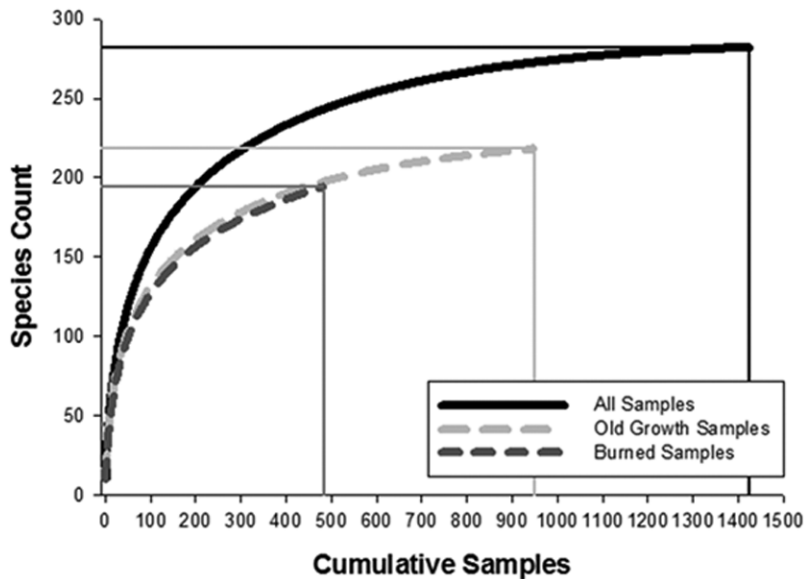


Fig. 3. Species accumulation curve for traps representative of the entire study (black solid line), old-growth habitats (light grey dashed line), and burned habitats (dark grey dashed line). The vertical and horizontal lines present on these graphs represent a secondary observational analysis conducted to determine the efficacy of our sampling regimes within these areas.

Psocoptera, Lepidoptera (larvae only), and Diptera. We eliminated taxa that were not associated with the ground-dwelling community (e.g., some houseflies, non-ground-based wasps, tree-dwellers). Our final taxa list included 61,335 individual arthropods comprising 270 morphospecies.

Species accumulation curves.—Species-accumulation curves may be calculated in both PC-Ord and Primer. This curve allowed us to determine if the number of samples was sufficient to characterize the entire surface community of each of our study areas. Ideally this curve would become horizontally asymptotic before the total number of trapping events is reached. This method allowed us to determine that 20 traps per site were sufficient to characterize the arthropod communities of each habitat. Species accumulation curves for Long Mesa Fire burn sites, old-growth areas, and all samples (Fig. 3) show a very gradual incline of less than 50 new species over 250, 500, and 750 trap efforts, respectively. This indicates that our trapping method was sufficient to characterize the common ground-dwelling arthropod community.

NMS and MRPP.—In order to test our second hypothesis that early successional arthropod

communities would differ from later successional communities we employed non-metric multidimensional scaling (NMS), using Primer 6 to measure community composition and the dissimilarity of those communities. No single-occurrence (singleton) or non-surface-dwelling arthropod taxa were included in this analysis. Ordinations were performed first with a square root transformation of the data and then a resemblance function was run on the data (Primer-E 2007). Our requirement for adequate differentiation was a stress level of no greater than 0.25 and a minimum stress of 0.01, indicating a sufficient degree of separation of points to draw general conclusions about the data. Included in each NMS analysis were the results of a Cluster analysis of the similarity matrix, performed in Primer. This Cluster analysis allowed for circles to be drawn around clusters of NMS points to better illustrate dissimilarity. Following NMS analyses we ran Multiple Response Permutation Procedures (MRPPs) on the same transformed dataset as above, with no adjustments. This was a way to confirm our observed groupings in the NMS analyses and examine the driving factors behind

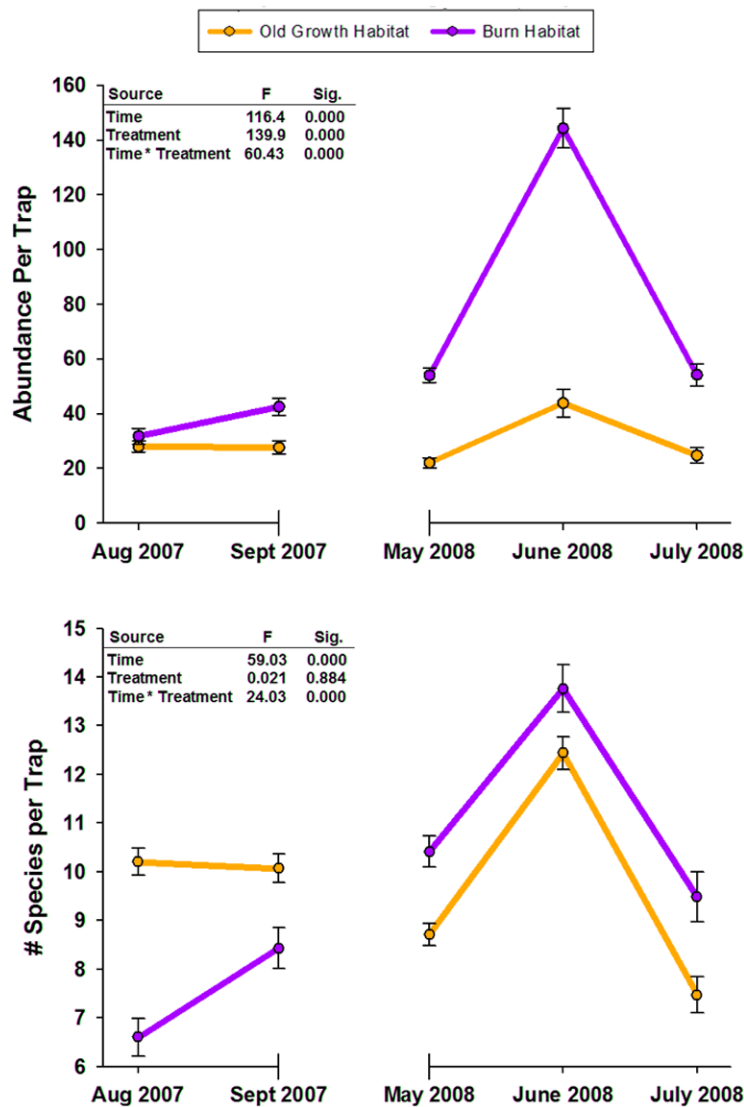


Fig. 4. Mean arthropod abundance and species richness over five collecting dates. These numbers are largely driven by grasshoppers. Bars show standard error of the mean.

the NMS point differentiations. We selected post hoc analyses to distinguish between our factors but otherwise used the default settings for MRPP available in the PC-ORD 5 data analysis package.

ANOVA.—We performed both repeated-measures ANOVA and one-way ANOVAs using PASW (Version 18.0 2009) to test the third hypothesis that abundance and species richness were greater in early successional habitats versus old-growth habitats. The repeated-measures analysis allowed us to consider the differences between arthropod communities based on date

collected, sampling location, and treatment of the site (burned or old-growth). Results were accepted as significantly different at the 0.05 probability level. All graphs derived from these methods show standard-of-the-mean error bars to visually differentiate significance. This model was used on a dataset that considered 20 traps per trapping plot per date (1,500 samples total).

Indicator species analysis.—Our fourth hypothesis predicted a substantial number of species that were indicators of their respective habitats and correlated with habitat characteristics. For this

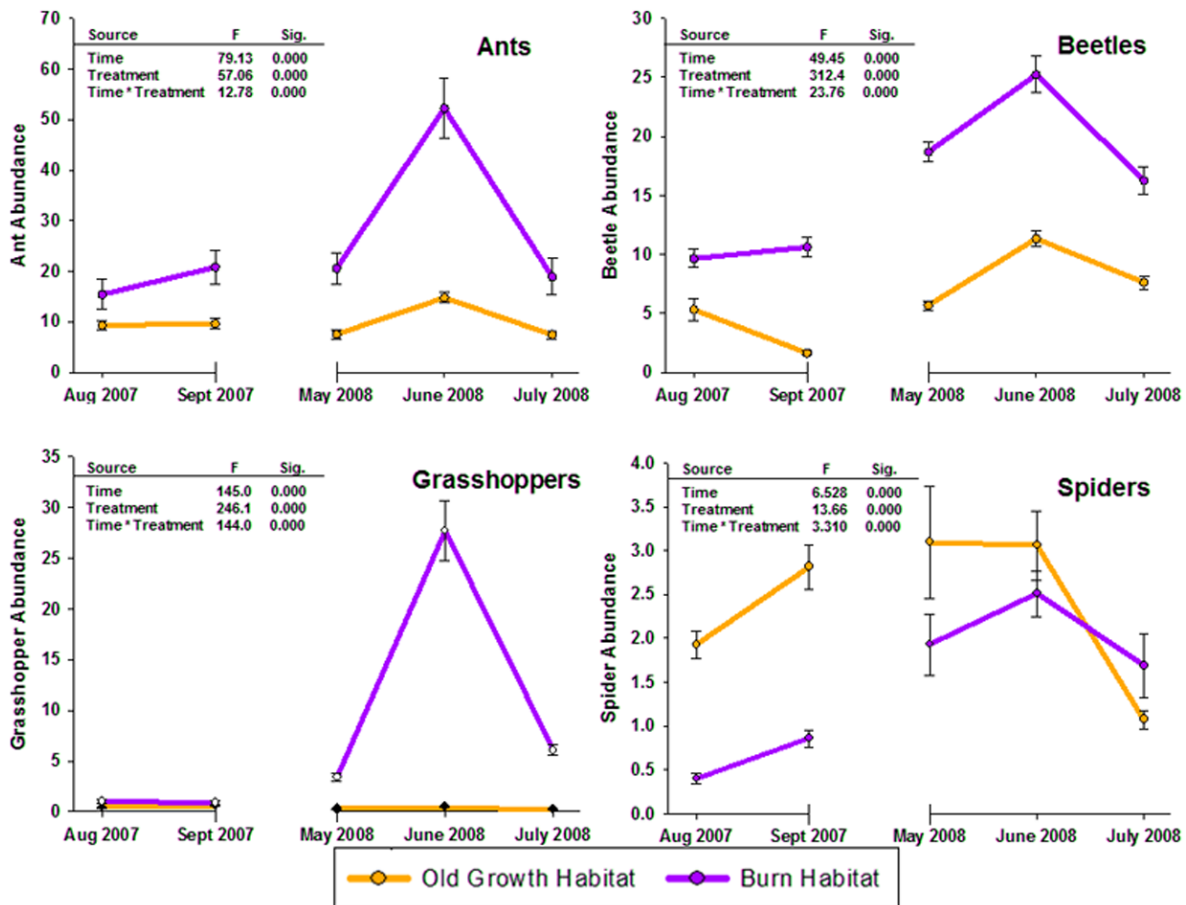


Fig. 5. Mean arthropod abundances of major taxa throughout our study, across the five collection dates. Ants, beetles, grasshoppers, and spiders all showed significant responses to fire. Bars show standard error of the mean.

study, indicator species are defined as those species which are significantly more abundant in one habitat. An indicator species analysis using PC-ORD 5 was performed to determine these species. Our dataset that considered all 1,427 samples that contained arthropods (73 traps contained no arthropods in this study) to determine the ability to predict location based on trap contents. The indicator values for all 270 species considered in this study were used to evaluate the effects of successional end-point habitat on arthropod communities (Appendix B). We used the results from this analysis in part to determine species affiliation for early and late successional habitats. Species were operationally defined as “affiliates” if they either had a significant indicator value (actual indicator species) or they were only found in one habitat (non-

indicators). All other species were considered ‘generalists’ in this context.

Habitat predictors.—We used the top indicator species from the analysis above to determine the degree to which their abundances could be predicted using habitat variables. We first employed stepwise linear regressions in PASW 18.0, accepting significant values at the 0.05 level. We examined the arthropod species with the highest indicator value and abundance from each successional habitat and the 47 habitat characteristics from each characterized trap. We also employed correlation analysis and tallied all significant correlations for each of the 14 indicator species (seven species from each habitat). Based on abundance values obtained from field measurements we classified each habitat variable as being characteristic of burn habitats, old-

Table 1. Tree measurements (mean and SE) for each 100-m² sampling area. The Long Mesa Fire area showed many significant reductions of all evaluated categories. It should be noted that canopy areas may be overestimated, as we did not correct for intersecting tree crowns. Significance values were generated using a one-way ANOVA in PASW 18.0 with significance being accepted at $P < 0.05$. Significant groups are denoted with superscript letters.

Tree measurement	Chapin Mesa old growth		Park Mesa old growth		Chapin Mesa burn		P
	Mean	SE	Mean	SE	Mean	SE	
Percent canopy cover							
Live pinyon	12.31 ^A	1.99	17.18 ^A	3.08	0.00 ^B	0.00	0.000
Live juniper	20.71 ^A	1.99	18.21 ^A	2.01	0.00 ^B	0.00	0.000
Bole volume (m ³ /ha)							
Live pinyon	3.584 ^A	1.489	1.206 ^A	0.297	0.000 ^B	0.000	0.016
Live juniper	10.460 ^A	1.567	11.171 ^A	2.133	0.000 ^B	0.000	0.001
Dead pinyon	0.999	0.487	1.193	0.245	1.051	0.362	0.918
Dead juniper	2.361 ^B	0.909	0.905 ^C	0.202	6.933 ^A	2.098	0.014
Basal area (m ² /ha)							
Live pinyon	1.732 ^A	0.277	3.483 ^A	0.825	0.000 ^B	0.000	0.000
Live juniper	10.187 ^A	1.327	12.256 ^A	1.694	0.000 ^B	0.000	0.000
Dead pinyon	1.377	0.295	1.290	0.578	0.518	0.128	0.152
Dead juniper	1.239 ^A	0.395	3.931 ^B	1.046	3.275 ^B	0.526	0.008

growth habitats, or in some cases neutral variables. For each set of seven species we counted the number of positive and negative correlations and whether they were associated with natal habitat variables (those variables from the habitat for which they are indicators).

Correlations.—We ran correlations in PASW on 23 habitat variables, 7 indicative of burn habitat and 16 indicative of old-growth habitat, to observe individual species habitat preference (Appendix C). Of these, there was no presence of Volume Class 1 fuels or Dead pinyon (PIED) Canopy in the burned habitat areas and almost no presence of any other canopy values in burned habitat. All other habitat values showed enough gradation among sampled sites to confidently observe habitat preference. Of the 14 indicator species, four were found only in their indicative habitats.

RESULTS

Abundance and species richness

In this study we collected 28,977 and 32,358 (total of 61,335) individual arthropods, comprising 270 morphospecies, in old-growth and burned habitats respectively. Of the 270 morphospecies, 83 were specific to old growth, 62 to burned, and 125 were common to both habitats. Because of the difference in the number of trapping sites, we also compared the average numbers of species found (58 old-growth, 41

burned) and average abundance (579.5 old-growth, 1294.3 burned) per site over the course of our study.

We did find that total abundance and species richness was greater early successional habitats. Although we were primarily interested in assessing overall differences between old-growth and burn habitats, we included a repeated-measures ANOVA to incorporate a time component (our five sampling periods) to understand how differences among habitats may change over time. Results indicated that arthropod abundance was generally, and at one sampling period nearly three times, higher in burn habitats compared to old-growth areas (Fig. 4). The large difference in abundance observed in the June 2008 sampling was primarily due to the increased presence of grasshoppers (primarily *Melanoplus sanguinipes*). Overall, species richness was not significantly different between habitats (mean species richness 10.03 and 10.3, $P = 0.38$), although species richness was higher in old-growth in August–September of 2007, while species richness was greater in burned habitats in spring, 2008 (Fig. 4).

We further examined differences in the four most abundant taxonomic groups, ants (Formicidae), beetles (Coleoptera), grasshoppers (Acrididae), and spiders (Araneae) (Fig. 5). For each of our major taxonomic groups we found similar abundance patterns to those of the overall arthropod community, with ants (Fig. 5), beetles

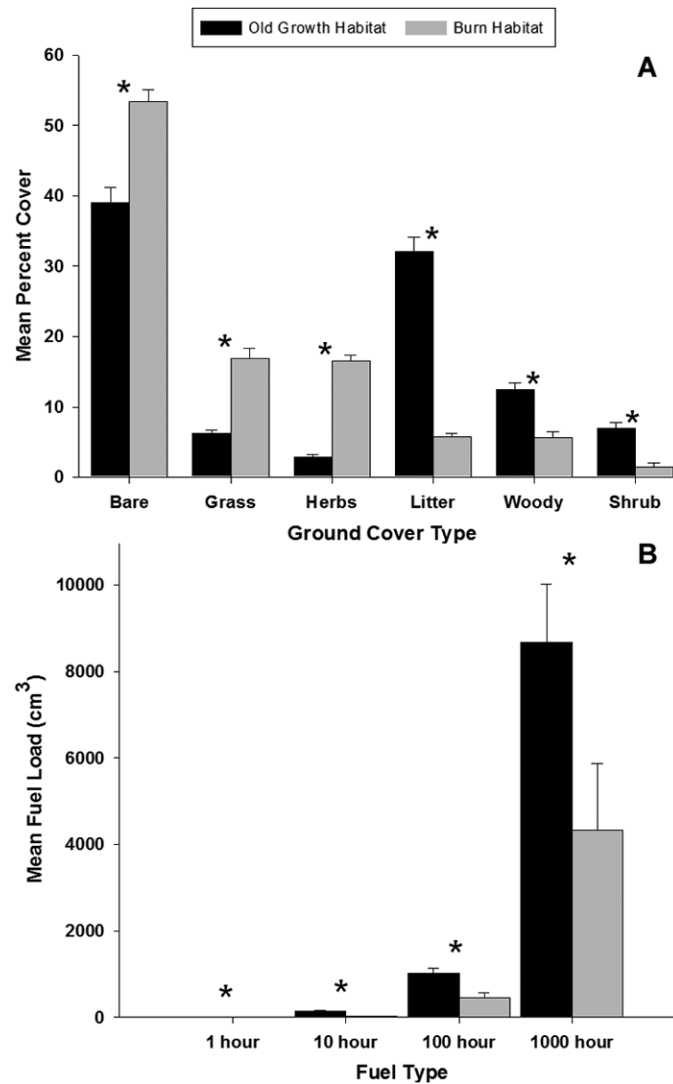


Fig. 6. Comparison of burn (black bars) and old-growth (grey bars) habitats with regard to (A) ground cover composition by percent and (B) dead and down woody debris by volume. Bars show standard error of the mean.

(Fig. 5), and grasshoppers (Fig. 5) showing positive trends in abundance in the early succession burned habitat and spiders (Fig. 5) showing a positive trend in abundance in the old-growth habitat.

Habitat characterization

Forest stand structure was very different between burned and old-growth habitats (Table 1). No trees in the burned area survived the Long Mesa Fire and no standing dead boles in that area retained any foliage ($P < 0.001$) resulting in zero canopy cover for burned areas. Additional-

ly, no saplings were present within characterized burned habitat plots. The average basal trunk diameter (BTD) of standing dead boles was significantly larger in old-growth areas ($P = 0.017$).

Ground cover was significantly different in the categories of grass, litter, dicot plants, and woody debris. In areas of the Long Mesa Fire, shrubs ($P = 0.032$), woody debris ($P = 0.001$), and litter ($P < 0.001$) were reduced while grass ($P = 0.003$), herbaceous plants ($P < 0.001$), and bare ground ($P = 0.046$) were increased. Rocky areas were not significantly impacted, though fire areas typical-

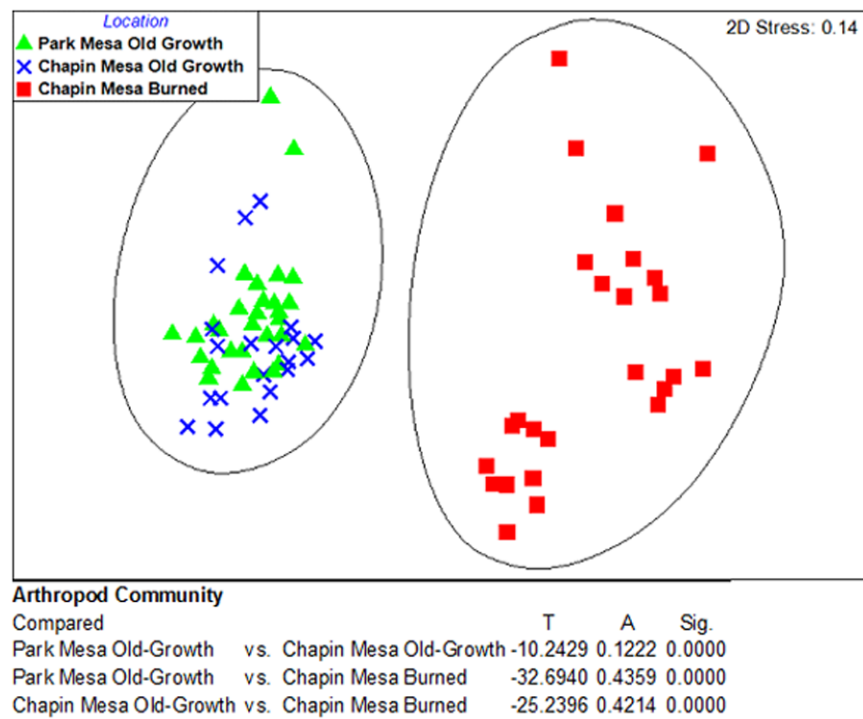


Fig. 7. Non-metric multidimensional scaling (NMS) showing differences in arthropod community among habitats for all collecting dates on two mesas. This ordination shows much more similarity between old-growth communities located on different mesas than between burned and old-growth communities even if they were present on the same mesa. Circles are drawn in Primer 6 based on a similarity score of 35.

ly had greater amounts of rock (Fig. 6A).

Woody debris was, overall, reduced in burned habitat areas (Fig. 6B), specifically, the 0.64–2.54 cm and 2.54–7.62 cm size categories were significantly reduced in burned plots ($P = 0.001$ and $P = 0.010$, respectively) while the <0.64 cm and >7.62 cm size categories, while reduced, were not significantly impacted ($P = 0.057$ and $P = 0.094$).

Soil composition in the burned habitat areas showed a significant trend toward coarser material. Overall, very few of the soil samples had any particles larger than 0.8 cm. Particle sizes found to be significant were $0.8 \text{ cm} > x < 0.4 \text{ cm}$ ($P < 0.001$: burn), $0.32 \text{ cm} > x < 0.23 \text{ cm}$ ($P = 0.002$: old-growth), and $0.23 \text{ cm} > x < 0.17 \text{ cm}$ ($P = 0.005$: old-growth). All of the above P -values were calculated by one-way ANOVA tests.

Composition of arthropod communities and habitat

Our NMS ordination, and subsequent MRPP analysis, showed that arthropod communities

were very different between burn and old-growth plots, indicating location was not as important as treatment (Fig. 7). Though the old-growth arthropod communities tested as significantly different between Park Mesa and Chapin Mesa, the low A statistic for this comparison suggested that, while different, old-growth habitat samples were still much more similar to each other than those in burned habitats. Although we found shifts in communities across sampling periods, communities from old-growth and burned were consistently different (sampling dates not differentiated in Fig. 7). The second pattern that emerged was that there was more arthropod community variation, mostly due to temporal shifts, in burned habitat than in old growth. This is expressed by the wider spread of burned NMS points, hence greater in-group dissimilarity, shown in the figure as well as the larger heterogeneity (A) statistic in the MRPP.

A second NMS ordination was conducted on key habitat variables considered to be important

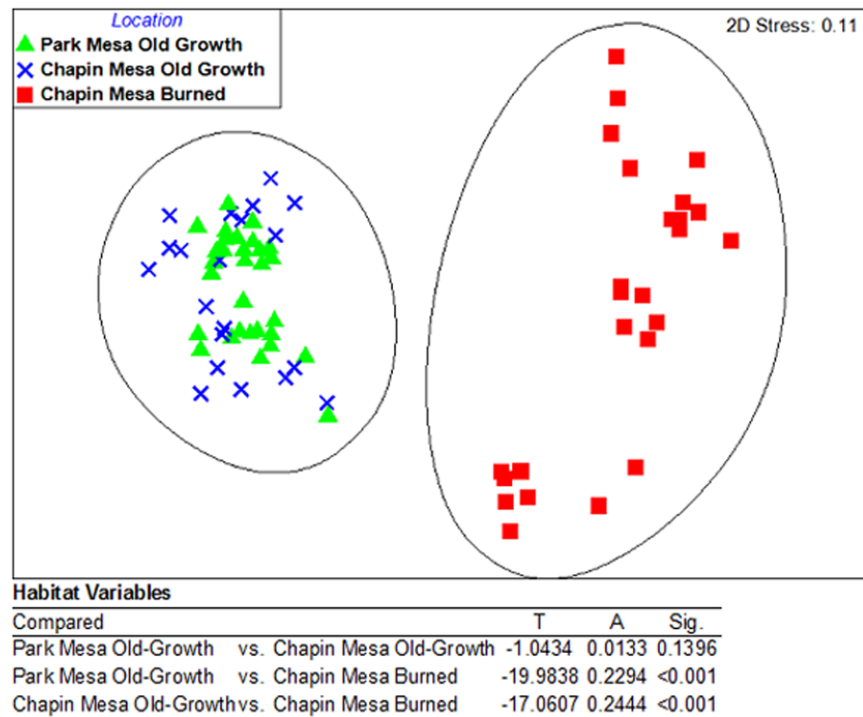


Fig. 8. Non-metric multidimensional scaling (NMS) showing differences in habitat variables for five subplots sampled at each of the 15 study sites. This ordination shows much more similarity between old-growth communities located on different mesas than between burned and old-growth communities even if they were present on the same mesa. Circles are drawn in Primer 6 based on a similarity score of 35.

to ground-dwelling arthropods. These habitat variables were stand structure; ground cover, including dead and down woody debris; and soil particle size composition. There was almost complete overlap of old-growth plots, regardless of which mesa they occurred on, and no overlap between old-growth habitats and burned habitats (Fig. 8). Also, there was much greater within-group variation among burn habitats than in old-growth habitats. The MRPP analysis of these habitats also found that old-growth habitats were not significantly different from each other, with the very low A statistic for the old-growth comparisons suggesting a very similar suite of habitat variables in these plots. Based on this strong congruence of arthropod communities with habitat variables, most of our ensuing analyses do not separate the old-growth plots from Chapin Mesa and Park Mesa.

Indicator species

There were 63 significant indicator species for old-growth and 77 significant indicator species

for burned areas based on our PC-ORD Indicator Species Analysis. These comprise 30% and 40% of the arthropod species sampled in old-growth and burned habitats respectively (Appendix B). Of these indicators, 30 species were found exclusively in old-growth and 41 species were found only in burned habitats. The remaining 69 indicator species were found in both habitats, but the abundances between those habitats strongly favored one habitat over the other.

To characterize the importance of habitat on the overall arthropod community, we compared the number of affiliate and generalist species. The result of this simple comparison (Fig. 9) suggests that both early and late successional habitats tended to be dominated by affiliate species with generalist species making up a small portion of the total diversity of each area.

Can habitat predict species distribution and abundance?

Stepwise linear regression and correlations with habitat variables were used to identify

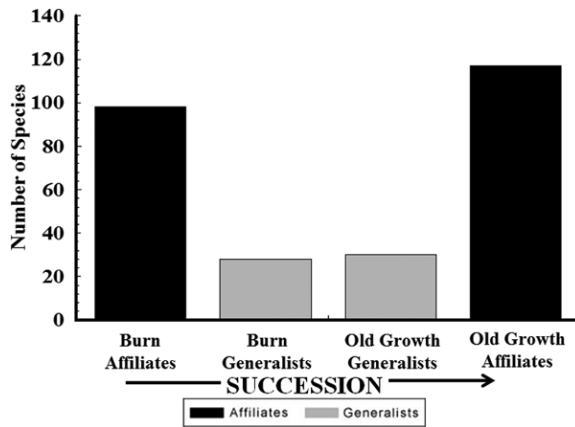


Fig. 9: Composition of species and the habitat preference of species between successional endpoints. For both habitats, species that were found to be habitat-specific dominated the arthropod community.

specific factors that influenced the abundances of the 7 most significant indicator species found to be most abundant in each habitat (14 total species). These 14 most significant indicator species for each habitat type are listed in Table 2 along with their indicator values. A multiple regression analysis using all the habitat variables showed that many of these variables were strongly correlated with those species' presence and explained between 42% and 82% of the variation in the abundance of these indicator species using all sites (Table 3). The number of

significantly correlated habitat variables showed that the natal indicator species responded positively to habitat variables found to be more prevalent in their natal habitat and negatively to habitat variables found to be prevalent in non-natal habitat (Fig. 10 and Appendix C). Old-growth species showed stronger positive correlations with “natal” habitat variables and burn indicator species had more negative significant correlations with non-natal variables. All significant correlations were in the direction we predicted for both burn and old-growth indicator taxa (e.g., burned variables were positive for burned habitat indicators and negative for old-growth indicators).

DISCUSSION

The major findings from this study were: (1) arthropod abundance and species richness were greater in early successional burn habitats, (2) we found predictable differences in habitat characteristics between recently burned and old-growth woodland habitats (burned habitats showed on average 15% more bare ground cover, 10% more grass, 6% less woody debris, and 30% less litter than old-growth habitats), (3) arthropod community structure reflected similar differences between the two habitats, (4) indicator species constituted 30% and 40% of species found in old-growth and burned habitats respectively, and (5) there were strong correlations between habitat

Table 2. Strong indicator species between burned and old-growth sites. Results of Monte Carlo tests are given as P-values. Below are the top seven indicators for both the Long Mesa Fire burned habitat and old-growth habitat. Also listed are the indicator values (IV), mean occurrence per trap per sample period, a presence/absence chart (presence in habitat indicated by X), and the indicator p-value from PC-ORD.

Indicator	Family	Major group	IV	Mean	Old growth	Burn	P
Old-growth							
<i>Camponotus vicinus</i>	Formicidae	ant	52.1	21.2	X	X	0.0002
<i>Machilinus aurantiacus</i>	Meinertellidae	bristletail	39.2	15.8	X	X	0.0002
Eryt 0002	Erythraeidae	mite	37.8	22.1	X	X	0.0002
Phor 0001	Phoridae	scuttle fly	23.4	8.7	X		0.0002
<i>Myrmica</i> sp.	Formicidae	ant	21.6	8.3	X	X	0.0002
Ceci 0001	Cecidomyiidae	fungus gnat	21.4	8.1	X		0.0002
Scia 0001	Sciaridae	fungus gnat	19.8	7.5	X		0.0002
Burned area							
<i>Eleodes extricatus</i>	Tenebrionidae	ground beetle	62.4	40.1	X	X	0.0002
<i>Melanoplus sanguinipes</i>	Acrididae	grasshopper	58.6	11		X	0.0002
<i>Monomorium cyaneum</i>	Formicidae	ant	55	29.6	X	X	0.0002
<i>Pheidole hyatti</i>	Formicidae	ant	50.4	15.5	X	X	0.0002
<i>Ischyropalpus</i> sp.	Anthicidae	beetle	34.1	6.9	X	X	0.0002
<i>Calathus</i> sp.	Carabidae	ground beetle	27.6	5.5	X	X	0.0002
<i>Emblethis</i> sp.	Rhyparochromidae	seed bug	19.9	4.2	X	X	0.0002

Table 3. Summary of multiple regression output analysis for the top seven indicator species for both old-growth and burn habitats. Predictor variables included all habitat variables.

Indicator species	R ²	SS	df	MS	F	P
Old-growth habitat						
<i>Camponotus vicinus</i>	0.720	1324.18	35	37.83	2.71	0.002
<i>Machilinus aurantiacus</i>	0.614	1910.90	30	63.70	2.23	0.008
Eryt 0002	0.627	4851.11	31	156.49	2.23	0.008
Phor 0001	0.772	258.04	35	7.37	3.59	<0.001
<i>Myrmica</i> sp.	0.589	146.51	28	5.23	2.25	0.008
Ceci 0001	0.661	213.15	33	6.46	2.30	0.007
Scia 0001	0.477	272.44	20	13.62	2.37	0.007
Burn habitat						
<i>Eleodes extricatus</i>	0.801	28870.97	35	824.88	4.25	<0.001
<i>Melanoplus sanguinipes</i>	0.768	45300.23	35	1294.29	3.51	<0.001
<i>Monomorium cyaneum</i>	0.820	191379.35	35	5467.98	4.81	<0.001
<i>Pheidole hyatti</i>	0.696	160706.05	35	4591.60	2.417	0.005
<i>Ischyropalpus</i> sp.	0.676	1609.36	34	47.33	2.33	0.006
<i>Calathus</i> sp.	0.721	471.53	35	13.47	2.73	0.002
<i>Emblethis</i> sp.	0.721	53.50	35	1.53	2.73	0.002

variables and indicator species for those habitats suggesting arthropod communities are structured and highly responsive to between-habitat differences (Appendix C).

Arthropod community composition and abundance

As compared with forest ecosystems, there is virtually nothing published on the community ecology of ground-dwelling arthropods in native woodlands (but see Clifford et al. 2008), however, some work has been conducted on ground-dwelling arthropod communities along successional gradients in other habitats. Most of these studies compare communities in disturbed and non-disturbed habitats, which in most cases represent successional endpoints or a gradient of successional snapshots (Seastedt and Crossley 1981, Sugg and Edwards 1998, Buddle 2001, Buddle and Hammond 2003, Moretti et al. 2004, Moretti et al. 2006, Pohl et al. 2007, Buddle and Shorthouse 2008, Gillette et al. 2008, Hirao et al. 2008, Hore and Uniyal 2008, Larrivee et al. 2008). These studies show that arthropods respond to disturbance based on the severity of the damage done to a habitat, disturbed habitats have new indicator species, abundance and species richness may fluctuate and both are generally higher at early stages of succession, and arthropod communities tend to stabilize over time as the habitat regenerates (Pohl et al. 2007). Generally, patterns seen in this study are consistent with those patterns seen in other regions and habitat types.

We found a higher overall and average-per-site abundance of arthropods in the early succession-

al habitat but greater overall and average-per-site species richness between the two successional habitats. Many studies have observed that post-disturbance, early succession habitats contain a greater abundance of herbivore and omnivore species (Malmström et al. 2009). Similar to these studies, our post-fire arthropod community composition contained a greater herbivore and omnivore presence, both in richness and abundance, with significantly greater abundance in early succession burned habitat than late succession old-growth habitat. For example, one of the strongest burn indicator species, *Melanoplus sanguinipes*, a broad generalist grasshopper (Acrididae) is noted to be a strong indicator of disturbed habitats that are rich in forbs (Craig et al. 1999) and is known to maintain populations in cheatgrass dominated areas (Fielding and Brusven 1992).

Another very abundant burn indicator, *Eleodes extricatus*, a darkling beetle (Tenebrionidae), showed significantly higher populations in burned than in old-growth sites. This may be caused by the greater amount of ground-level plant matter available in post-fire habitats as well as increased soil temperature caused by the elimination of canopy. Our data for *E. extricatus* was similar to the pattern found by Chen et al. (2006) for *E. extricatus* in Ponderosa pine forests. We found abundance to be nearly three times higher in the burned areas than in the old-growth habitat with much of this abundance accounted by the presence of *E. extricatus*.

Although seasonal differences were noted,

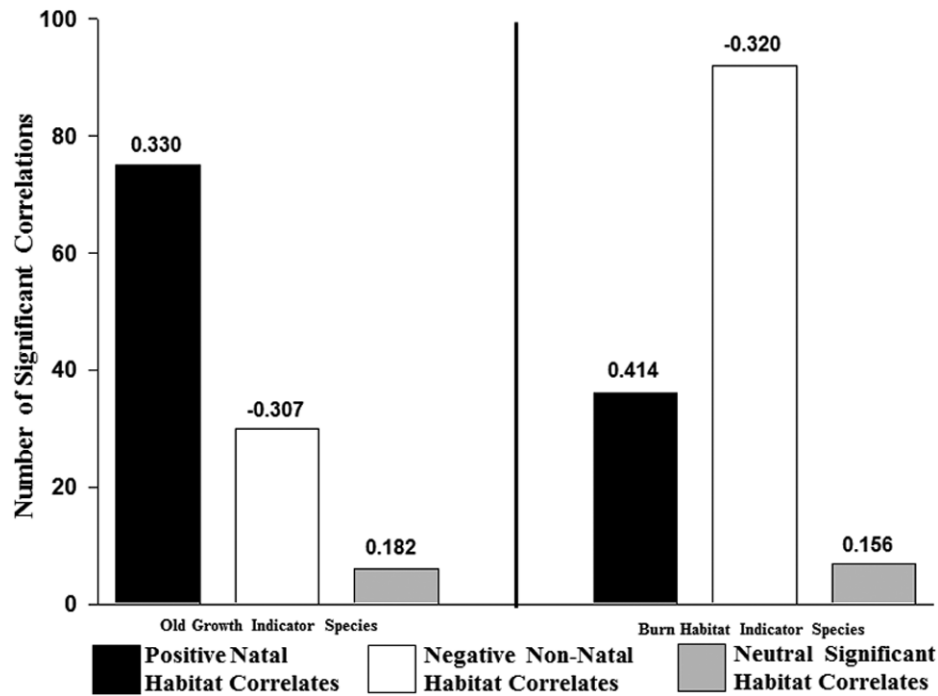


Fig. 10: Habitat correlations with regard to the seven strongest indicator species and the associated average Pearson's correlation value for each category. Each group of indicator species was measured by the number of significant habitat factors in either a positive (black) or negative (white) correlation direction. The habitat factors were divided between "natal", "non-natal", and "neutral" variables. Natal habitat variables were those found to be more prevalent in an indicator species' preferred habitat (i.e., old-growth variables for old-growth indicator species), non-natal variables were those found to be less prevalent in an indicator species' preferred habitat, and neutral variables are those either largely unchanged by fire disturbance or which are too few to be statistically distinguished but still measured as significant for at least one indicator species. The numbers at the top of each bar represent the mean correlation score for the significant habitat correlates.

overall, we found that old-growth supported 208 species and 187 in burned habitat, an average of 58 species per site in old-growth and 41 in burned habitat). We believe this to be due to the increased habitat heterogeneity present in old-growth being more important to the ground-dwelling community than the increased herbaceous cover (Franklin and Van Pelt 2004).

Indicator species and habitat correlates

Our indicator species analysis showed that the species with the highest indicator values were very different between sites with 63 (30%) of the 270 species found primarily in old-growth habitat and 77 (40%) of the 270 species found primarily in burned areas. This does support our hypothesis that the two habitats have different arthropod communities. Additionally, the num-

bers of affiliate species (described in *Data analysis*) trapped only in one of the two habitats outnumbered generalist species common to both habitats.

Spiders tend to respond negatively to fire as a disturbance (Gillette et al. 2008, Hore and Uniyal 2008, Larrivee et al. 2008). Our study, which included 32 spider species, also found significantly lower abundance and richness of spiders in the early succession burned habitat. Of those, only four were found to be significantly positively correlated with burned habitats and 16 showed a significant negative correlation. Thus, our results are consistent with the literature that have found reduced spider diversity and abundance in a post-fire habitat is linked to the reduction of preferred shelter areas, such as a reduction in tree bark or downed woody debris,

in disturbed habitats.

The increased grasses and herbaceous vegetation were expected to be strongly correlated to the presence and size of populations of grasshoppers. A literature review found no other studies comparing woodland and grassland habitat responses of acridid species, but rather studies that only addressed disturbances in grassland areas where these species were already established. We have found that the dominant species of grasshoppers exhibit similar feeding preferences to those found in Fielding and Brusven's (1992) study of cheatgrass as a food source. Indeed, *Melanoplus sanguinipes* was an indicator of the cheatgrass dominated areas over the same time periods in both studies and *Aulocara elliotti*, while not found to be an indicator in our study, was present in the earliest seasonal time-period we surveyed and was an early season indicator in their study. Only two Orthoptera were found to be indicators of old-growth habitats; both were camel crickets (Raphidophoridae) and known to be omnivores. These Orthoptera require continuous moist, dark conditions which are typically exhibited in the downed woody debris of the old-growth habitat.

MontBlanc et al. (2007) found that ants were more likely to occur in burned areas due to removal of leaf litter, changes in food availability, and increased soil insolation. Of the 22 ant species collected, eight species showed a significant positive response to burned areas and six species showed a significant positive response to old-growth. Overall, we found a significant increase in species abundances of ants in burned areas. Species that typically depend on wood for shelter or that feed on honeydew, were significantly reduced in burned habitat (e.g., *Camponotus*, *Formica*, and *Crematogaster*). Those species that responded more positively to fire tended to be ground-dwelling opportunists and seed feeders (*Pogonomyrmex*, *Lasius*, *Hypoponera*, *Solenopsis*, and *Pheidole*) and species that may cohabitate with others (*Monomorium*).

The beetle community exhibited a significant increase in species richness in response to burned habitat. Of the 105 beetle taxa identified, only 10 species were found to be indicators of old-growth habitat and 39 were found to be indicators of burned areas. Tenebrionidae were the most abundant beetles, especially *Eleodes extricatus*, a

burned habitat indicator which was the most common species in the entire study and present in both habitats. The abundance of *E. extricatus* was a driving factor in determining the greater tenebrionid response as the two other tenebrionid species that were indicators were both indicators for old-growth habitat. Parmenter et al. (1989) found that in *Eleodes* species in sagebrush-steppe habitats, different microhabitat characteristics had an effect on which species was captured with differences in temperature and litter depth reduction accounting for greater presence of *E. extricatus*. Chen et al. (2006) also observed a positive response of tenebrionids, especially *Eleodes* species, to increases in bare-ground, which they correlated with increased soil temperature and increased density of understory vegetation.

Carabidae also showed increased abundance in burned habitats, but not to the same degree shown by tenebrionids. Of the 11 species examined in this study, six are indicator species for burned habitat and two are indicator species for old-growth habitat. Niwa and Peck (2002) and Holliday (1992) found that, in a post-fire habitat, carabid abundances tended to be greatly reduced, due to a change in the dominant understory vegetation. However, Beaudry et al. (1997) observed a greater carabid presence in burned and clear-cut areas of Jack-Pine and found that the increase was due to old-growth adapted species being replaced by more generalist species. In summary, our results indicate a high degree of habitat affiliation by arthropods and concomitant strong correlations between putative successional specialists and habitat variables (e.g., woody debris).

The role of fire as a disturbance

We reviewed the literature documenting arthropod responses to all types of stand-replacing disturbances, including fire, clear-cutting, hurricane blow-down, and drought impact on stand mortality. The study by Malmström et al. (2009) examined the effects of both clear-cutting and fire on experimental plots in boreal forest habitat. Similar to our study, they examined the effects of these disturbances on arthropod feeding guilds, with each guild showing significant differences between successional endpoints. Their findings on fire effects show a negative correlation

between fire effects and the predator and fungivore (listed in this study as detritivores) communities. Our study did find a negative correlation of burn habitats and predator species richness, primarily driven by spiders (Fig. 9), but also recognized a positive correlation between burn habitat and detritivore abundance, in contrast to the Malmström et al. (2009) study. One of the strong indicator species for burned habitat, a collembolan, is in direct contrast with the collembolan response noted by Malmström et al. (2009), suggesting ecologically significant differences between burned habitat dynamics in pinyon-juniper woodland compared to boreal forest.

Sugg and Edwards (1998) studied the effects on, and recovery of, arthropod fauna following the stand-replacing eruption of Mount St. Helens in 1980. They found many primary re-colonizers of the disturbed area were carabids (predatory ground beetles), tenebrionids (omnivorous darkling beetles), and geocorids (predatory Hemiptera); groups that were also found in burned habitats in Mesa Verde. Our study also found *Cicindela* beetles and *Geocoris* hemipterans in burned habitats.

Hurricane blow-down effects on forest arthropods were examined by Hirao et al. (2008). It was found that the herbivore community tended to react positively to disturbance, likely due to increased understory vegetation and negative predator response to disturbance. This is similar to the findings at Mesa Verde in that burned habitat had higher abundance of herbivores and omnivores as well as lower abundance of predators. Stepwise linear regression showed that reduction in canopy cover and increase in herbaceous vegetation were most strongly correlated with these results in their study.

Another paper (R. Delph, M. Clifford, N. Cobb, and P. Ford, *unpublished manuscript*) examined drought impacts on pinyon-juniper woodland arthropod communities. Their results showed many arthropod response patterns similar to the fire responses found in this study, including arachnids as indicators of undisturbed (analogous to old-growth) habitat, changes in dominant ant populations as indicators of habitat change, and an increase of herbivores in drought-disturbed areas correlated with an increase in herbaceous vegetation.

Implications under a global change scenario

Pinyon-juniper woodlands tend to show a much longer cycle of stand regeneration compared to most forest vegetation types, with a typical regeneration cycle occurring over 200 years or more, with old-growth condition being typically reached after 300 years (Floyd et al. 2004). Due to the long-term nature of pinyon-juniper regeneration and the semi-arid climates they occupy, regenerating pinyon-juniper woodlands may require centuries to reach a state of ecological equilibrium. Because of this long term regeneration, and the hypothesized future increase in disturbance due to climate change (Rehfeldt et al. 2006), pinyon-juniper woodlands may be less likely to reach these late successional states before experiencing another disturbance. Trends of increasing aridity and warmth in the region have produced conditions that favor a wildfire disturbed regime over recent decades. As much as 18% of southwestern US forests and woodlands have experienced fire-related mortality between 1984 and 2006 (Williams 2010).

There have been no definitive inventory studies quantifying old-growth woodland on the Colorado Plateau, though consensus among ecologists is that old-growth woodlands are uncommon (Floyd et al. 2000, Floyd 2003). With Mesa Verde having experienced fire-induced mortality in as much as 80% of the park area over the last century, there may be a trend for these woodlands becoming more rare (G. San Miguel, *personal communication*). From these observations we believe it is likely that the fire cycle of this region has been greatly sped up.

Drought stress, human use, and climate change may shorten fire return intervals, causing greater habitat loss. Approximately 80% of old-growth woodland habitat within Mesa Verde National Park has been converted from late successional stages into an early to mid-successional state (G. San Miguel, *personal communication*). It should be noted that the old-growth stands investigated in this study differed in age by up to 100 years based on pre-settlement fire evidence, suggesting that large fires in centuries past were less frequent than currently.

Final remarks

Catastrophic fire is the most extensive and intensive natural disturbance within pinyon-

juniper woodlands and typically resets the successional cycle with the removal of trees and shrubs. Fire and other disturbances have greatly reduced old-growth woodlands regionally. We compared community composition in ground-dwelling arthropods in recently burned early-successional habitats and late-successional old-growth woodland. The transition from a tree-dominated habitat to open habitats is reflected in the arthropod communities which were distinctly different in early successional habitats compared to old-growth habitats. Burned habitats were characterized by greater overall arthropod abundance and greater abundances in all major taxa and functional groups except for spiders/predators, which were more abundant in old-growth habitats. Species composition was significantly different between burned and old-growth habitats and, coupled with the finding of little variation in species richness, this suggests both habitats were similarly diverse but comprised distinct assemblages. This was further supported with the finding that 70% of the taxa from both habitats were indicators of their respective habitats. Burned habitats were dominated by grasshoppers, beetles, and ants reflecting the increase in herbaceous ground cover and bare ground, while old-growth arthropod communities were characterized by more mesic species of detritivores/fungivores and spiders. Although pinyon-juniper woodlands are not mesic habitats, relative to open recently burned habitats, they most likely provide micro-habitats that are cooler and retain moisture in duff and woody debris. These differences were maintained despite seasonal shifts in species composition for both habitats. These results support old-growth communities as being distinct from earlier successional habitats and provide further evidence for the need to preserve diminishing old-growth woodlands.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Taxonomic list of surface-dwelling arthropods collected from pitfall traps used in this study. Specimens were identified to the species level when possible and confirmed by S.L. Brantley (arachnids), J. Labonte (Carabidae), C. O'Brien (Curculionidae), and D.C. Lightfoot (Orthoptera). The few specimens that were unidentified to genus level such as immature or damaged specimens were given operational taxonomic unit (O.T.U.) codes, which is a common technique used to separate species by morphological characteristics (Wilkie et al. 2003). A permanent reference collection of specimens from this study is housed at the Colorado Plateau Museum of Arthropod Biodiversity at Northern Arizona University. The means represent the number of individuals collected over a three-week period during all the sampling periods at all study sites within the area.

Taxonomic information		Park Mesa old growth		Chapin Mesa old growth		Chapin Mesa fire 2002		P
Family	Species/O.T.U.	Mean	SE	Mean	SE	Mean	SE	
Vaejovidae	<i>Vaejovis coahuilae</i>	0	0	0.125	0.02	0	0	0
Dictynidae	<i>Dictyna apachea</i>	0.06	0.014	0.068	0.016	0.024	0.01	0.053
Gnaphosidae	<i>Gnaphosa californica</i>	0.163	0.019	0.045	0.012	0.012	0.005	0
Gnaphosidae	<i>Gnaphosa</i> sp. 1	0.053	0.011	0.133	0.022	0.028	0.011	0
Gnaphosidae	<i>Micaria nanella</i>	0.038	0.009	0.033	0.01	0.054	0.013	0.374
Gnaphosidae	<i>Castianeira dorsata</i>	0.147	0.017	0.09	0.017	0.054	0.011	0
Gnaphosidae	<i>Drassodes saccatus</i>	0.052	0.01	0.048	0.012	0.008	0.004	0.001
Gnaphosidae	<i>Drassodes</i> sp. 1	0.208	0.02	0.893	0.103	0.264	0.028	0
Gnaphosidae	<i>Drassodes</i> sp. 2	0	0	0	0	0.004	0.004	0.368
Gnaphosidae	<i>Drassodes</i> sp. 3	0	0	0	0	0.068	0.017	0
Gnaphosidae	<i>Drassyllus lamprus</i>	0	0	0	0	0.038	0.01	0
Gnaphosidae	<i>Gnaphosid</i> sp. 1	0.023	0.009	0.035	0.012	0	0	0.016
Gnaphosidae	<i>Herpyllus</i> sp. 1	0.608	0.222	0.268	0.168	0.072	0.064	0.074
Lycosidae	<i>Paradosa xerophila</i>	0.043	0.01	0.02	0.008	0.002	0.002	0.001
Lycosidae	<i>Schizocosa chiricahua</i>	0.503	0.037	0.345	0.038	0.37	0.045	0.009
Lycosidae	<i>Schizocosa</i> sp. 1	0.017	0.006	0.023	0.01	0	0	0.035
Lycosidae	<i>Lycosidae</i> sp. 1	0.015	0.005	0.023	0.007	0	0	0.01
Pholcidae	<i>Psilochorus imitatus</i>	0.172	0.019	0.153	0.023	0.172	0.02	0.774
Salticidae	<i>Habronattus virgulatus</i>	0.052	0.01	0.19	0.027	0.028	0.008	0
Salticidae	<i>Habronattus</i> sp. 1	0.015	0.005	0.06	0.018	0	0	0
Salticidae	<i>Habronattus</i> sp. 2	0.013	0.005	0.025	0.008	0	0	0.003
Salticidae	<i>Habronattus</i> sp. 3	0.005	0.003	0.01	0.006	0	0	0.155
Theridiidae	<i>Latrodectus hesperus</i>	0.016	0.005	0.009	0.004	0.092	0.015	0
Theridiidae	<i>Steatoda</i> sp. 1	0	0	0	0	0.008	0.005	0.069
Thomisidae	<i>Xysticus locuples</i>	0.063	0.01	0.043	0.012	0.076	0.014	0.173
Thomisidae	<i>Xysticus</i> sp. 1	0.003	0.002	0.005	0.004	0	0	0.324
Thomisidae	<i>Thomisid</i> sp. 1	0.002	0.002	0	0	0.002	0.002	0.687
Philodromidae	<i>Ebo</i> sp. 1	0.003	0.002	0.005	0.004	0.004	0.004	0.939
	Araneae sp. 1	0.003	0.002	0.005	0.004	0.062	0.058	0.37
	Araneae sp. 2	0	0	0	0	0.004	0.004	0.368
	Araneae sp. 3	0.003	0.002	0	0	0	0	0.223
	Araneae sp. 4	0.002	0.002	0.003	0.003	0	0	0.57
	Araneae Immature sp. 5	0	0	0	0	0.032	0.032	0.368
Anystidae	<i>Anystid</i> sp. 1	0.777	0.185	0.335	0.112	2.56	0.831	0.005
Erythraeoidea	<i>Erythraeoid</i> sp. 1	0.04	0.01	0.038	0.018	0.058	0.023	0.654
Erythraeoidea	<i>Erythraeoid</i> sp. 2	2.657	0.252	1.645	0.168	0.628	0.081	0
Trombidiidae	<i>Trombidiid</i> sp. 1	0.182	0.033	0.315	0.063	0.054	0.013	0
Trombidiidae	<i>Trombidiid</i> sp. 2	0.013	0.007	0.163	0.097	0	0	0.03
Trombidiidae	<i>Trombidiid</i> sp. 3	0.01	0.006	0.055	0.025	0	0	0.007
	Oribatida sp. 1	0.013	0.006	0.028	0.01	0	0	0.016
	<i>Opilones</i> sp. 1	0.01	0.004	0	0	0	0	0.011
Ixodidae	<i>Ixodida</i> sp. 1	0.002	0.002	0.005	0.004	0	0	0.242
Chernetidae	<i>Chernetid</i> sp. 1	0.02	0.006	0.015	0.009	0.004	0.003	0.145

Table A1. Continued.

Taxonomic information		Park Mesa old growth		Chapin Mesa old growth		Chapin Mesa fire 2002		P
Family	Species/O.T.U.	Mean	SE	Mean	SE	Mean	SE	
Chernetidae	Chernetid sp. 2	0.017	0.006	0.018	0.009	0	0	0.054
Eremobatidae	<i>Eremobates mormonus</i>	0.02	0.007	0.035	0.011	0.002	0.002	0.006
Polyxenidae	<i>Polyxenus</i> sp. 1	0.022	0.01	0.935	0.139	0.11	0.033	0
Parajulidae	<i>Oriulus</i> sp. 1	0.19	0.029	0.013	0.006	0	0	0
Lithobiidae	Lithobiid sp. 1	0.002	0.002	0	0	0.014	0.005	0.005
Lithobiidae	Lithobiid sp. 2	0.012	0.004	0.003	0.003	0	0	0.02
Lithobiidae	Lithobiid sp. 3	0.008	0.004	0	0	0	0	0.068
Entomobryidae	Entomobryid sp. 1	0.888	0.113	2.528	0.383	8.336	1.164	0
Sminthuridae	Sminthurid sp. 1	0.113	0.017	0.143	0.027	0.026	0.026	0.001
Hypogastruridae	Hypogastrurid sp. 1	0.04	0.009	0.01	0.005	0.002	0.002	0
Meinertellidae	<i>Machilinus aurantiacus</i>	1.9	0.207	1.018	0.253	0.064	0.021	0
	<i>Thysanura</i> sp. 1	0.043	0.009	0.015	0.007	0	0	0
Acrididae	<i>Arphia conspersa</i>	0.073	0.011	0.08	0.016	0.098	0.019	0.482
Acrididae	<i>Aulocara ellioti</i>	0	0	0	0	0.008	0.008	0.368
Acrididae	<i>Trimerotropis cincta</i>	0	0	0	0	0.022	0.013	0.052
Acrididae	<i>Trimerotropis modesta</i>	0	0	0	0	0.008	0.006	0.202
Acrididae	<i>Trimerotropis pallidipennis</i>	0	0	0	0	0.092	0.02	0
Acrididae	<i>Melanoplus bivittatus</i>	0.005	0.003	0	0	0.044	0.011	0
Acrididae	<i>Melanoplus flavoides</i>	0	0	0	0	0.022	0.008	0
Acrididae	<i>Melanoplus sanguinipes</i>	0	0	0	0	7.016	0.736	0
Acrididae	<i>Xanthippus corallipes</i>	0.002	0.002	0.005	0.004	0.028	0.009	0.001
Acrididae	Acridid sp. 1	0.048	0.009	0.028	0.008	0	0	0
Rhaphidophoridae	<i>Ceuthophilus</i> sp. 1	0.02	0.006	0.025	0.008	0.042	0.014	0.214
Rhaphidophoridae	<i>Styracosceles neomexicanus</i>	0.265	0.028	0.125	0.022	0.05	0.014	0
Tettigoniidae	<i>Eremopedes</i> sp. 1	0.003	0.003	0.008	0.004	0.056	0.015	0
Gryllidae	<i>Gryllus</i> sp. 1	0.01	0.004	0.023	0.007	0.3	0.039	0
Gryllidae	<i>Oecanthus</i> sp. 1	0.018	0.007	0.023	0.009	0.024	0.009	0.866
Stenopelmaticidae	<i>Stenopelmatus</i> sp. 1	0.005	0.003	0.003	0.003	0.004	0.003	0.829
Rhinotermitidae	<i>Reticulitermes tibialis</i>	0.012	0.005	0.015	0.007	0.006	0.004	0.521
Polyphagidae	<i>Arenivaga</i> sp. 1	0.005	0.004	0	0	0.012	0.005	0.104
Mantidae	<i>Litaneutria</i> sp. 1	0	0	0.003	0.003	0.002	0.002	0.503
Miridae	<i>Phytocoris</i> sp. 1	0.057	0.015	0.08	0.022	0.048	0.013	0.41
Miridae	<i>Phytocoris</i> sp. 2	0.008	0.004	0.003	0.003	0.002	0.002	0.234
Cydnidae	<i>Dallasiellus discrepans</i>	0.135	0.023	0.378	0.043	0.038	0.009	0
Rhyparochromidae	<i>Eremocoris</i> sp. 1	0.035	0.009	0.02	0.008	0.028	0.012	0.567
Rhyparochromidae	<i>Eremocoris</i> sp. 2	0.003	0.002	0.003	0.003	0.002	0.002	0.91
Nabidae	<i>Pagasa fusca</i>	0	0	0	0	0.044	0.012	0
Pentatomidae	Pentatomid sp. 1	0.007	0.003	0	0	0	0	0.049
Reduviidae	<i>Rhynocoris ventralis</i>	0	0	0.005	0.004	0	0	0.064
Reduviidae	<i>Rhynocoris</i> sp. 1	0	0	0.005	0.004	0	0	0.064
Reduviidae	<i>Apiomerus</i> sp. 1	0.008	0.004	0.015	0.006	0.002	0.002	0.093
Lygaeidae	<i>Nysius</i> sp. 1	0	0	0	0	0.022	0.007	0
Nabidae	<i>Nabis</i> sp. 1	0	0	0	0	0.01	0.005	0.028
Rhyparochromidae	<i>Emblethis</i> sp. 1	0.005	0.003	0.005	0.004	0.318	0.036	0
Rhyparochromidae	<i>Emblethis</i> sp. 2	0	0	0	0	0.01	0.004	0.007
Rhyparochromidae	<i>Sisannes claviger</i>	0.008	0.004	0.013	0.006	0.064	0.013	0
Lygaeidae	<i>Lygaeus kalmii</i>	0.005	0.003	0.003	0.003	0.018	0.007	0.051
Geocoridae	<i>Geocoris</i> sp. 1	0	0	0	0	0.218	0.033	0
Cicadellidae	Cicadellid sp. 1	0.24	0.028	0.165	0.03	0.456	0.073	0
Cicadellidae	Cicadellid sp. 2	0.055	0.011	0.055	0.015	0.048	0.015	0.913
Cicadellidae	Cicadellid sp. 3	0.002	0.002	0	0	0.02	0.011	0.053
Cicadellidae	Cicadellid sp. 4	0.012	0.005	0.003	0.003	0.014	0.007	0.315
Cicadellidae	Cicadellid sp. 5	0.002	0.002	0	0	0.002	0.002	0.687
Cicadellidae	Cicadellid sp. 6	0.002	0.002	0	0	0.364	0.056	0
Cicadellidae	Cicadellid sp. 8	0.01	0.006	0.008	0.004	0.002	0.002	0.475
Cicadellidae	Cicadellid sp. 10	0	0	0.013	0.007	0	0	0.007
Cicadellidae	Cicadellid sp. 30	0	0	0	0	0.006	0.004	0.165
Fulgoridae	Fulgorid sp. 1	0	0	0	0	0.004	0.003	0.135
	Psocoptera sp. 1	0.245	0.06	0.183	0.031	0.004	0.003	0
	Psocoptera sp. 2	0.005	0.005	0	0	0	0	0.473
Carabidae	<i>Pasimachus obsoletus</i>	0.058	0.012	0	0	0.006	0.003	0
Carabidae	<i>Calosoma</i> sp. 1	0.002	0.002	0.008	0.004	0.16	0.035	0
Carabidae	<i>Harpalus somnulentus</i>	0.13	0.048	0.215	0.04	0.134	0.023	0.288
Carabidae	<i>Cymindis</i> sp. 1	0.008	0.004	0.055	0.015	0.06	0.014	0.001
Carabidae	<i>Piosoma</i> sp. 1	0	0	0	0	0.004	0.003	0.135
Carabidae	<i>Harpalus fraternus</i>	0.003	0.002	0.008	0.008	0.89	0.087	0

Table A1. Continued.

Taxonomic information		Park Mesa old growth		Chapin Mesa old growth		Chapin Mesa fire 2002		P
Family	Species/O.T.U.	Mean	SE	Mean	SE	Mean	SE	
Carabidae	<i>Cicindela punctulata</i>	0	0	0	0	0.286	0.073	0
Carabidae	<i>Amblycheila picolomini</i>	0.002	0.002	0.028	0.012	0	0	0.002
Carabidae	<i>Agonum placidum</i>	0	0	0	0	0.014	0.005	0.001
Carabidae	Carabid sp. 1	0.02	0.009	0.085	0.024	0.004	0.004	0
Carabidae	Carabid sp. 2	0.005	0.003	0.005	0.004	0.07	0.015	0
Scarabaeidae	<i>Euphoria inda</i>	0	0	0	0	0.258	0.06	0
Scarabaeidae	Aphodiinae sp. 1	0	0	0	0	0.144	0.038	0
Scarabaeidae	<i>Canthon</i> sp. 1	0	0	0	0	0.008	0.004	0.018
Scarabaeidae	<i>Copris</i> sp. 1	0.017	0.017	0	0	0	0	0.473
Scarabaeidae	<i>Diplotaxis obscura</i>	0	0	0	0	0.004	0.003	0.135
Scarabaeidae	<i>Diplotaxis</i> sp. 1	0.01	0.005	0	0	0.002	0.002	0.086
Scarabaeidae	<i>Diplotaxis</i> sp. 2	0.043	0.011	0.02	0.008	0.012	0.006	0.034
Scarabaeidae	Scarabaeid sp. 1	0	0	0.005	0.005	0.008	0.004	0.184
Scarabaeidae	Scarabaeid sp. 2	0.002	0.002	0.003	0.003	0.002	0.002	0.959
Scarabaeidae	Scarabaeid sp. 3	0.012	0.006	0.008	0.006	0	0	0.244
Scarabaeidae	Scarabaeid sp. 4	0.008	0.007	0	0	0	0	0.332
Scarabaeidae	Scarabaeid sp. 5	0	0	0.038	0.01	0.004	0.004	0
Melyridae	<i>Collops bipunctatus</i>	0	0	0	0	0.01	0.005	0.028
Melyridae	Melyrid sp. 1	0	0	0	0	0.008	0.006	0.202
Staphylinidae	Aleocharinae sp. 1	0	0	0	0	0.068	0.016	0
Staphylinidae	Aleocharinae sp. 2	0	0	0	0	0.03	0.009	0
Staphylinidae	Aleocharinae sp. 3	0	0	0	0	0.004	0.004	0.368
Staphylinidae	<i>Lobrathium</i> sp. 1	0.002	0.002	0.003	0.003	0.026	0.01	0.007
Staphylinidae	Staphylinidae sp. 1	0.013	0.005	0.01	0.006	0	0	0.092
Staphylinidae	Staphylinidae sp. 2	0	0	0	0	0.01	0.004	0.007
Elateridae	<i>Ctenicera</i> sp. 1	0.005	0.003	0.003	0.003	0.006	0.003	0.738
Elateridae	<i>Ctenicera</i> sp. 2	0.015	0.007	0	0	0	0	0.028
Elateridae	<i>Ctenicera</i> sp. 3	0.055	0.012	0.01	0.006	0	0	0
Elateridae	<i>Ctenicera</i> sp. 4	0.065	0.012	0.013	0.007	0.006	0.003	0
Elateridae	<i>Ctenicera</i> sp. 5	0.047	0.014	0.01	0.005	0.004	0.004	0.003
Elateridae	Elaterid sp. 1	0.003	0.002	0	0	0	0	0.223
Lathridiidae	Lathridiid sp. 1	0.003	0.002	0.008	0.006	0	0	0.262
Tenebrionidae	<i>Eleodes extricatus</i>	3.275	0.174	7.193	0.394	11.38	0.458	0
Tenebrionidae	<i>Eleodes snowii</i>	0.122	0.021	0.223	0.043	0.002	0.002	0
Tenebrionidae	<i>Eleodes longicollis</i>	0.032	0.009	0.038	0.01	0.042	0.011	0.739
Tenebrionidae	<i>Eleodes</i> sp. 1	0	0	0.003	0.003	0.008	0.005	0.148
Tenebrionidae	<i>Embaphion</i> sp. 1	0.073	0.013	0.038	0.011	0.018	0.006	0.001
Tenebrionidae	<i>Embaphion</i> sp. 2	0.007	0.004	0	0	0.002	0.002	0.276
Tenebrionidae	<i>Statira</i> sp. 1	0.012	0.005	0.008	0.004	0	0	0.095
Tenebrionidae	<i>Triorophus</i> sp. 1	0	0	0.005	0.004	0	0	0.064
Zopheridae	<i>Zopherus concolor</i>	0	0	0	0	0.04	0.034	0.254
Curculionidae	<i>Cimbochera</i> sp. 1	0.093	0.014	0.075	0.018	0.06	0.014	0.27
Curculionidae	<i>Curculio</i> sp. 1	0.01	0.004	0.02	0.013	0.012	0.005	0.605
Curculionidae	<i>Diamimus subsorsisus</i>	0	0	0	0	0.028	0.008	0
Curculionidae	<i>Zascalis</i> sp. 1	0.003	0.002	0	0	0.004	0.003	0.472
Curculionidae	Curculionid sp. 1	0.017	0.015	0	0	0	0	0.401
Curculionidae	Curculionid sp. 2	0.037	0.025	0.02	0.012	0.002	0.002	0.384
Curculionidae	Curculionid sp. 3	0.012	0.005	0.02	0.007	0.01	0.005	0.454
Curculionidae	Curculionid sp. 4	0	0	0	0	0.006	0.004	0.165
Anthicidae	<i>Ischyropalpus</i> sp. 1	0.012	0.004	0.005	0.004	1.11	0.116	0
Anthicidae	Anthicid sp. 1	0.06	0.023	0.068	0.017	0.082	0.022	0.759
Anthicidae	Anthicid sp. 2	0.038	0.009	0.073	0.046	0.006	0.003	0.138
Cantharidae	Cantharid sp. 1	0.053	0.017	0.055	0.017	0.002	0.002	0.013
Cantharidae	Cantharid sp. 2	0.005	0.004	0.003	0.003	0.01	0.007	0.551
Cantharidae	Cantharid sp. 3	0	0	0.003	0.003	0.002	0.002	0.503
Nitidulidae	<i>Carpophilus</i> sp. 1	0.002	0.002	0	0	0.004	0.004	0.577
Nitidulidae	Nitidulid sp. 1	0	0	0.003	0.003	0.004	0.003	0.324
Trogidae	<i>Trox</i> sp. 1	0.023	0.008	0.033	0.015	0.016	0.016	0.69
Lycidae	Lycid sp. 1	0.003	0.002	0	0	0	0	0.223
	Coleoptera Larva sp. 1	0.003	0.002	0.003	0.003	0	0	0.453
	Coleoptera Larva sp. 2	0	0	0	0	0.004	0.003	0.135
	Coleoptera Larva sp. 3	0.003	0.003	0	0	0.002	0.002	0.67
	Coleoptera Larva sp. 4	0	0	0	0	0.024	0.013	0.027
	Coleoptera Larva sp. 5	0.003	0.002	0	0	0.002	0.002	0.513
	Coleoptera Larva sp. 6	0.003	0.002	0.005	0.004	0.204	0.03	0
	Coleoptera Larva sp. 7	0	0	0.005	0.004	0.002	0.002	0.223

Table A1. Continued.

Taxonomic information		Park Mesa old growth		Chapin Mesa old growth		Chapin Mesa fire 2002		
Family	Species/O.T.U.	Mean	SE	Mean	SE	Mean	SE	P
	Coleoptera Larva sp. 8	0	0	0	0	0.006	0.003	0.049
	Coleoptera Larva sp. 9	0	0	0	0	0.006	0.003	0.049
	Coleoptera Larva sp. 10	0	0	0	0	0.066	0.017	0
	Coleoptera Larva sp. 11	0	0	0	0	0.014	0.005	0.001
	Coleoptera Larva sp. 12	0	0	0	0	0.034	0.01	0
	Coleoptera Larva sp. 13	0.005	0.003	0.025	0.009	0.22	0.038	0
	Coleoptera Larva sp. 14	0	0	0	0	0.01	0.004	0.007
	Coleoptera Larva sp. 15	0	0	0	0	0.024	0.009	0.001
Carabidae	Carabid Larva sp. 1	0	0	0	0	0.012	0.005	0.002
Tenebrionidae	Tenebrionid Larva sp. 1	0.002	0.002	0.003	0.003	0.014	0.005	0.018
Lampyridae	Lampyrid Larva sp. 1	0.007	0.003	0.003	0.003	0.002	0.002	0.407
Lampyridae	Lampyrid Larva sp. 2	0.008	0.004	0.005	0.004	0	0	0.13
	Coleoptera sp. 1	0.002	0.002	0	0	0.028	0.008	0
	Coleoptera sp. 2	0.002	0.002	0.003	0.003	0	0	0.57
	Coleoptera sp. 3	0	0	0.008	0.004	0.002	0.002	0.074
	Coleoptera sp. 4	0	0	0.005	0.004	0	0	0.064
	Coleoptera sp. 5	0.002	0.002	0.013	0.007	0	0	0.023
	Coleoptera sp. 6	0.002	0.002	0	0	0.002	0.002	0.687
	Coleoptera sp. 7	0.003	0.002	0	0	0	0	0.223
	Coleoptera sp. 8	0	0	0	0	0.018	0.016	0.288
	Coleoptera sp. 9	0	0	0	0	0.008	0.004	0.018
	Coleoptera sp. 10	0	0	0	0	0.008	0.006	0.135
	Coleoptera sp. 11	0	0	0	0	0.044	0.011	0
	Coleoptera sp. 12	0	0	0	0	0.006	0.003	0.049
	Coleoptera sp. 13	0	0	0	0	0.012	0.005	0.002
	Coleoptera sp. 14	0.257	0.257	0	0	0	0	0.473
	Coleoptera sp. 15	0	0	0	0	0.004	0.004	0.368
	Coleoptera sp. 16	0	0	0	0	0.004	0.003	0.135
	Coleoptera sp. 17	0	0	0	0	0.004	0.003	0.135
	Coleoptera sp. 18	0	0	0	0	0.01	0.004	0.007
	Coleoptera sp. 19	0	0	0	0	0.01	0.005	0.028
	Coleoptera sp. 20	0	0	0.003	0.003	0.01	0.007	0.168
	Coleoptera sp. 21	0.018	0.018	0	0	0	0	0.473
Myrmeleontidae	Myrmeleontid sp. 1	0.005	0.003	0	0	0.006	0.003	0.324
Myrmeleontidae	Myrmeleontid sp. 2	0.002	0.002	0	0	0.002	0.002	0.687
Myrmeleontidae	Myrmeleontid sp. 3	0.003	0.002	0	0	0	0	0.223
Myrmeleontidae	Myrmeleontid sp. 4	0.053	0.016	0.028	0.01	0	0	0.004
Mutillidae	<i>Dasymutilla vestita</i>	0.045	0.009	0.043	0.013	0.198	0.03	0
Mutillidae	<i>Dasymutilla</i> sp. 1	0.015	0.005	0.01	0.005	0.022	0.008	0.458
Mutillidae	<i>Dasymutilla</i> sp. 2	0.005	0.003	0.008	0.004	0	0	0.184
Mutillidae	<i>Dasymutilla</i> sp. 3	0.005	0.003	0.003	0.003	0	0	0.277
Mutillidae	<i>Dasymutilla</i> sp. 4	0.005	0.003	0	0	0	0	0.105
Mutillidae	<i>Pseudomethoca</i> sp. 1	0.002	0.002	0.003	0.003	0.036	0.01	0
Mutillidae	<i>Pseudomethoca</i> sp. 2	0	0	0	0	0.004	0.003	0.135
Mutillidae	<i>Sphaerophilama</i> sp.	0	0	0	0	0.044	0.01	0
Mutillidae	Mutillid sp. 1	0	0	0.005	0.004	0	0	0.064
Mutillidae	Mutillid sp. 2	0	0	0.005	0.004	0.002	0.002	0.223
Formicidae	<i>Lasius latipes</i>	0.003	0.002	0.003	0.003	0.002	0.002	0.91
Formicidae	<i>Lasius nigriscens</i>	0	0	0	0	0.006	0.003	0.049
Formicidae	<i>Crematogaster depilis</i>	0.093	0.024	0.588	0.099	0.018	0.008	0
Formicidae	<i>Leptothorax muscorum</i>	0.675	0.107	0.443	0.05	0.664	0.196	0.445
Formicidae	<i>Leptothorax</i> sp. 1	0.022	0.011	0.005	0.004	0	0	0.104
Formicidae	<i>Monomorium cyaneum</i>	2.253	0.262	2.925	0.395	10.472	1.008	0
Formicidae	<i>Pheidole</i> sp. 1	0.017	0.01	0.088	0.076	0	0	0.228
Formicidae	<i>Pheidole hyatti</i>	1.033	0.183	0.86	0.211	10.568	1.126	0
Formicidae	<i>Solenopsis molesta</i>	0.063	0.012	0.118	0.037	0.386	0.082	0
Formicidae	<i>Forelius pruinosus</i>	1.9	0.239	1.435	0.208	1.838	0.449	0.577
Formicidae	<i>Camponotus vicinus</i>	1.345	0.085	1.41	0.084	0.118	0.025	0
Formicidae	<i>Camponotus modoc</i>	0.298	0.039	0.228	0.047	0.14	0.134	0.386
Formicidae	<i>Camponotus ocreatus</i>	0.007	0.003	0.373	0.061	0	0	0
Formicidae	<i>Formica argentea</i>	0.307	0.035	1.655	0.351	0.294	0.036	0
Formicidae	<i>Formica podzolica</i>	0.028	0.01	1.063	0.491	1.002	0.388	0.029
Formicidae	<i>Formica gnava</i>	0	0	0	0	0.008	0.006	0.202
Formicidae	<i>Tapinoma sessile</i>	0	0	0	0	0.016	0.014	0.278
Formicidae	<i>Pogonomyrmex</i> sp. 1	0.002	0.002	0.005	0.005	0.026	0.01	0.011
Formicidae	<i>Myrmica</i> sp. 1	0.44	0.043	0.325	0.042	0.006	0.003	0

Table A1. Continued.

Taxonomic information		Park Mesa old growth		Chapin Mesa old growth		Chapin Mesa fire 2002		P
Family	Species/O.T.U.	Mean	SE	Mean	SE	Mean	SE	
Formicidae	<i>Dorymyrmex</i> sp. 1	0.022	0.016	0.013	0.01	0	0	0.404
Formicidae	<i>Dorymyrmex</i> sp. 2	0	0	0.005	0.004	0	0	0.064
Formicidae	<i>Hypoponera</i> sp. 1	0	0	0	0	0.014	0.007	0.011
Dryinidae	Dryinid sp. 1	0.008	0.004	0	0	0.002	0.002	0.085
Geometridae	Geometrid sp. 1	0.002	0.002	0.003	0.003	0	0	0.57
Erebidae	<i>Lophocampa ingens</i>	0.007	0.003	0	0	0	0	0.049
Erebidae	Erebid sp. 1	0.005	0.003	0.005	0.004	0	0	0.286
Erebidae	Erebid sp. 2	0.037	0.008	0.043	0.011	0	0	0
Lasiocampidae	<i>Malacasoma</i> sp. 1	0.02	0.006	0.013	0.007	0	0	0.019
Noctuidae	Noctuid sp. 1	0.02	0.006	0.013	0.006	0	0	0.007
Noctuidae	Noctuid sp. 2	0.008	0.006	0.003	0.003	0	0	0.283
Noctuidae	Noctuid sp. 3	0.007	0.003	0.003	0.003	0	0	0.153
Noctuidae	Noctuid sp. 4	0.005	0.004	0	0	0	0	0.259
Noctuidae	Noctuid sp. 5	0.012	0.004	0.003	0.003	0	0	0.02
Noctuidae	Noctuid sp. 6	0.003	0.002	0.003	0.003	0	0	0.453
Noctuidae	Noctuid sp. 7	0.022	0.006	0.008	0.004	0	0	0.004
Cecidomyiidae	Cecidomyiid sp. 1	0.27	0.043	0.705	0.088	0	0	0
Cecidomyiidae	Cecidomyiid sp. 2	0.018	0.01	0.01	0.005	0	0	0.201
Sciaridae	Sciarid sp. 1	0.518	0.078	0.33	0.053	0	0	0
Sciaridae	Sciarid sp. 2	0.06	0.015	0.055	0.013	0	0	0
Sciaridae	Sciarid sp. 3	0.15	0.019	0.69	0.088	0	0	0
Sciaridae	Sciarid sp. 4	0.002	0.002	0.003	0.003	0	0	0.57
Sciaridae	Sciarid sp. 5	0	0	0.005	0.005	0	0	0.253
Sciaridae	Sciarid sp. 6	0.028	0.025	0	0	0	0	0.385
Sciaridae	Sciarid sp. 7	0	0	0.008	0.004	0	0	0.016
Phoridae	Phorid sp. 1	0.425	0.046	0.445	0.055	0	0	0
Phoridae	Phorid sp. 2	0.025	0.009	0.093	0.046	0	0	0.016
Phoridae	Phorid sp. 3	0.038	0.011	0.07	0.017	0	0	0
Phoridae	Phorid sp. 4	0.027	0.008	0.015	0.007	0	0	0.01

APPENDIX B

Table B1. Taxonomic list of indicator species arranged by habitat, indicator value, and significance. The mean value represents the average number of specimens of each species per pitfall trap collected.

Species	Indicator value	P
Old-growth habitat indicators		
<i>Camponotus vicinus</i>	52.1	0.0002
<i>Machilinus aurantiacus</i>	39.2	0.0002
Erythraeoid sp. 2	37.8	0.0002
Phorid sp. 1	23.4	0.0002
<i>Myrmica</i> sp. 1	21.6	0.0002
Cecidomyiid sp. 1	21.4	0.0002
Sciarid sp. 1	19.8	0.0002
Sciarid sp. 3	17.1	0.0002
<i>Dallasiellus discrepans</i>	13	0.0002
<i>Styracosceles neomexicanus</i>	12	0.0002
Psocoptera sp. 1	11.3	0.0002
Trombidiid sp. 1	10.7	0.0002
<i>Polyxenus</i> sp. 1	10.6	0.0002
<i>Eleodes snowii</i>	8.9	0.0002
<i>Crematogaster depilis</i>	8.8	0.0002
<i>Castianeira</i> sp.	8.4	0.0002
Sminthurid sp. 1	7.3	0.0002
<i>Oriulus</i> sp. 1	7.2	0.0002
<i>Camponotus ocreatus</i>	6.1	0.0002
<i>Vaejovis coahuilae</i>	4.1	0.0002
Acridid sp. 1	3.9	0.0004
Erebid sp. 2	3.6	0.0004

Table B1. Continued.

Species	Indicator value	P
Phorid sp. 3	3.5	0.0004
Thysanura sp. 1	2.8	0.0004
<i>Habronattus virgulatus</i>	6.6	0.0006
Sciarid sp. 2	4.1	0.0006
Myrmeleontid sp. 4	3	0.0006
<i>Pardosa orophila</i>	2.8	0.0006
<i>Ctenicera</i> sp. 3	2.8	0.0008
<i>Drassyllus</i> sp. 1	5.1	0.001
<i>Castianeira dorsata</i>	4	0.001
<i>Camponotus modoc</i>	8.6	0.0014
<i>Micaria nanella</i>	7.1	0.002
Cantharid sp. 1	3	0.002
Phorid sp. 2	2.4	0.002
<i>Herpyllus</i> sp. 1	4.5	0.0024
<i>Habronattus</i> sp. 1	2.4	0.0024
Hypogasturid sp. 1	2.3	0.0024
<i>Formica argentea</i>	15.1	0.0026
<i>Ctenicera</i> sp. 4	3.1	0.003
Gnaphosid sp. 1	1.9	0.0034
<i>Habronattus</i> sp. 2	1.8	0.004
Carabid sp. 1	2.5	0.0042
Phorid sp. 4	1.8	0.0042
<i>Embaphion</i> sp. 1	3.7	0.006
<i>Eremobates mormonus</i>	2	0.006
<i>Drassodes saccatus</i>	14.4	0.0076
<i>Malacasoma</i> sp. 1	1.5	0.0076
<i>Pasimachus obsoletus</i>	2.3	0.008
Lycosidae sp. 1	1.7	0.008
Noctuid sp. 1	1.7	0.0082
Oribatida sp. 1	1.5	0.0096
<i>Schizocosa</i> sp. 1	1.5	0.01
<i>Ctenicera</i> sp. 5	2	0.0112
Anthicid sp. 1	2.6	0.0116
Trombidiid sp. 2	1.9	0.0126
Noctuid sp. 7	1.5	0.0136
Trombidiid sp. 3	1.4	0.0148
Chernetid sp. 2	1.4	0.015
<i>Dictyna apachea</i>	3.6	0.0168
Staphylinid sp. 1	1	0.038
<i>Schizocosa chiricahua</i>	15.5	0.0412
Burn habitat indicators		
<i>Eleodes extricatus</i>	62.4	0.0002
<i>Melanoplus sanguinipes</i>	58.6	0.0002
<i>Monomorium cyaneum</i>	55	0.0002
<i>Pheidole hyatti</i>	50.4	0.0002
Entomobryid sp. 1	47.6	0.0002
<i>Ischyropalpus</i> sp. 1	34.1	0.0002
Anystid sp. 1	28.2	0.0002
<i>Calathus</i> sp. 1	27.6	0.0002
<i>Emblethis</i> sp. 1	19.9	0.0002
<i>Gryllus</i> sp. 1	14.7	0.0002
Cicadellid sp. 6	13.8	0.0002
<i>Geocoris</i> sp. 1	12.4	0.0002
<i>Solenopsis molesta</i>	12.1	0.0002
Coleoptera Larva sp. 6	11.4	0.0002
<i>Dasyneura vestita</i>	9.3	0.0002
<i>Cicindela punctulatus</i>	8.2	0.0002
<i>Euphoria inda</i>	7.8	0.0002
<i>Formica podzolica</i>	7.5	0.0002
<i>Calosoma</i> sp. 1	7.4	0.0002
<i>Latrodectus hesperus</i>	6.7	0.0002
<i>Trimerotropis pallidipennis</i>	5.2	0.0002
Aphodiinae sp. 1	5.2	0.0002
Carabid sp. 2	4.9	0.0002
<i>Sisamnes claviger</i>	4.3	0.0002
Aleocharinae sp. 1	4.2	0.0002
<i>Sphaerophthama</i> sp. 1	4.2	0.0002
<i>Drassodes</i> sp. 3	4	0.0002

Table B1. Continued.

Species	Indicator value	P
Coleoptera Larva sp. 10	3.8	0.0002
<i>Eremopedes</i> sp. 1	3.7	0.0002
<i>Pagasa fusca</i>	3.6	0.0002
Coleoptera sp. 11	3.6	0.0002
<i>Melanoplus bivittatus</i>	3.4	0.0002
<i>Drassyllus lamprus</i>	3	0.0002
<i>Pseudomethoca</i> sp. 1	2.8	0.0002
Aleocharinae sp. 2	2.6	0.0002
Coleoptera Larva sp. 12	2.4	0.0002
Coleoptera sp. 1	2.3	0.0002
<i>Nysius</i> sp. 1	2.2	0.0002
<i>Melanoplus flavidus</i>	1.8	0.0002
<i>Xanthippus corallipes</i>	2.2	0.0004
Coleoptera Larva sp. 15	1.6	0.0004
<i>Agonum</i> sp. 1	1.4	0.0004
Coleoptera Larva sp. 11	1.4	0.0004
<i>Lobrathium</i> sp. 1	1.7	0.0006
<i>Trimerotropis cincta</i>	1.2	0.0012
Coleoptera sp. 13	1.2	0.0014
<i>Pogonomyrmex</i> sp. 1	1.4	0.0024
Lithobiid sp. 1	1.3	0.0024
Staphylinidae sp. 2	1	0.0034
Coleoptera Larva sp. 14	1	0.0034
<i>Emblethis</i> sp. 2	1	0.0038
<i>Hypoponera</i> sp. 1	1	0.0042
Coleoptera sp. 18	1	0.0044
Coleoptera Larva sp. 4	1	0.0048
Cicadellid sp. 3	1.1	0.005
Cicadellid sp. 1	10	0.0054
<i>Cymindis</i> sp. 1	3.2	0.0072
Tenebrionid Larva sp. 1	1.2	0.0092
<i>Nabis</i> sp. 1	0.8	0.0102
<i>Zopherus concolor</i>	0.8	0.0106
Coleoptera sp. 9	0.8	0.0118
<i>Canthon</i> sp. 1	0.8	0.0124
Coleoptera sp. 19	0.8	0.0124
<i>Collops bipunctatus</i>	0.8	0.013
<i>Nicrophorus guttula</i>	2.1	0.0142
<i>Arenivaga</i> sp. 1	1	0.0186
<i>Lygaeus kalmia</i>	1.1	0.0228
<i>Lasius nigriscens</i>	0.6	0.0356
Coleoptera sp. 12	0.6	0.0374
Coleoptera Larva sp. 9	0.6	0.0386
Coleoptera Larva sp. 8	0.6	0.0392
<i>Steatoda</i> sp. 1	0.6	0.0394
Scarabaeid sp. 1	0.6	0.0432

APPENDIX C

Table C1. A comparison of correlative values among the top seven habitat indicator species for the old-growth (OG) and burned habitats. These species were correlated with habitat values we believe to be indicative of one habitat over the other. The species of grasses, shrubs, and herbaceous vegetation were not accounted for in this analysis.

Habitat value	B1	B2	B3	B4	B5	B6	B7	O1	O2	O3	O4	O5	O6	O7
Ground cover (burn indicative)														
Grass	++	++	+	+	-	+	++	-	-	-	--	--	+	--
Herb	++	++	++	++	++	++	++	--	--	-	--	--	--	--
Bare ground	-	+	-	-	+	+	+	-	--	+	--	-	--	-
Soil coarseness (burn indicative)														
@#5	+	-	-	+	++	++	-	+	-	-	+	-	-	+
@#10	++	-	-	-	++	+	-	+	-	+	+	+	+	++
@#35	++	++	++	+	++	++	++	--	--	--	-	-	-	-
@#60	-	+	+	++	++	+	-	-	+	-	-	-	-	--
Ground cover (OG indicative)														
Shrub	-	-	-	-	-	-	-	++	++	+	+	-	-	+
Woody	-	-	--	-	-	--	--	-	+	+	+	+	+	+
Leaf litter	--	--	-	-	--	--	--	++	++	+	++	++	++	++
Woody debris (OG indicative)														
Total volume	+	+	-	-	-	-	-	-	+	-	-	-	+	-
Canopy classes (OG indicative)														
Total canopy	--	--	--	--	--	--	--	++	++	+	++	++	++	++
Soil coarseness (OG indicative)														
@#120	--	--	--	--	--	--	--	++	++	++	+	+	+	+
@#230	--	--	--	-	--	--	-	+	+	+	+	++	+	++
Finest soil	--	-	-	-	--	--	-	+	+	+	+	+	+	++

Notes: Burned species abbreviations are: B1, *E.extricator*; B2, *M.sanguinipes*; B3, *M.cyaneum*; B4, *Phayatti*; B5, *Ischryopalpus* sp.1; B6, *Calathus* sp.1; B7, *Emblethis* sp.1. Old-growth species abbreviations are: O1, *C.vicinus*; O2, *M.aurantiacus*; O3, *Myrmica* sp.1; O4, *Erythraeidae* sp.2; O5, *Cecidomyidae* sp.1; O6, *Sciaridae* sp.1; O7, *Phoridae* sp.1.