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## Effects of Prescribed Fire on the Diversity of Soil-Dwelling Arthropods in the University of South Florida Ecological Research Area, Tampa, Florida

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Effects of Prescribed Fire on the Diversity of Soil-Dwelling Arthropods in the University of South Florida  
Ecological Research Area, Tampa, Florida

by

Celina Bellanceau

A thesis submitted in partial fulfillment  
of the requirements for the degree of  
Master of Science  
Department of Biology  
College of Arts and Science  
University of South Florida

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Effects of Prescribed Fire on the Diversity of Soil-Dwelling Arthropods in the University of South Florida  
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Celina Bellanceau

**ABSTRACT**

Leaf litter samples were used to study arthropod diversity in the University of South Florida Ecological Research Area. Arthropods were collected from different plots of different prescribed burn frequencies (1 year, 2 year, 5 year, 7 year and no burn frequencies). Differential responses of arthropods to burn frequency were studied. It was expected that burn frequency would affect arthropod richness and diversity and that the pattern of diversity and richness would follow the Intermediated Disturbance Hypothesis. It was also expected that richness and diversity would be correlated with the amount of leaf litter present. Preliminary results suggest that there are short-term and long-term differences among arthropod communities in response to fire history and vegetation and that the amount of leaf litter may influence the distribution of arthropod taxa.



## INTRODUCTION

### **Sandhill Community**

Sandhill habitat is found in the temperate climate of the southeastern United States in areas with deep, well-drained sandy soil depleted of nutrients and with almost no organic matter. The soils are marine deposits of once Plio-Pleistocene beach sand formations (Myers 1990).

Sandhill is often called Longleaf pine/Turkey oak habitat because of the floral composition of the habitat. The overstory of sandhill habitat is mainly composed of Longleaf pine (*Pinus palustris*) with some slash pine (*Pinus elliotti*) while the understory is made up of turkey oak (*Quercus laevis*) and a few blackjack oaks (*Quercus incana*) or sand live oaks (*Quercus geminata*) (Schmidt 2005). Persimmon (*Diospyros Virginia*) and saw palmetto (*Serenoa repens*) also occur (Hay-Smith & Tanner 1997b). Underwood plant species can include sparkleberry (*Vaccinium arboreum*) and pawpaw (*Asimina incarna*) (Myers 1990).

Although sandhill habitats have low diversity of trees, they do have high total diversity attributed to the species-rich herbaceous layer. Groundcover plants include wiregrasses *Aristida stricta* and *Sporobolus gracilis*, and can include other herbaceous plants such as lopsided Indian grass (*Sorghastrum secundum*), greeneyes (*Berlandiera pumila*), golden aster (*Chrysopsis scabrella*), blazing star (*Liatris pauciflora*), paintbrush (*Carphephorus corymbosus*), and sandhill milkweed (*Asclepias humistrata*) as well as others (Hay-Smith & Tanner 1997b).

Breeding amphibians use temporary ponds in sandhill habitat as a source of water that is free from predaceous fish and insects (Dodd & Charest 1988) and many fossorial animals require the loose sands of sandhill to “swim” or to burrow through (Myers 1990). The burrows of the Florida mouse (*Peromyscus floridanus*), gopher tortoises (*Gopherus polyphemus*), and the pocket gopher (*Geomys pineti*) serve as refuge for many other species, which also serve essential roles in sandhills (Hay-Smith & Tanner 1997b). Other sensitive animals that utilize sandhill habitat include the Florida gopher frog (*Rana capito*), the threatened eastern indigo snake (*Drymarchon corais*) and the Sherman’s fox squirrel (*Sciurus niger shermanii*) (Hay-Smith & Tanner 1997b). Gopher frogs and the eastern indigo snakes are important commensals of gopher tortoise burrows. Scarab beetles such as *Aephodius troglodytes*, *Copris gopheri*, and *Onthophagus polyphemus* are some invertebrate commensals of gopher tortoise burrows (Myers 1990). Many of these animals help with seed dispersal, and refugia and nest cavity construction (Hay-Smith & Tanner 1997b).

Endangered species of sandhill habitat include red-cockaded woodpeckers (*Picoides borealis*) and Florida mice (*Peromyscus floridanus*) (Hay-Smith & Tanner 1997a), which will readily use gopher tortoise burrows instead of digging their own. Endangered plant species, which are endemic to sandhill, include claspingleaf (*Warea amplexifolia*) and Carter’s mustard (*W. carteri*) (Liberton Undated).

### **Importance of fire**

Sandhill communities are pyrogenic; the organisms living within it have evolved in the presence of fire, so that the habitat is fire-maintained and fire-dependent (Agee 1993; Myers 1990). Sandhill requires frequent, low-intensity fires in one to ten year intervals to maintain its open overstory of mainly longleaf pines, understory of deciduous oaks and ground cover of wire grasses and forbs (Myers 1990).

Fire often produces a mosaic of habitat (Mushinsky & Gibson 1991; Tansley 1924), which is important to biodiversity, including the diversity of arthropods. Complexity of habitat has been found to be positively associated with species richness (Hansen 2000; Humphrey et al. 1999; Huston 1994; Uetz 1979). The structure of the vegetation in an area influences populations of terrestrial arthropods. Different arthropods have specific microhabitat requirements and habitat heterogeneity allows for many different microhabitat types (Samways 2005).

Fire has been found to be a significant abiotic agent of selection for many species and can be considered an ecological process (Agee 1993 {Myers, 1990 #51}). Fire can influence the structure of many communities as well as the evolution of the species within the community. Fire can alter the size, age, and spatial distribution of habitats and the extent of the alteration is correlated with fire frequency (Mushinsky & Gibson 1991).

Of course, each plant community is different, so the ecological effect of fire on habitat structure consequently differs. The plant species and litter of a community determine the temperature of a fire and the rate at which it spreads. Even within a community, the temperature and rate of spread is irregular and inconsistent which leads to the mosaic habitat patterns found in sandhill (Mushinsky & Gibson 1991). The lack of homogenous fire temperatures in a single stand of plants may be related to the type and height of vegetation (Hobbs & Gimingham 1984) and the subsequent moisture content of the litter layer (Hobbs et al. 1984).

The plants living in sandhill provide the fuel for the low intensity, frequent fires that are necessary to maintain viable sandhill habitat. Sandhill and ponderosa pine communities produce well-aerated litter beds with their resinous needles which allow for increased flammability of the communities (Agee 1993). Lightning was historically the igniting force for sandhill fires and usually struck the lightning-rod like longleaf pines (Myers 1990). Native Americans have also ignited the forests for thousands of years (Kalisz 1986; Komarek 1974; Ware et al. 1989), so anthropogenic influences are nothing new to sandhill.

It has been found that communities that are exposed to any interval of fire are more similar to each other than to communities that are not exposed to fire (Hanula 2003). It has also been found that species richness and diversity can increase following a fire (Force 1981). Different genera differ in their response to fire, however, and it can seem to be an almost species-specific response (Ahlgren 1974; Hanula 2003; Niwa & Peck 2002; Siemann et al. 1997; Warren et al. 1987).

Studies have been inconsistent in determining the relationship between fire and the Intermediate Disturbance Hypothesis (IDH), which states that the highest diversity should be found in areas of intermediate disturbance. There are studies which have found that species richness increases with fire frequency, without an ensuing decline in species richness at higher fire frequencies (Kerstyn & Stiling 1999; Mehlman 1992; Nuzzo et al. 1996; Tester 1996). Other studies have found the lowest species richness to be at sites with intermediate disturbance (Schwilk et al. 1997), and others have actually found a decline in species richness with an increase in fire frequency (Collins et al. 1995). Another study found a decline in certain species when fire was suppress or occurred late (Andersen & Muller 2000). One reason for such inconsistent results could be the inclusion of dormant season fires, in some studies, which may impact fauna and flora differently than growing season fires (Beckage & Stout 2000). Differing time since last fire, which is known to affect species diversity could also be attributed to the mixed results found (Gibson & Hulbert 1987; Mehlman 1992).

Beckage and Stout (2000) found no direct relationship between the number of fires and understory flowering stem species richness, diversity or abundance. They did find an increased species richness and unimodal increase in flowering stem abundance and diversity resulting from fire, yet their model selection criterion favored the null model. Instead of a direct effect of fire, Beckage and Stout (2000) found indirect effects from open overstory. They found that overstory density and composition were most affected by varied fire frequency and this affected the understory composition.

Reduced overstory density and composition impacts the composition and abundance of understory species by decreasing competition for light and soil resources. Increased overstory density leads to decreased understory because of the light and soil resources that are being blocked or used. Support for this indirect relationship between disturbance and understory diversity was also found when using herbicides to reduce overstory density. Increased species richness and ground cover were also found to result from herbicidal declines in overstory oaks from a sandhill community (Brockway et al. 1998).

Many studies have also found variation in responses to disturbance by arthropods. Schowalter (1994; 1995) found that Lepidopteran, detritivore and predator abundances decreased while sap-sucking insect abundances increased in response to canopy-opening disturbances such as hurricanes and timber harvesting. Studies on effects of prescribed fire have also found this trend for grasshopper (Kerstyn & Stiling 1999; Nagel 1973), leaf miner (Kerstyn & Stiling 1999) and herpetofaunal (Mushinsky & Gibson 1991); abundances were found to be higher in the more frequently burned sites.

Reasons for the lack of support for the IDH could have been that the hypothesis does not operate in the Florida pine savanna system in which Beckage and Stout (2000) were studying. Another possibility could be that the relationship between the response variables and fire could be too subtle to detect with their experimental design, or there could have been low power attributed to the relatively small sample size of the study (Beckage & Stout 2000)

### **Fire Effects on Sandhill Flora**

Disturbances such as fire are a selective force. The timing, frequency, and intensity of fire can have a huge effect on the species composition, abundances and the structure of sandhill communities. Fire is an abiotic disturbance that influences the habitat structure and, in turn, the evolution of strategies to survive. Species have evolved to be tolerant to fire in ecosystems with a history of fire (Mushinsky & Gibson 1991). Fire affects the germination of herbaceous plants, the regeneration of longleaf pines, the phenologies of forbs (Daubenmire 1968; Hartnett 1987; Platt et al. 1988), and the morphologies of flowering plants (Mushinsky & Gibson 1991; Platt et al. 1988).

Longleaf pine is considered fire-resistant because it has evolved several adaptations to fire. Longleaf pines, like other fire adapted or resistant plants actually require fire to allow for the germination and establishment of its seedlings (Myers 1990(Agee 1993)). Seeds of longleaf pines need the open well-drained, coarse-grained soil to land on because the seeds are so large and have a persistent wing which cannot penetrate dense groundcover to reach the soil beneath. Seedlings require moderate shade, provided by palmettos and oaks, to protect them from the heat (Myers 1990). After a seedling has established itself it develops into its grass stage where it stays for two years to ten years. This grass stage provides it protection from fire because the terminal bud is nestled in the center of the dense, long needles, which collect moisture. During the grass stage, the longleaf pine grows a long, thick taproot which provides energy stores for later bolting into a sapling. Bolting entails sending up a single straight stem that can grow up to one meter or more in a single growing season. The resulting sapling has a terminal bud which is likely to be above the fire line. Thick bark helps to insulate the tree and scaly plates are produced which flake off as they burn to dissipate heat. Thus, it is seen that longleaf pine communities require frequent, low intensity fires to persist. If fire is disrupted for any reason and litter is allowed to accumulate, recruitment could be decreased and a high temperature, high intensity fire could kill the longleaf pines (Myers 1990; Agee 1993).

Sandhill habitats generally have groundcover consisting of wiregrass, which allows for other groundcover such as forbs, low shrubs and other grasses to coexist. Some of these other groundcover species include bracken fern (*Pteridium aquilinum*), bluestems (*Andropogon* spp.), dwarf live oak (*Q. minima*), golden aster and low-bush blueberry (*Vaccinium myrsinites*). Wiregrass is extremely sensitive to disturbances such as bedding, scraping and scarification of soils, and may not return to a site once it has been extirpated. Perplexingly, wiregrass has a low reproductive capacity yet it can often be found as a dense ground cover. Disturbance such as low intensity fire, grazing and minor soil disturbance during the growing season, April to mid-August, allows it bloom profusely (Myers 1990).

After a fire, the degree of regeneration depends on the types of species present before the fire. Some plants have lignotubers which contain buds and energy stores, which allow for viable dormant buds below the surface. These buds are then stimulated to sprout by the loss of above ground shoots (Agee 1993). Habitats that have many fire tolerant plant species can resprout so rapidly that they can return quickly to its pre-fire condition (Abrahamson 1984a, b; Keeley 1986; Malanson & Trabaud 1987). Plants with adventitious or latent axillary buds are able to regenerate by sprouting buds along the plant body (Agee 1993). This rapid return to the habitats original state leads to high productivity levels (Buchholz 1983). For many plant species, dispersal of seeds (Bradstock & Myerscough 1981(Agee 1993)) and flowering (Gill 1977; Knapp & Hulbert 1986; Wein & Bliss 1973) may increase following a fire. A larger seed bank can result and may lead to new individuals becoming established in an area (Cheplick & Quinn 1987).

Phenology and growth patterns may also change in species of plants enduring after a fire. Following a fire, new shoots, flowers and fruits may appear earlier during than they would if there had not been a fire. Burnt plants may also maintain their green color longer than plants that have not been burned (Daubenmire 1968).

When fire is suppressed, less dominant sandhill species and invader species from adjacent upland communities take over, causing a decline in the fire-adapted species a change in the overall vegetation. Because oaks thrive without fire, upland oak dominated sandhills can result if fire is suppressed. Upland oaks in the USF Eco Area are mainly turkey oaks and sand live oaks. These oaks are deciduous and generally of low stature and have multiple stems. Other hardwoods, such as persimmon also generally increase in abundance when fires are interrupted (Myers 1990).

### **Importance of Soil Fauna**

Litter is composed of any decaying vegetative matter on the ground, such as leaves, woody material, fruit, and flowers. Soil and litter-dwelling arthropods are important in ecosystem processes such as decomposition of organic matter and the associated nutrient cycling, horizontal and vertical movement of soil, and accumulation of soil which leads to soil stability in terrestrial ecosystems. Nutrient cycling is important and soil and litter-dwelling arthropods break down vegetative litter and decaying animal material including chitin into pieces that are more manageable for bacteria, protists and fungi, which further degrade the matter (Eisenbeis & Wichard 1985; Gullan & Cranston 2000; Hale 1976; Samways 2005; Wallwork 1967). Many arthropods also help in the distribution of fungi (Hale 1976; Wallwork 1967). Arthropods are found in just about every soil type in all parts of the world, (Gullan & Cranston 2000; Longino & Colwell 1997; Samways 2005; Wallwork 1976). They are small, fecund and respond quickly to environmental change and so are often used as subjects for studying biodiversity (Longino & Colwell 1997).

Important arthropods of litter and humus-rich soils are acariformes (mites), isopteran (termites), formicidae (ants), collembola (springtails), protura, diplura (doubletails), thysanoptera (thrips), many coleoptera (beetles), as well as immature stages of coleoptera, diptera (flies), and lepidoptera (butterflies and moths). Collembola and Mites are major orders associated with soils and litter and are among the most abundant groups of soil fauna (Eisenbeis & Wichard 1985; Wallwork 1976). Collembola can actually constitute up to 80% of total number of animals in the soil (Hale 1976). Soil arthropods that are restricted to terrestrial soils include many blattodea (roaches), orthoptera (crickets and grasshoppers), and dermaptera (earwigs) (Gullan & Cranston 2000). Rather than being defined by geographic proximity, many communities of arthropods have been found to be best defined by habitat type (Hughes et al. 2000).

Spatial scale is important to consider when discussing soil and leaf litter-dwelling arthropods because different morphs and species differ in their behaviors and habitat requirements (Chust et al. 2003). Some arthropods may be confined to a particular soil layer or depth and show morphological and behavioral adaptations specific to that layer or depth. Morphological adaptations can include larvae with well-developed legs for moving through soil and pupae with adaptations that allow them to move to the surface for emergence. Subterranean insects can also exhibit seasonal shifts in distribution. Drier layers are used for pupation and deeper soils, which offer constant temperatures, are used more in the winter (Gullan & Cranston 2000; Hale 1976).

Collembola and Mites often exhibit a vertical stratification of species in leaf litter. Generally, organisms with larger body sizes are found in greater concentrations in the upper layers of leaf litter, whereas smaller forms are found deeper. These organisms differ morphologically as well, with epedaphic organisms occurring closer to the surface having better developed eyes, springing organs (collembola), antennae and often more stronger pigmentation. Euedaphic organisms are found deeper in the litter often are less pigmented and have reduced sensory and springing organs (Eisenbeis & Wichard 1985; Wallwork 1976). Most soil mites are mainly hemiedaphic; living in the organic layer associated with the soil surface (Wallwork 1967). Seasonal changes in distribution have been seen for some organisms. Collembola have been found to peak in abundance in autumn with their lowest abundance in summer, although different species can vary in the timing of their peak abundances (Hale 1976).

Arthropods vary in their feeding habits. Coleoptera can be predaceous, saprophagous, and coprophagous and their diets can vary depending on the life stage. Diptera can be parasitic, insectivorous, coprophagous, herbivorous, and saprophagous or scavengers. Mites can be predaceous, herbivorous or saprophagous (Raw 1967). Soil-dwelling arthropods including collembola, beetle larvae, certain termites and ants can be saprophages or detritivores and get their nutrition from eating large volumes of soil containing dead and decaying vegetable and animal debris, although it may be the soil-associated fungal and bacterial microorganisms which are being selected (Gullan & Cranston 2000; Raw 1967; Wallwork 1976).

Microarthropod densities have been found to be higher close to rhizospheres; the rhizosphere of a plant is the zone including root hairs, mycorrhizae and rhizobacteria. Collembola, along with other microarthropods can be beneficial to plants because they aid in the transport of beneficial fungi to and bacteria and removal of harmful fungi and bacteria from the rhizosphere during selective grazing by the collembola on root and subterranean fungi, including pathogenic fungi. The interactions between microarthropods and fungi could make certain elements available for plants to utilize because of the mineralization of nitrogen and phosphates by microarthropods, although this relationship is not fully understood (Gullan & Cranston 2000).

There are many other potential causes of arthropod distributions including moisture content, temperature, light, and presence and distribution of resources or predators. McCoy (1987) found that Polopinus species were negatively correlated with reptilian predators of arthropods.

Arachnids that are associated with soil and litter are spiders, mites and pseudoscorpions (*Pseudoscorpiones*). Spiders living in the soil zone are mostly tubular web spinning spiders such as Atypidae, Clubionidae, Eresidae, Agelenidae, Hahniidae as well as migratory spiders such as jumping (Salticidae) and wolf spiders (Lycosidae) (Eisenbeis & Wichard 1985; Wallwork 1976). Although spiders and pseudoscorpions are strictly carnivorous (the latter mainly eating mites, collembola and nematodes) and are major predators of other soil fauna, there is a wide array of dietary groups for mites, including parasitism and predation (Wallwork 1976). Predatory mites generally feed on the same prey as pseudoscorpions. Other predators of soil fauna include certain ants, and adult Carabid (Carabidae) and rove (Staphylinidae) beetles (Eisenbeis & Wichard 1985; Wallwork 1976).

### **Fire Effects on Sandhill Litter and Soil Fauna**

The effects of fire on arthropods function through various mechanisms, at different times. Immediate effects of fire can be direct mortality (Miller 1955), forced emigration (Gillon 1970), and immigration of pyrophilous species attracted to the smoke or heat of fires. Short term effects after fires can include fire-induced changes to the habitat which can strongly affect food quality and accessibility (Benzie 1986; Evans 1984; Rice 1932; Schowalter 2000), foraging sites (Andersen 1988, 1991), predation rates (Knutson & Campbell 1976; Schowalter 2000), microclimate (Andersen 1991; Samways 1990) and composition of predator and detritivore communities (Agee 1993; McCoy 1987). Longer term effects include changes in ecosystem processes, including primary production and nutrient cycling (Miller 1955).

Often there are small or no long-term effects of fire on ordinal-level abundances of arthropods in temperate woodlands and open forests of south Australia (Andersen & Muller 2000), but fire management can sometimes have large effects on insects and their mediated processes in North America. One study that has found outbreaks of herbivorous insects resulting from fire suppression in North American forests also found that the outbreak, in turn, can lead to increased vulnerability of the forests (McCullough et al. 1998). Another study found that fire suppression resulted in a decrease in the abundance of ants while late fires resulted in a reduction in spider, homopteran and silverfish abundances. Overall, most fauna were not found to be affected by fire (Andersen & Muller 2000).

There has been some concern that repeated prescribed burns may be detrimental to invertebrate populations (Dietrich et al. 1998; Opler 1981; Reed 1997; Swengel 1994, 1996) but it seems that this may not always be the case. Although Hanula (2003) found the lowest diversity and evenness in the one-year fire frequency plots and highest in the control plots, Friend (1996) found that the overall composition of assemblages were often resilient to fire, even if substantial changes in arthropod abundances at the species level occurred. A greater number of hemiptera and homoptera were found on burned sites than unburned sites in one study (Cancelado & Yonke 1970). Higher biomass of herbivorous arthropods was also found on burned versus unburned sites (Nagel 1973). It has been found that fire intervals of 2 to 3 years do not affect species richness or composition. Most populations, especially those arthropod populations that are common in an area, have been found to recover within a growing season, although some may take up to 2 years or more (Hanula 2003; Panzer, 2002). Uncommon species recovery time may take longer or not occur at all (Bess et al. 2002).

In a study of prescribed burning effects on spider and carabid beetles, it was found that the effects of burning can differ within taxonomic families. It was found that four out of seven spider families were more abundant on unburned sites than burned, while three of the seven families were more abundant on burned sites. It was also found that four of five beetle families were more abundant on unburned sites, while there was no difference found for the other family. Although abundances differed, species richness and diversity did not differ significantly for either spiders or carabid beetles (Niwa & Peck 2002).

It does seem important for conservation of soil arthropods in fragmented habitats to provide for the various needs of the different arthropods in a habitat. It is also important to include different intensities and timing of prescribed burns and to include areas without burns to allow for recruitment (Hanula 2003; Howe 1994; Panzer 2002; Swengel 1996). Perhaps the optimal fire frequency of 3 years found for many prairie-inhabiting birds (Swengel 1996) could be compatible with that of arthropods on fragmented land as well (Panzer 2002).

The dry sand of sandhill makes it a target for development. Fire suppression, logging, habitat destruction for development, as well as other human induced modifications have decreased Longleaf pine/Turkey oak sandhill habitat to about 3% of its historic range. Considering Florida and Georgia, in acreage alone, it has been estimated that a 90% decrease in sandhill acreage has occurred in the last 60 years (Jensen & Carson 2001).

Maintaining the existing sandhill habitat is essential to conserving this species-rich habitat. This is a difficult task because of the ever looming threat of past and present land usage and development and because of the necessity for regular low intensity fires (Jensen & Carson 2001).

In this thesis I will address the question of whether sandhill soil and litter-dwelling arthropod communities differ depending on prescribed fire frequency, time since fire, seasonal and/or amount of leaf litter. It is hypothesized that time since the last fire and amount of leaf litter will affect the arthropod communities more than fire frequency or season. The amount of time since the last fire is predicted to affect community composition the most because it affects canopy cover and amount of leaf litter which could affect the composition of the litter-dwelling arthropods.

## METHODS

The study site was located within the University of South Florida Ecological Research Area (USF Eco Area figure 1), which is located in west-central Florida. It is composed of approximately 200 ha of pine flatwoods, riverine swamp, and Longleaf pine (*Pinus palustris*)/turkey oak (*Quercus laevis*) sandhill. Sandhill occurs in approximately 20 ha of the USF Eco Area (Schmidt, 2005). Longleaf pine and slash pine (*Pinus elliotti*) dominate the overstory and turkey oaks dominate the midstory, along with scattered cabbage palms (*Sabal palmetto*). An understory is composed of mostly wiregrass, *Aristida stricta*, forbs and saw palmetto (*Serenoa repens*) (Mushinsky, 1992; Mushinsky, 1985). About 12.4 ha of the sandhill habitat along the southern border of the USF Eco Area is divided into experimental burn plots. Since the mid-1970s, the plots have been subjected to different prescribed fire regimes. Prescribed burns occur in one-year, two-year, five-year and seven-year intervals and there are two replicates of each treatment. Two reference plots have not been burned since at least 1965 (Mushinsky, 1985). Plot sizes range from approximately 0.7 to 1.9 ha (Figure 2).

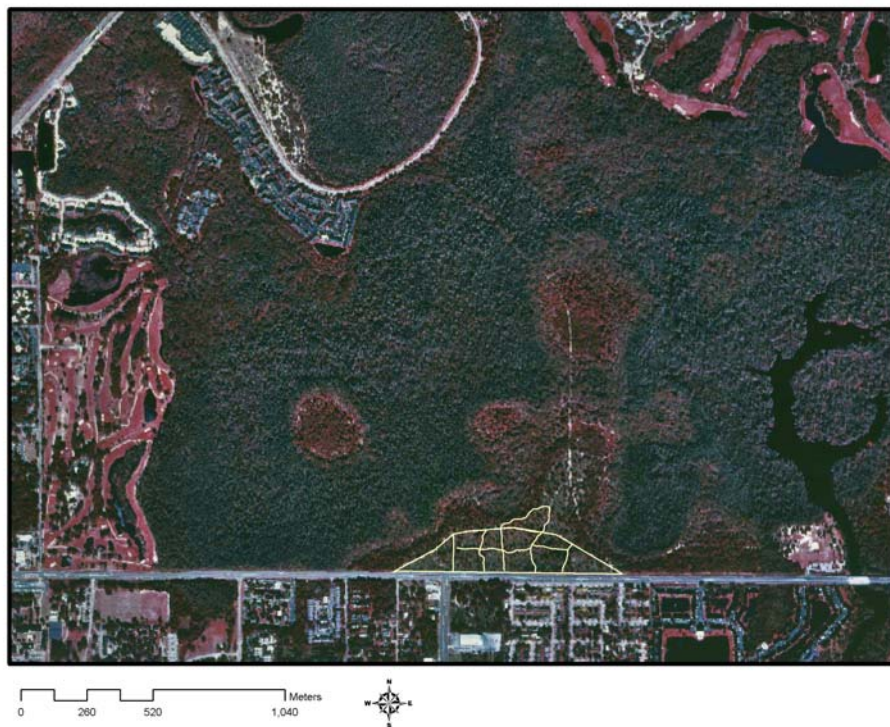


Figure 1. Aerial photograph of the University of South Florida Ecological Research Area in northeast Tampa, FL. The experimental sandhill plots used in this study are outlined in yellow.

Although the intended prescribed fire frequencies are in one-, two-, five-, and seven-year intervals, the actual fire frequencies have not always followed this pattern. Appendix A shows the actual fire frequencies in the USF Eco Area. Delays in burn dates occurred for some plots and there were no burns in some years. There were no burns in 1994, 1995, 1997, 2000, 2001, 2002, 2004 or 2005. The delays were associated with the lack of burn for 1997, 1999, 2000 and 2001. There was a one year delay for the two and seven-year burn plots intended to be burned in 1997 and delays of 3 years for the one-year plots intended to be burned in 1999. The two-year and five-year plots intended to be burned in 2000 and 2001, respectively, were burned three and two years late, respectively. The last fire occurred in 2003, at which time the one-, two-, and five-year plots were burned.

### Experimental Design

There were five regularly-spaced sample locations in each plot/treatment, approximately 20-30 m apart. The five sample locations were set up to allow for a representative sample of the different areas in each treatment, while trying to keep the distance between each sample far enough so that the sample locations would not influence the others. This resulted in five treatments: Reference, 1-year, 2-year, 5-year and 7-year fire frequencies and two replicates: East and West (Figure 2). There were a total of seven sampling occasions. Sampling occurred in September (leaf litter only), and November of 2004, and in January, April, August, November of 2005.

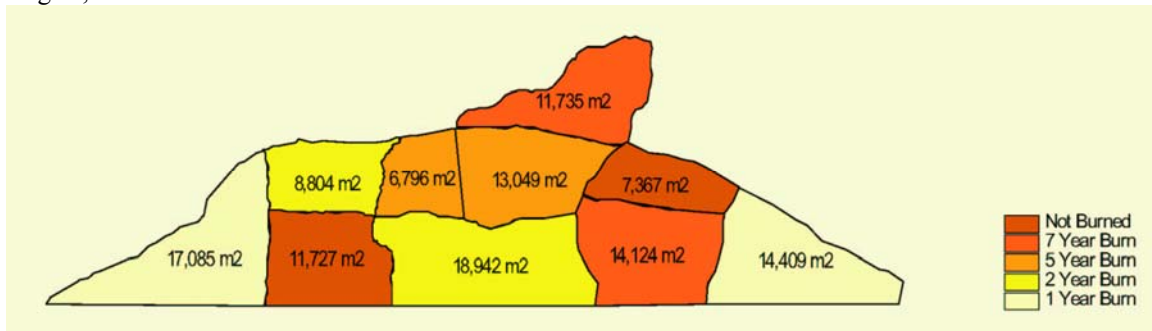


Figure 2. Map of the burn plots. By Emily Minor {, 2000 #142}. Based on GPS points of the outline of the plots; the areas are calculated by ArcView based on those data

In each treatment five small pitfall traps (16 oz plastic cups) were set in the ground with the top of each cup flush with the ground. These cups were filled with about half an inch of antifreeze to preserve the specimens. The pitfall traps were shaded with 2 gallon bucket lids, propped up with sticks, and were left out for 5 consecutive days during each season (Figures 3 and 4). Between seasons, the pitfall traps were closed. The traps were checked daily when open. If rain occurred and the cups were more than 1/3 full of water, the contents were collected and the trap reset. If disturbance occurred, the traps were repaired and reset.



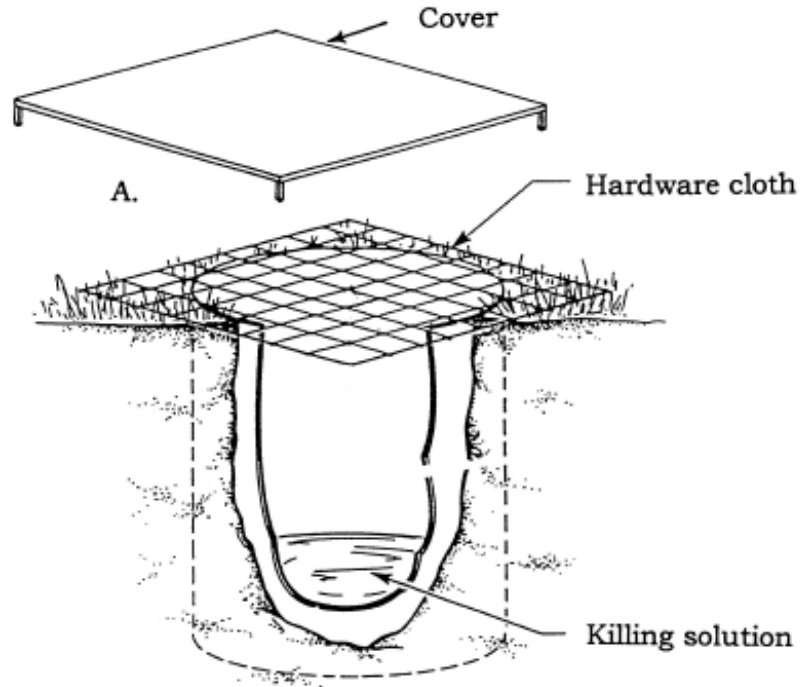


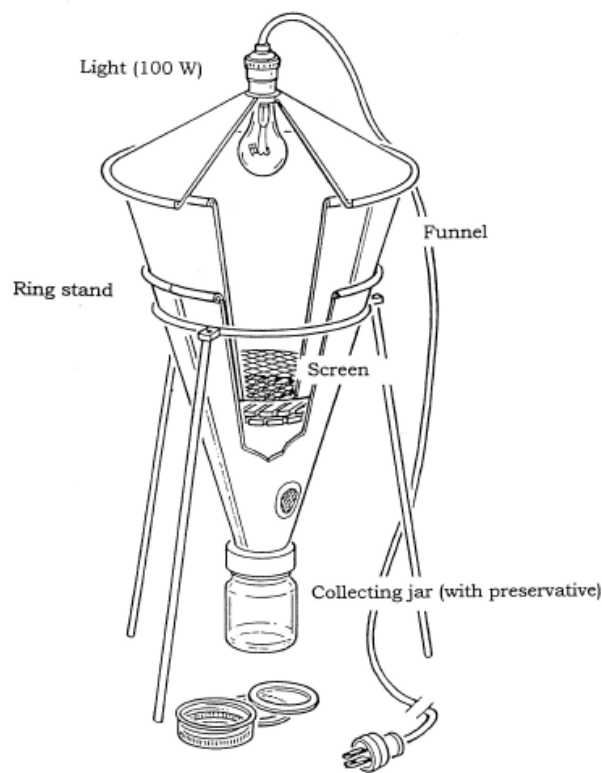
Figure 3. The general set up of a pitfall trap. The traps used in this study contained antifreeze as the killing solution and did not have a hardware cloth mesh covering.



Figure 4. The presentation of a pitfall trap. The pitfall traps used in this study were 16oz plastic cups, filled 1/8 full of antifreeze. A two gallon bucket lid, propped up by sticks was used to shield the trap contents from sun and rain.

Leaf litter was sampled using a 625 cm<sup>2</sup> quadrat made from PVC pipes, which allowed one or two plots to be sampled for leaf litter each day during the time that pitfall traps were checked for damage or inundation with rain water. The quadrat was thrown haphazardly near each of the five sample areas per plot, and all leaf litter within the quadrat was collected. These samples were brought back to the lab on the same day they were collected. The mass and major vegetation type of each leaf litter sample were recorded for the April, August and November samples.

To extract the arthropods from the leaf litter Tullgren funnel traps (Sutherland, 1996) were used. The traps had 100 watt bulbs that functioned to drive the arthropods out of the leaf litter and into the 70% ethanol preservative in the collecting jars below the funnel (Figures 5-7). The collecting jar of the funnel traps were composed of 16 ounce plastic cups filled with approximately one inch of ethanol. Leaf litter was left in the trap for 24 hours. The ethanol and preserved arthropods were poured into a vial and stored in a refrigerator. The samples were then presorted to extract the arthropods from the alcohol and leaf litter debris. The arthropods were placed into a smaller vial filled with ethanol (70%). Arthropods were later identified into taxonomic order.



(Quayle, 2001)

Figure 5. Tullgren funnel apparatus. The apparatus used in this experiment consisted of a beaker and a plastic funnel with hardware cloth screen.



Figure 6. Tullgren funnel set up for this experiment. Each 16 oz cup contained about an inch of 70% alcohol. Hardware cloth with mesh size 0.25 inch was used as a screen in the funnel. A 100 watt light bulb is placed directly over the funnel to drive insects down into the alcohol.



Figure 7. Tullgren funnel trap station.

## Data Analysis

### *Univariate Statistics*

Order richness (S) was calculated as the number of arthropod orders. Diversity indices were employed to measure diversity using the number of orders in the sample and the evenness of their distribution for the different treatments. Order abundances were calculated and used to calculate Shannon-Wiener coefficients of diversity ( $H'$ ), Hills number 1 ( $N_1$ ) and Hills number 2 ( $N_2$ ). The Shannon-Wiener index  $H' = -\sum_i p_i \log(p_i)$  was used because variances can be calculated and t-tests can be used to determine if the values are significantly different. Shannon-Wiener is also one of the diversity indices with the best discriminatory ability and ease of computation (Clarke and Warwick 2001).  $N_1$  is a transformation of the Shannon-Wiener diversity index:  $[\exp(H')]$  and  $N_2$  is the reciprocal of the Simpsons diversity index:  $[1/\lambda]$ . Hill's evenness index ( $H_e$ ) was used to calculate the evenness of relative abundances. Hill's numbers were used because they are easier to interpret than other diversity index values (Hill 1973).

A univariate ANOVA was used to test for treatment effects of fire frequency, and time since the last fire on arthropod abundance, the number of arthropod orders present for all seasons pooled and for seasons separately. Shannon-Wiener index values were used to statistically analyze the data using a univariate ANOVA (Clarke and Warwick 2001). ANOVA tests were performed on arthropod abundances from each plot to test for the effect of fire frequency on the arthropod abundance. The different fire frequencies were the different levels of the burn factor. Although the data are not normal and do not have homogeneity of variance, post-hoc multiple comparison test that do not assume homogeneity of variances are not very efficient and do not have high power. ANOVA is robust to heterogeneity of variances and non-normality of data, so post-hoc multiple comparison tests that assume homogeneity of variances can be used (Zar 1999).

If one uses an  $\alpha$  of 0.05 for an ANOVA and computes multiple t-tests, the probability of committing a type I error is increased for the entire experiment. Because of this, it is often invalid to perform multiple t-tests. Post-hoc tests use  $\alpha$  levels that are more conservative than 0.05. These are used so that, if the null hypothesis is rejected, the chance of committing a type I error is still 0.05 and not higher. If an ANOVA is found to be significant, Post-hoc tests are used to compare all groups (Madrigal 1998). There is no consensus as to which post-hoc procedure is the best to use but the Student-Newman-Keuls, Tukey's and Tukey's b tests are common methods. Tukey's test is one of the more robust of the multiple comparison tests and it was used in my analyses (Zar 1999).

A repeated measures ANOVA was used to test for differences within Shannon-Weiner diversity index values between sampling periods (Zar 1999). This would account for time effects and lack of independence of replicates over time. If there was a time effect, this effect can be accounted for and then a test for treatment effect can be done.

Spearman Rank Correlations were employed to test for correlations between arthropod abundance, number of arthropod orders, separately, and then leaf litter mass and fire frequency treatments and years since last fire, separately. The Spearman Rank correlation coefficient,  $r_s$ , is an estimate rank correlation coefficient for the population and ranges from -1 to +1 (Zar 1999).

Spearman Rank Correlations were employed to test for correlations between Shannon-Wiener diversity values and leaf litter mass treatments and leaf litter mass treatments and arthropod abundances.

The Friedman two-way analysis of variance is similar to a repeated measures ANOVA in that it was used to test for different community compositions among fire frequencies and time since the last fire (Zar 1999).

The nonparametric Kendall's coefficient of concordance (W) tests for agreement among rankings of all groups being considered. W values range from 0 for no agreement to 1 for full agreement among the ranking of all groups or complete (Zar 1999).

The Wilcoxon signed-rank test was used to test the symmetry of dispersion and is a nonparametric alternative to the paired Students t-test (Zar 1999).

### ***Multivariate Statistics***

Similarity between sampling units (traps, plots and fire frequency treatments) was measured with the Bray-Curtis index (Bray and Curtis 1957) using the dispersion weighted, square-root transformed counts of order abundances to decrease the relative importance of overdispersed or highly clumped orders and to reduce the effects of very abundant orders, respectively (Clarke et al. 2006).

Dispersion weighting is a procedure that addresses the differences in the variance structure of individual order counts. Dispersion weighting downweights only the overdispersed or clumped orders, thereby, increasing the importance of rarer but consistent orders which have a more Poisson-like distribution. The clumped order counts were divided by their average index of dispersion  $D$ , which is the average variance to mean ratio for treatment groups, in order to get Poisson like values. Without changing the relative differences between mean responses within treatment groups, dispersion weighting results in a matrix with a Poisson-like variance structure across all orders. Dispersion weighting downweights counts with high variability, thereby causing a small increase in power which can increase the significance in ANOSIM tests of group differences. The downweighting of highly variable counts is similar to increasing power in univariate statistics by decreasing error (Clarke et al. 2006).

The order similarity matrix was generated from which later multivariate analyses in PRIMER (Primer-E) were performed. The unweighted group average method of cluster analysis was used to identify groups of traps, plots, and treatments with the most different community compositions. Post-hoc randomization was performed using the similarity profile test (SIMPROF) of PRIMER. SIMPROF performs 1000 random rearrangements of each variable, separately, across the samples to test for significant differences in the composition of the community at each cluster dendrogram node (Clarke and Gorley 2006). For ordination, non-metric multi-dimensional scaling (MDS) was used as suggested by Ludwig and Reynolds (1998). The nonparametric analysis of similarities (ANOSIM) was performed to test for different community compositions among plots, fire frequencies and time since last fire treatments (Clarke et al. 2006).

The RELATE routine of PRIMER was used to test for directional change in community composition by comparing the Bray Curtis similarity matrix to a constructed model matrix. Separate model matrices were constructed for burn frequency and the number of months since fire between all pairs of plots. Each model matrix was correlated with the Bray Curtis similarity matrix.

Similarity equals one if two samples are completely similar and equals zero if the two samples have no orders in common. Similarities between replicates within a site are expected to be higher than the similarities between replicates at different sites. Two orders are considered similar if they are represented at a significant amount of same sites and dissimilar if they never occur together (Clarke and Warwick 2001).

The Bray-Curtis similarity coefficient was used because of its common use in ecology and because it is one of the few measurements that can satisfy the following conditions: when two samples have no orders in common it takes the value of zero, when an order is absent from the two samples and is included or excluded, the value is unchanged. The similarity between samples A and B are not changed if a third sample, C, is included or excluded in the data array and when the relative abundances for all orders are the same, it is elastic enough to show differences in total abundance for two samples as an imperfect similarity. Many of the other coefficients that also satisfy these criteria are either too similar to the Bray-Curtis coefficient or have drawbacks that make them undesirable (Clarke and Warwick 2001).

Overall, the similarity measurement was utilized in order to replace the original data set with a pairwise similarity matrix that will be easier to work with for further analyses. The similarities are chosen to reflect similarity in arthropod abundances in the community (Clarke and Warwick 2001). The similarity matrix was used to differentiate between sites and times. The similarity indices were used because they take into account shared order abundances, thereby decreasing any distortion caused by inadequately sampled rare species. Similarities within each group are expected to be higher than those between groups.

The program PRIMER was used to measure the similarities in order abundances or richness in different treatments (PRIMER-E 2006). This was used to measure the number of orders and individuals common to the communities compared. Similarities within and among treatment groups were calculated, using the Bray-Curtis coefficient and the absolute data values between every pair of the samples in the data matrix. Values range from 0-1, arranged in a similarity matrix. The similarity matrix is a triangular arrangement of similarities between every pair of orders. It describes the pattern of occurrences of all orders in combination across the given set of samples (Clarke and Warwick 2001).

The unweighted group average cluster method with a SIMPROF post-hoc randomization procedure was used to perform cluster analysis to group plots and treatments with similar communities. Clustering was used because the similarity matrix was too large to easily determine patterns of similarity. Replicate samples within a site that form a cluster that is distinct from replicates within other sites can be considered to have different community compositions from the other sites. Sites or times can then be put into groups with similar community structure and order assemblages can be defined. (Clarke and Warwick 2001).

The non-metric multi-dimensional scaling (MDS) ordination technique was performed to produce a graphical representation of the degree of similarity between sites (Clarke and Warwick 2001). Ordination techniques arrange data in relation to axes so that the relative positions of the data to each other, and to the axes, give the most information about their similarities. Ordination brings large data sets to simpler one-, two-, or S-dimensional figures that can be used to visualize similarity among communities (Krebs 1999). The relative placement of samples on the ordination map reflects the similarity of their communities. Distances between samples on the ordination axes are a reflection of the dissimilarities in the community structures (Clarke and Warwick 2001).

To test for different community compositions among plots, fire frequency and time since last fire treatments, analysis of similarities (ANOSIM) was used. ANOSIM is analogous to the parametric analysis of variance procedure (ANOVA). ANOSIM was used because there are fewer assumptions to satisfy than there are for ANOVA.  $R$  is the test statistic for ANOSIM and it contrasts the differences among rank similarities *between* treatments with differences among replicates *within* treatments.  $R = 1$  if all rank similarities within treatments are more similar than rank similarities between treatments.  $R = 0$  if the null hypothesis of no treatment effects occurs. ANOSIM performs permutations of all possible arrangements of variable labels and calculates an  $R$  statistic for each arrangement. ANOSIM calculates an  $R$  statistic among all treatments, which is called the Global  $R$ . If the Global  $R$  is significant,  $R$  statistics are then calculated for each pairwise permutation of the treatments (Clarke and Warwick 2001).

To test for directional change in community composition, the Bray Curtis similarity matrix was correlated with a constructed model matrix using the RELATE routine of PRIMER. A Monte Carlo randomization procedure calculates the Spearman rank correlation of the model matrix and Bray Curtis matrix and performs 999 permutations of random rearrangements of plot labels in the Bray Curtis matrix and calculates a  $p$  statistic for each arrangement. (Clarke and Gorley, 2006). The test statistic for RELATE is the  $p$  statistic. When  $p$  is greater than 0.95, a very high degree of correlation between the model and Bray Curtis matrices exists (Clarke and Warwick 2001).

Similar model matrices were constructed for fire frequency and months since the last fire between all trap pairs and the RELATE procedure was performed for their correlations to the Bray Curtis similarity matrix.

## RESULTS

### Overall

A total of 15735 individuals from 14 orders, sampled over five occasions, were used in the analyses (Table 1). Arthropod abundance values ranged from 688 to 7689 individuals per sampling occasion (Table 1), and 2264 to 3554 for each fire frequency treatment across all sampling occasions (Tables 2-6).

Collembola, hymenoptera and acariformes were the most abundant orders. Collembola had a peak abundance of 5559 in August 2005. Hymenopteran abundance peaked in April and August 2005 (1004 and 1126, respectively). Acariformes peaked in abundance in January 2005 with 681 individuals. These orders were the most abundant in the winter months as well. Spiders joined collembola and hymenoptera as dominators in spring, while collembola dominated in summer, followed by hymenoptera.

Arthropod abundance was higher in the most frequently burned treatment and the unburned reference treatment (one- and over 30 year fire frequencies) than in the intermediate fire frequencies (two-, five-, and seven-year fire frequency) (Table 2).

Arthropod abundances increased over time across all fire frequency treatments until August 2005, with one exception (the seven-year fire frequency in April 2005) (Table 5).

Shannon-Weiner diversity was not different among fire frequency treatments ( $p$ : 0.091). The time since the last fire did affect Shannon-Weiner diversity during the January 2005 ( $p$  = 0.031), and April 2005 sampling occasion ( $p$  = 0.013).

Shannon-Weiner diversity was not correlated with leaf litter mass treatments. The arthropod community distribution of plots was generally even (Table 3).

Arthropod abundances in the November 2004 sampling occasion were positively correlated with fire frequency ( $r_s$ : 0.900,  $p$ : 0.031) and time since the last fire ( $r_s$ : 0.894,  $p$ : 0.041). In all other sampling occasions arthropod abundances were not correlated with fire frequency or time since the last fire. Arthropod abundances were not correlated with leaf litter mass treatments.

The Friedman and Kendall's  $W$  test revealed that arthropod abundances were different, overall, among sampling occasions across fire frequencies ( $p$ : 0.001). Specifically, the Wilcoxon test revealed that arthropod abundances were different for the November 2004 and January 2005, April and August 2005, August and November 2005, and for the November 2004 and November 2005 sampling occasions ( $p$ : 0.063 for each pair) across fire frequencies.

The mean number of orders ranged from 10-12 orders for fire frequency treatments overall (Table 8) and varied for each sampling occasion (Table 9).

The number of arthropod orders in any of the sampling occasion was not correlated with fire frequency. The number of arthropod orders in the January 2005 sampling occasion was positively correlated with time since the last fire ( $r_s$ : 0.894,  $p$ : 0.041). In all other sampling occasions the number of arthropod orders was not correlated with time since the last fire.

The number of arthropod orders was different, overall, among sampling occasions across fire frequencies ( $p$ : 0.043). The number of arthropod orders was different for the November 2004 and January 2005 sampling occasions ( $p$ : 0.077) and for the November 2004 and November 2005 sampling occasions ( $p$ : 0.042) across fire frequencies.

Leaf litter mass in all sampling occasions where leaf litter mass was recorded was positively correlated with fire frequency (Table 13). Leaf litter mass was also correlated with time since last fire for the April and August 2005 sampling occasions ( $r_s$ : 0.894,  $p$ : 0.041 for both).

Leaf litter masses were different, overall, among all sampling occasions across fire frequencies ( $p$ : 0.074) and time since last fire ( $p$ : 0.074). Specifically, leaf litter masses were different for the April and November 2005 sampling occasions across fire frequencies ( $p$ : 0.043) and time since last fire ( $p$ : 0.043). Leaf litter masses from the August 2005 and November 2005 sampling occasions were different among time since last fire treatments ( $p$ : 0.003 and  $p$ : 0.013, respectively).

### ***Dispersion***

The dispersion weighting downweighted the highly variable orders. Dispersion weighting corrected for the clumped distributions of arthropods. The data indicate that all orders have significantly aggregated patterns of dispersion (all  $D$  values are greater than 1 (Table 14)).  $D$  is the degree to which an individual order tends to be aggregated. The null hypothesis of random dispersion is supported if  $D = 1$ . The resulting dispersion weighted similarity matrix is found in Appendix B.

### ***Cluster analysis***

The cluster analyses of community composition among experimental plots indicated two major groups. One group is made up of plots with the more extreme fire frequencies: 1 year and 7 years between fires and unburned plots. The other group is made up of plots with more the intermediate fire frequencies of 2 and 5 years between fires. All two- and five-year plots were burned one year prior to data collection, as well as the one-year plots (SimProf at  $\alpha = 0.05$ ) (Figure 8).

Cluster analysis dendrogram of experimental traps. The X-axis is labeled with traps. Solid lines indicate significant differences among plots at  $p = 0.05$ . Symbols indicate the amount of years since the last fire. There are two major groups. One group consists of the CWE trap, one of the traps that has not been burned for at least 30 years. The other group consists of all other traps with all the other times since last fire: 1 year, 7 year or at least 30 years (Figure 9).

### ***MDS***

The results of the nonmetric multidimensional scaling of experimental plots indicate significantly different groups. One group is made up of plots with fire frequencies of two- and five-years. The other group is made up of the other plots with fire frequencies of one-, seven-, and greater than 30-years. The goodness-of-fit is high, indicated by the stress measure of 0.05. Higher goodness of fit is indicated by lower stress (figure 10).

The results of the nonmetric multidimensional scaling of experimental traps indicate loose groups. The goodness-of-fit is relatively low, indicated by the stress measure of 0.24. Lower goodness of fit is indicated by higher stress (figure 11).

### ***ANOSIM***

The results of the two-way nested ANOSIM using traps as samples indicate no effect of plots on arthropod abundances (Global  $R = -0.042$ ,  $p = 0.731$ ; 999 permutations). Arthropod abundances in the fire frequency treatments were different when considering traps as samples (Global  $R = 0.67$ ,  $p = 0.002$ ; 945 permutations) which allowed a one-way ANOSIM to be performed with traps as samples.

The results of the one-way ANOSIM indicate that arthropod abundances were different among plots across all fire frequency treatments (Global  $R = 0.21$ ,  $p = 0.002$ ; 999 permutations) (Table 17). Community composition was different between unburned reference plots and all plots burned in November 2003, and between the seven year fire frequency and the two and five year treatments (Table 18).



### ***RELATE***

The results of the RELATE procedure, randomized Spearman Rank correlation values of similarities among fire frequency treatments, indicate a correlation of Bray-Curtis similarities among plots and the pattern of differences among fire frequency treatments ( $\rho = 0.356$ ,  $p = 0.021$ ; 999 permutations).

The results of the Relate procedure, randomized Spearman Rank correlation values of similarities among years since the last fire, indicate a strong correlation of Bray-Curtis similarities among plots and the pattern of differences among years since fire ( $\rho = 0.492$ ,  $p = 0.007$ ; 999 permutations).

### ***Repeated Measures ANOVA***

Multivariate Tests indicate no significant effect of season on arthropod diversity ( $p = 0.121$ ).

Tests of within-subjects effects indicate an effect of season on arthropod diversity for all criterion ( $p = 0.001$ ,  $0.008$ ,  $0.044$ ) but no effect of the interaction of season and plot ( $p = 0.465$ ,  $0.459$ ,  $0.451$ ) (Table 15). Post hoc tests did not indicate any difference among burn frequencies ( $p = 0.124$ ).

### ***Seasonal***

#### ***Cluster analysis***

Without any a priori knowledge, the results of the cluster analysis that was performed for the seasonal data indicated that arthropod abundances from plots within similar sampling occasions were generally more similar to one another than to plots from different sampling occasions. If another sampling occasion was found within a group, it was usually a sampling occasion adjacent to that of the group. Any outliers that were present were closest to the group of the same sampling occasion (Figure 12).

### ***MDS***

The results of the nonmetric multidimensional scaling indicate a general pattern of change over time, with the exception of the November 2005 sampling occasion. Again, samples clumped together in groups from the same sampling occasion. Samples within the same sampling occasions also became more similar as time goes on (stress = 0.13) (Figure 13).

### ***ANOSIM***

The results of the 2-way crossed ANOSIM indicate no difference among fire frequency groups across all sampling occasions (Global  $R = 0.048$ ,  $p = 0.308$ ; 999 permutations).

Tests for differences among sample occasions indicated that sampling occasions were different across all fire frequency groups. (Global  $R = 0.538$ ,  $p = 0.001$ ; 999 permutations). All sampling occasions were different except November 2004 and Jan 2005, and August 2005 and November 2005 (Table 16).

### ***Results of RELATE Spearman rank correlation***

The results of the Relate procedure, randomized Spearman Rank correlation values of similarities among for time of year, indicate a correlation of Bray-Curtis similarities among plots and the pattern at each time of year. ( $\rho = 0.078$ ,  $p = 0.076$ ; 999 permutations).

The results of the Relate procedure, randomized Spearman Rank correlation values of similarities among months since fire, indicate a correlation of Bray-Curtis similarities among plots in each sampling occasion and the pattern of differences among months since fire ( $\rho = 0.078$ ,  $p = 0.076$ ; 999 permutations).

### Traps

Table 1. 15735 individuals used in the analyses. The data from the September 2004 sampling occasion were not included in the analyses because pitfall traps were not employed during that sampling occasion.

	Number of Individuals
Nov-04	688
Jan-05	1785
Apr-05	2167
Aug-05	7689
Nov-05	3406
<b>Total</b>	<b>15735</b>

Table 2. Total and Mean Arthropod Abundance per Fire Frequency.

Fire Frequency	Total Abundance	Mean Abundance
One Year	3554	710.8
Two Year	2727	545.4
Five Year	2264	452.8
Seven Year	3318	663.6
Reference – No Fire	3413	682.6

Table 3. Diversity, Richness and Evenness measures. S is the number of orders represented. N is the number of individual arthropods represented. H' is the Shannon-Weiner diversity index, N1 and N2 are Hills Diversity indices, respectively. E5 is the evenness index. J' is the Jaccard evenness index.

Plot	S	N	J'	H'(loge)	1-Lambda'	N1	N2	E5	Fire Frequency (years)	Years Since Fire
1E	14	2347	0.44	1.16	0.51	3.21	2.05	0.48	1	1
1W	14	1419	0.64	1.69	0.76	5.41	4.08	0.70	1	1
2E	13	1650	0.44	1.13	0.52	3.09	2.06	0.51	2	1
2W	14	1116	0.55	1.46	0.65	4.32	2.85	0.56	2	1
5E	13	1306	0.50	1.29	0.59	3.63	2.46	0.56	5	1
5W	14	1079	0.56	1.49	0.68	4.43	3.15	0.63	5	1
7E	13	2179	0.58	1.49	0.65	4.45	2.82	0.53	7	7
7W	14	1518	0.63	1.67	0.74	5.33	3.84	0.66	7	7
CE	14	1889	0.58	1.54	0.72	4.66	3.56	0.70	30	30
CW	13	2169	0.62	1.59	0.69	4.88	3.25	0.58	30	30

Table 4. Leaf litter mass is found to increase from April 2005 to August 2005 from means of 97.34g to 126.76g. The leaf litter mass between August 2005 and November 2005 were similar.

Sampling Occasion	S	N	J'	H'(loge)	1-Lambda'	N1	N2	E5	Total Leaf Litter Mass (g)	Mean Leaf Litter Mass (g)
Nov-04	13	627	0.52	1.34	0.65	3.81	2.88	0.67	N/A	N/A
Jan-05	14	2030	0.71	1.87	0.80	6.49	4.91	0.71	N/A	N/A
Apr-05	14	2093	0.62	1.64	0.72	5.16	3.54	0.61	486.71	97.34
Aug-05	14	7565	0.37	0.98	0.44	2.67	1.77	0.46	633.80	126.76
Nov-05	14	3318	0.49	1.29	0.53	3.63	2.14	0.43	616.06	123.21

Table 5. Arthropod Abundances per Fire Frequency.

<b>Fire Frequency</b>	<b>Nov-04</b>	<b>Jan-05</b>	<b>Apr-05</b>	<b>Aug-05</b>	<b>Nov-05</b>
One Year	53	406	585	1841	669
Two Year	33	194	303	1373	824
Five Year	118	165	443	1151	387
Seven Year	166	502	330	1479	841
Reference – No Fire	257	406	432	1721	597

Table 6. Mean Arthropod Abundances per Time Since Last Fire.

<b>Time Since Last Fire</b>	<b>Nov-04</b>	<b>Jan-05</b>	<b>Apr-05</b>	<b>Aug-05</b>	<b>Nov-05</b>	<b>Total</b>
One Year	68	255	444	1455	627	2849
Seven Years	166	502	330	1479	841	3318
Reference > 30 Years	257	406	432	1721	597	3413

Table 7. Mean Arthropod Order Richness per Fire Frequency.

<b>Fire Frequency</b>	<b>Mean Order Richness</b>
One Year	12
Two Year	10
Five Year	10
Seven Year	12
Reference – No Fire	12

Table 8. Mean Order Richness per Sampling Occasion.

<b>Fire Frequency</b>	<b>Nov-04</b>	<b>Jan-05</b>	<b>Apr-05</b>	<b>Aug-05</b>	<b>Nov-05</b>
One Year	6	13	13	14	14
Two Year	5	10	12	12	13
Five Year	9	8	13	10	12
Seven Year	9	14	13	13	13
Reference – No Fire	7	14	12	13	13

Table 9. Total and Mean Leaf Litter Mass for each Plot and Sampling Occasion.

<b>Sampling Occasion</b>	<b>Plot</b>	<b>Total (g)</b>	<b>Mean(g)</b>
Apr-05	1E	273	54.6
	1W	200	40.0
	2E	300	60.0
	2W	204	40.8
	5E	325	65.0
	5W	657	131.4
	7E	634	158.5
	7W	627	125.4
	CE	437	87.4
	CW	1070	214.0
<b>Apr-05 Overall</b>		<b>4727</b>	<b>472.7</b>
Aug-05	1E	386	77.2
	1W	419	83.8
	2E	300	60.0
	2W	400	80.0
	5E	446	89.2
	5W	530	106.0
	7E	786	157.2
	7W	432	86.4
	CE	996	199.2
	CW	1643	328.6
<b>Aug-05 Overall</b>		<b>6338</b>	<b>633.8</b>
Nov-05	1E	371	74.2
	1W	444	88.8
	2E	467	93.4
	2W	463	92.6
	5E	644	128.8
	5W	350	70.0
	7E	1151	230.2
	7W	725	145.0
	CE	645	129.0
	CW	746	186.5
<b>Nov-05 Overall</b>		<b>6006</b>	<b>600.6</b>

Table 10. Mean Leaf Litter Mass per Fire Frequency.

<b>Fire Frequency</b>	<b>Mean Leaf Litter Mass (g)</b>
One Year	69.77
Two Year	71.13
Five Year	98.40
Seven Year	149.84
Reference – No Fire	189.72

Table 11. Mean Leaf Litter Mass per Fire Frequency for each Sampling Occasion.

<b>Sampling Occasion</b>	<b>Fire Frequency</b>	<b>Mean Leaf Litter Mass (g)</b>
Apr-05	1 Year	47.30
	2 Year	50.40
	5 Year	98.20
	7 Year	140.11
	Reference - No Fire	150.70
Aug-05	1 Year	80.50
	2 Year	70.00
	5 Year	97.60
	7 Year	121.80
	Reference - No Fire	263.90
Nov-05	1 Year	81.50
	2 Year	93.00
	5 Year	99.40
	7 Year	187.60
	Reference - No Fire	154.56

Table 12. Mean Leaf Litter Mass per Time Since Last Fire.

<b>Time Since Last Fire</b>	<b>Mean Leaf Litter Mass (g)</b>
One Year	79.77
Seven Years	149.84
Reference – No Fire	189.72

Table 13. Spearman Rank correlations for leaf litter mass and fire frequency for sampling occasions where leaf litter mass was recorded.

<b>Spearman Rank Correlations for Leaf Litter</b>		
	<b><math>r_s</math></b>	<b>P</b>
Apr-05	1.0	> 0.001
Aug-05	0.9	0.037
Nov-05	0.9	0.37

Table 14. Dispersion weighting is used to downweight highly variable orders. The null hypothesis of random dispersion is supported if  $D = 1$ .

<b>Index of Dispersion (D) Coefficients</b>			
	<b>D</b>	<b>Sig%</b>	<b>Divisor</b>
Collembola	109.176	0.000	109.176
Acariformes	23.183	3.381 E-187	23.183
Spiders	1.987	0.009	1.987
Formicidae	11.908	3.148 E-83	11.908
Hymenoptera	5.004	8.450 E-24	5.004
Diptera	3.492	2.414 E-12	3.492
Coleoptera	4.977	1.375 E-23	4.977
Homoptera	1.450	1.700	1.450
Hemiptera	1.959	0.000	1.959
Thysanoptera	9.632	5.830 E-63	9.632
Psocoptera	5.099	0.000	5.099
Isoptera	2.963	0.000	2.963
Blattodea	2.159	0.000	2.159
Orthoptera	1.998	0.008	1.998

Null = dispersion is random ( $D = 1$ ). Significant: not random ( $\% > 5$  = not significant;  $p > 0,05$ )

## Plots

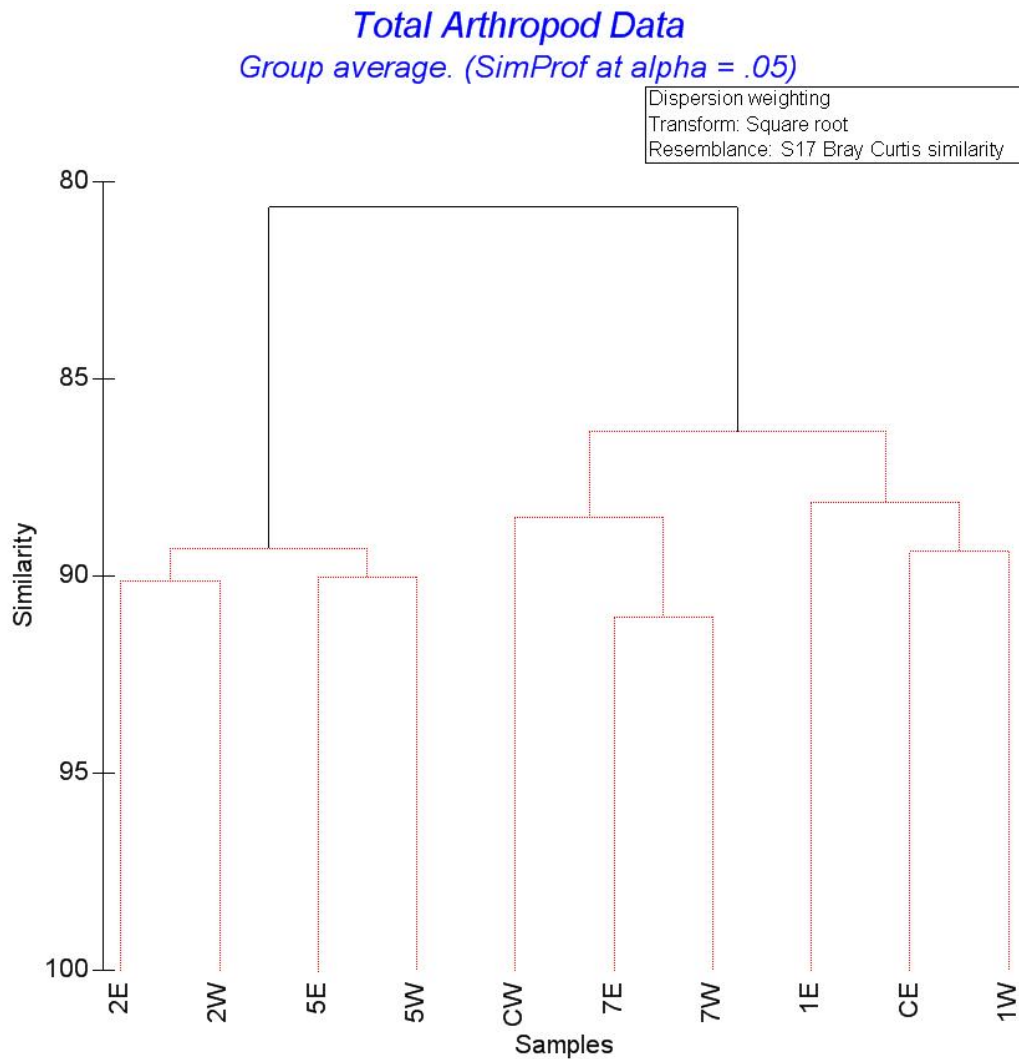


Figure 8. Cluster analysis dendrogram of arthropod community composition among experimental plots. Labels indicate plot. Solid lines indicate significant differences among plots at  $p = 0.05$ . There are two major groups. One group consists of plots with the more extreme fire frequencies: 1 year and 7 years between fires and unburned plots. The other group consists of plots with more intermediate fire frequencies of 2 and 5 years between fires. All two- and five-year plots were burned one year prior to data collection, as well as the one-year plots.

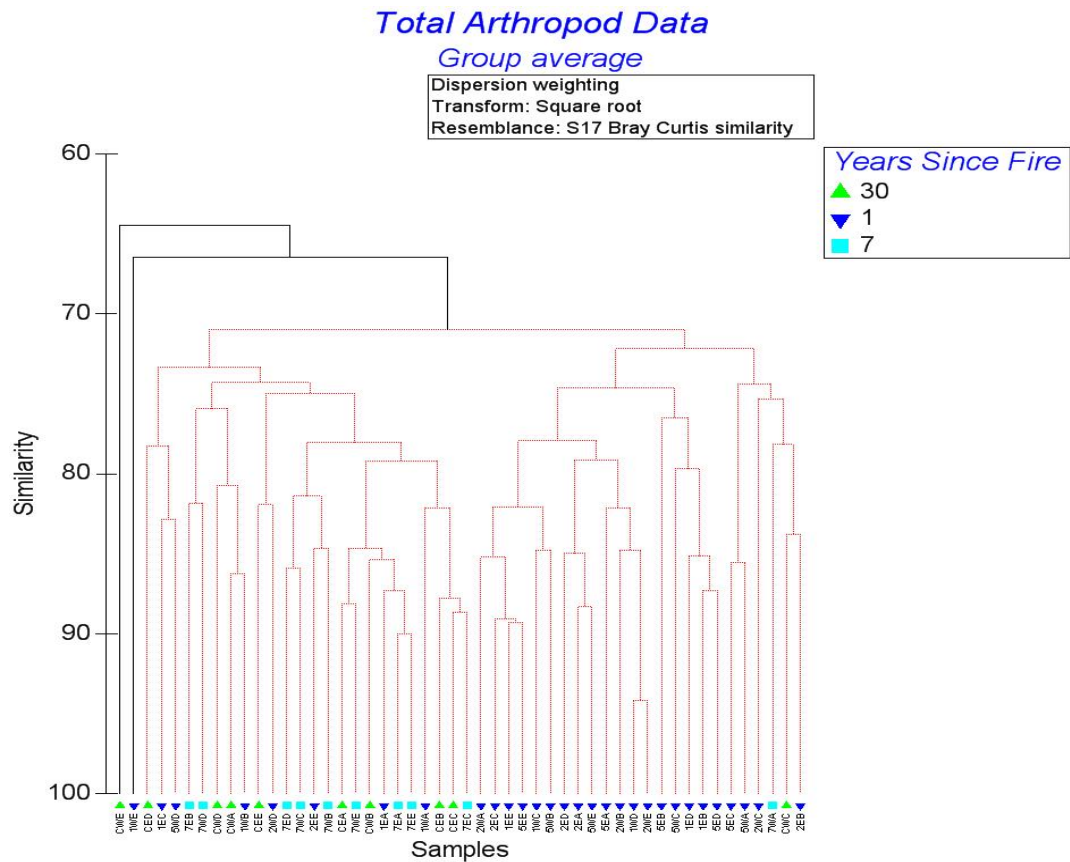


Figure 9. Cluster analysis dendrogram of experimental traps. X-axis is labeled with traps. Solid lines indicate significant differences among plots at  $p = 0.05$ . Symbols indicate the amount of years since the last fire. There are two major groups. One group consists of the CWE trap, one of the traps that has not been burned for at least 30 years. The other group consists of all other traps with all the other times since last fire: 1 year, 7 year or at least 30 years.



*Bray-Curtis Similarity Between Plots*  
*85% Similarity contour delineates significantly different groups (SimProf at alpha = .05)*

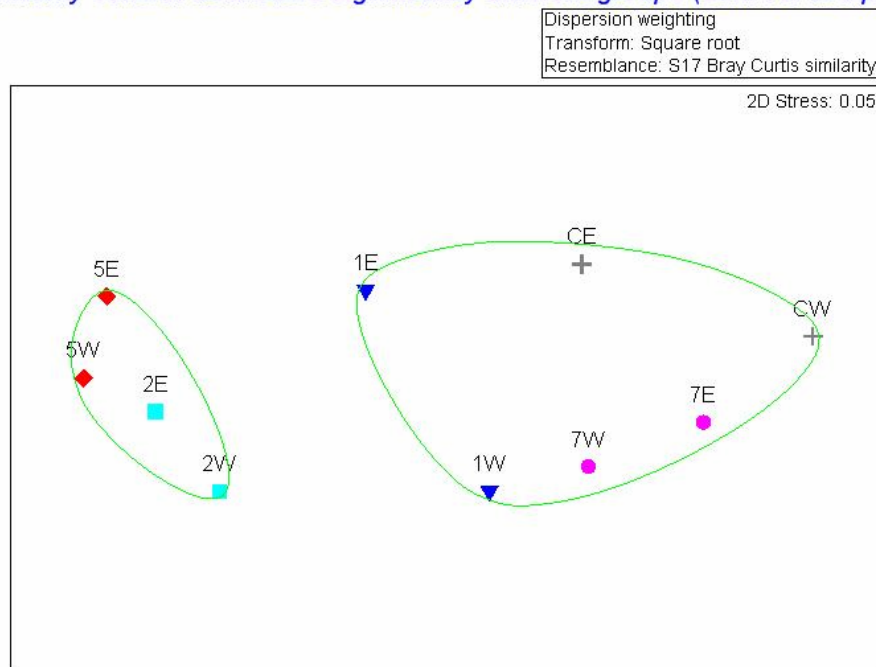


Figure 10. Plot of nonmetric multidimensional scaling of experimental plots. Plot designations are labeled with colors and shapes. Dark blue triangles refer to plots with 1 year fire frequencies, teal squares refer to plots with 2 year fire frequencies, red diamonds refer to plots with 5 year fire frequencies, purple circles refer to plots with 7 year fire frequencies, and gray plus signs refer to the reference plots without a fire for at least 30 years. Contour lines indicate significantly different groups (SimProf at alpha = 0.05). The goodness-of-fit is high, indicated by the stress measure of 0.05. Higher goodness of fit is indicated by lower stress.

## Traps

### **Arthropod Communities by Burn Frequency - Sampling Occasions Pooled**

*Data points represent trap arrays*

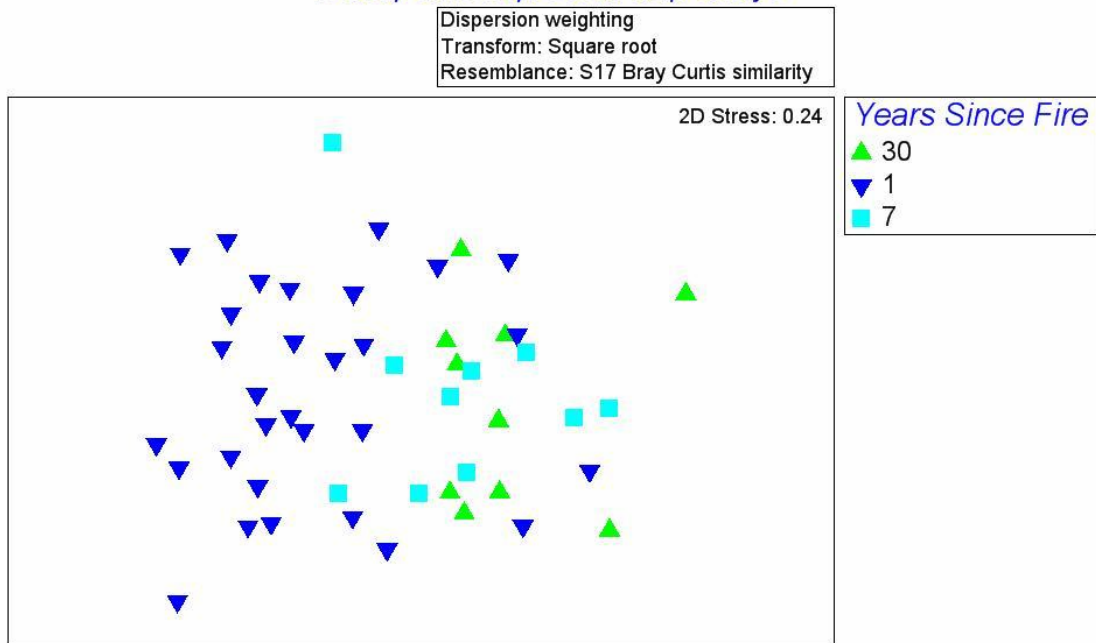


Figure 11. Plot of nonmetric multidimensional scaling of experimental traps. Trap designations are labeled with colors and shapes. Dark blue triangles refer to plots that were burned 1 year prior to data collection, teal squares refer to plots that had not been burned for 7 years prior to data collection, and red diamonds refer to plots that have not had a fire for at least 30 years prior to data collection. The goodness-of-fit is relatively low, indicated by the stress measure of 0.24. Lower goodness of fit is indicated by higher stress.

Table 15. Repeated measures analysis of variance (MANOVA) for differences within fire frequencies between sampling periods. Tests of Within-Subjects Effects indicate significant effects of season.

Source	Measure	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power(a)
Season	Sphericity Assumed	1.891	4	0.473	7.161	0.001	28.643	0.98
	Greenhouse-Geisser	1.891	2.333	0.811	7.161	0.008	16.703	0.88
	Huynh-Feldt	1.891	4	0.473	7.161	0.001	28.643	0.98
	Lower-bound	1.891	1	1.891	7.161	0.044	7.161	0.577
Season * DumPlot	Sphericity Assumed	1.111	16	0.069	1.052	0.451	16.834	0.448
	Greenhouse-Geisser	1.111	9.33	0.119	1.052	0.459	9.817	0.3
	Huynh-Feldt	1.111	16	0.069	1.052	0.451	16.834	0.448
	Lower-bound	1.111	4	0.278	1.052	0.465	4.209	0.166
Error (Season)	Sphericity Assumed	1.32	20	0.066				
	Greenhouse-Geisser	1.32	11.663	0.113				
	Huynh-Feldt	1.32	20	0.066				
	Lower-bound	1.32	5	0.264				
a	Computed using alpha = .05							

## Seasonal

Nov 04 - Nov 05 (PF+LL)

Group average

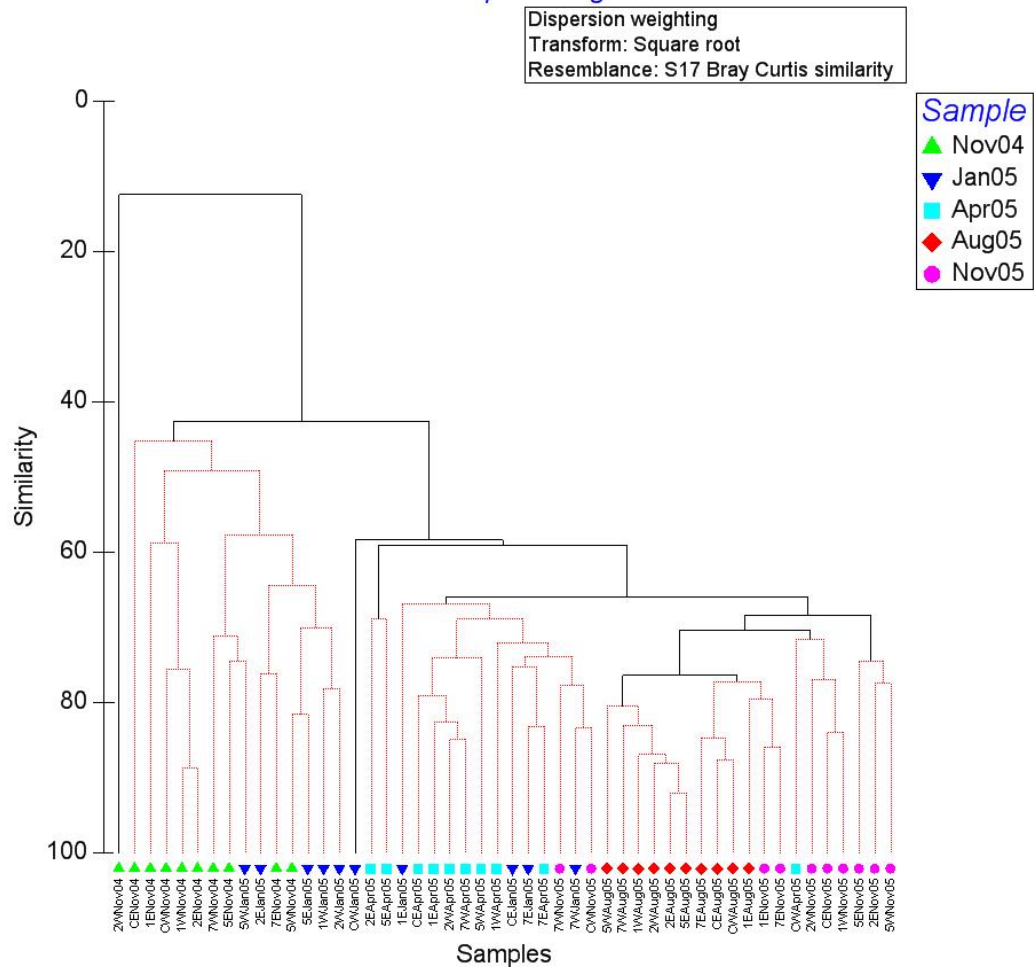


Figure 12. Cluster analysis dendrogram of plots for each sampling occasion. X-axis is labeled with plots for each sampling occasions. Solid lines indicate significant differences among plots at  $p = 0.05$ . Plots seem to clump with other plots of the same sampling occasion with the exception of a few plots which are usually from an adjacent sampling occasion. Any outliers that are present are closest to the group of the same sampling occasion.

## MDS

The results of the nonmetric multidimensional scaling of sampling occasions indicate seasonal groupings that correspond with arthropod abundance.

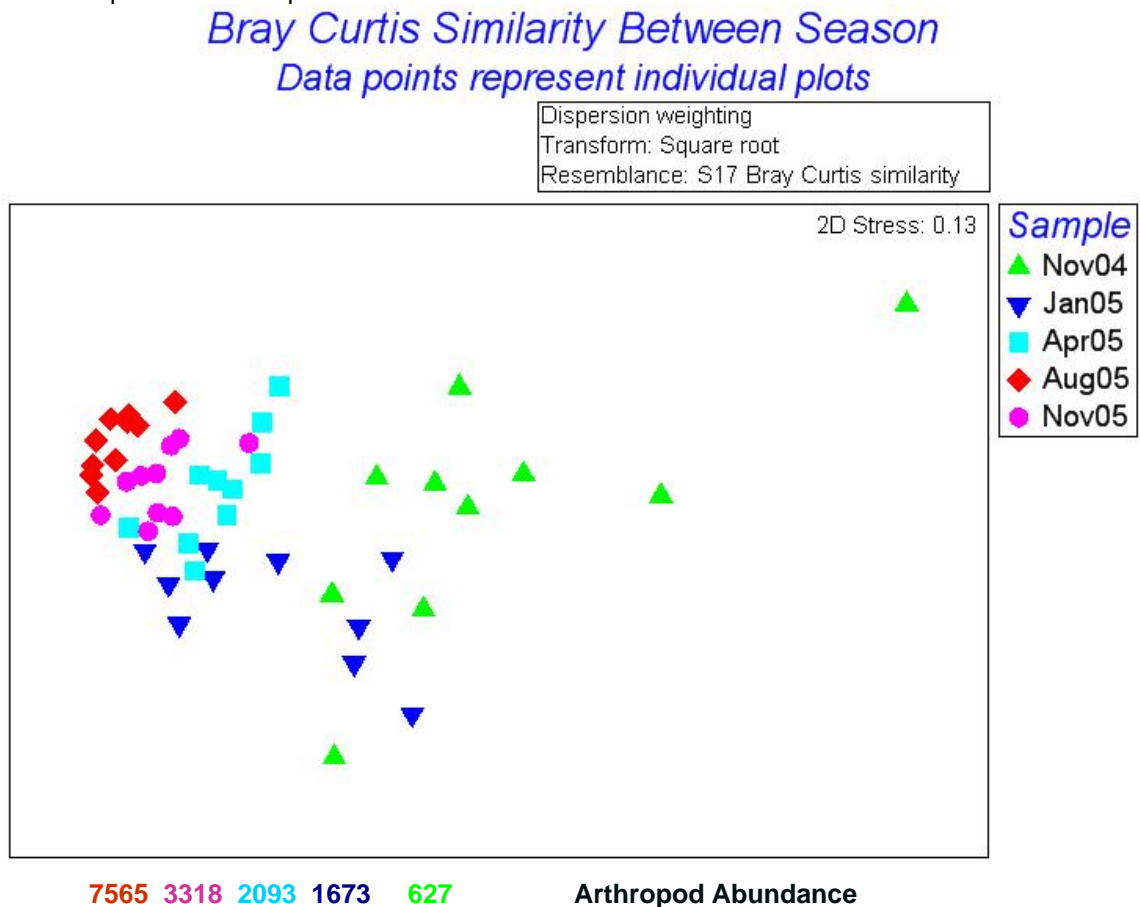


Figure 13. Plot of nonmetric multidimensional scaling of sampling occasions. Sampling occasion designations are labeled with colors and shapes. The goodness-of-fit is relatively good, indicated by the stress measure of 0.13. Higher goodness of fit is indicated by lower stress.

## Two-Way Crossed ANOSIM: Seasonal

Table 16. Pairwise tests of sampling occasions across all fire frequency groups.

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	#>=Obs
Nov04, Jan05	0.4	0.095	243	243	23
Nov04, Apr05	0.6	0.016	243	243	4
Nov04, Aug05	0.95	0.004	243	243	1
Nov04, Nov05	0.7	0.004	243	243	1
Jan05, Apr05	0.6	0.012	243	243	3
Jan05, Aug05	0.8	0.004	243	243	1
Jan05, Nov05	0.65	0.016	243	243	4
Apr05, Aug05	0.6	0.008	243	243	2
Apr05, Nov05	0.5	0.025	243	243	6
Aug05, Nov05	0.4	0.074	243	243	18

# **One Way ANOSIM: Seasonal**

Table 17. Pairwise tests of sampling occasions.

Groups	R Statistic	Sig Level %	Possible Permut	Actual Permut	#>=Obs
Nov04, Jan05	0.392	0.001	92378	999	0
Nov04, Apr05	0.598	0.001	92378	999	0
Nov04, Aug05	0.793	0.001	92378	999	0
Nov04, Nov05	0.693	0.001	92378	999	0
Jan05, Apr05	0.409	0.001	92378	999	0
Jan05, Aug05	0.752	0.001	92378	999	0
Jan05, Nov05	0.514	0.001	92378	999	0
Apr05, Aug05	0.755	0.001	92378	999	0
Apr05, Nov05	0.455	0.001	92378	999	0
Aug05, Nov05	0.546	0.001	92378	999	0

Table 18. Pairwise tests of fire frequency and arthropod abundances.

Groups	R Statistic	Sig Level %	Possible Permut	Actual Permut	#>=Obs
30, 1	0.15	2.5	92378	999	24
30, 2	0.412	0.1	92378	999	0
30, 5	0.587	0.1	92378	999	0
30, 7	0.074	9.8	92378	999	97
1, 2	-0.003	45.6	92378	999	455
1, 5	0.083	9.5	92378	999	94
1, 7	0.072	11.5	92378	999	114
2, 5	-0.054	76.4	92378	999	763
2, 7	0.318	0.3	92378	999	2
5, 7	0.455	0.1	92378	999	0

## DISCUSSION

Fire determined the number of arthropods and the community composition without affecting the species-abundance distribution. When all sampling occasions were pooled, arthropod abundance and Shannon-Wiener diversity were not affected by fire frequency. This result has been found in other studies as well. In an inland mixed conifer forest, although abundances differed, species richness and diversity did not differ significantly for either spiders or carabid beetles (Niwa & Peck 2002). Community composition in my study, however, was affected by fire frequency. This is because orthopterans were more abundant in plots that were burned in November 2003, while all other orders of arthropods were more abundant in plots that were not burned recently. Orthopterans increase in abundance shortly after fire (Kerstyn & Stiling 1999; Knight & Holt 2005). Fire increases biomass of herbaceous vegetation (Glitzenstein et al. 2003) and quality of forage (Radho-Toly et al. 2001). The experimental plots were relatively small, which may have allowed many arthropods that respond positively to fire to move into areas with higher fire frequencies and those that respond negatively to move into areas with lower fire frequencies.

Arthropod abundance and diversity were affected by season. At different times of the year arthropod abundances and diversity were different. Certain groups of orders peaked at different times of the year. Orders that peaked in summer and fall (late in the vegetative growing season) included collembolans, orthopterans, coleopterans and dipterans. Many of these orders feed on vegetation and their peaks in abundance follow peaks in new vegetative growth. Orders that peaked in the dormant season (late fall through spring) included isopterans, psocopterans, mites and thysanopterans. Many species in these groups feed on dead plant matter which is more abundant in the dormant season. Two groups peaked in abundance during the early growing season: hymenopterans and spiders. Many hymenopterans and all spiders are predaceous and their peaks in abundance may be tracking peaks in abundance of their prey. It is also likely that many species in these orders may be responding to annual variation in climate, such as summer rainfall, which can vary significantly from one year to the next at the study site (Halstead 2007).

The effects of fire on arthropods function through various mechanisms that occur at different times. Immediate effects of fire can be direct mortality (Miller 1955), forced emigration (Gillon 1970), and immigration of pyrophilous species attracted to the smoke or heat of fires. Short term effects after fires can include fire-induced changes to the habitat which can strongly affect food quality and accessibility (Benzie 1986; Evans 1984; Rice 1932; Schowalter 2000), foraging sites (Andersen 1988, 1991), predation rates (Knutson & Campbell 1976; Schowalter 2000), microclimate (Andersen 1991; Samways 1990) and composition of predator and detritivore communities (Agee 1993; McCoy 1987).

Because orders peak in abundance at certain times of the year, the season in which plots are burned may have different effects on arthropod communities. Orders and life stages that are dispersal-limited may be negatively affected if fires occur when they are near their peak abundance or at their lowest abundances. A dormant season fire may affect some orders more than others, and vice versa. Season of fire affects plant communities. Dormant season fires can allow hardwoods to persist at greater distances (Myers 1990). Changes in plant species composition associated with timing of fire are also very likely to affect community compositions of arthropods utilizing these plant species.

Arthropod responses to disturbance can vary. Lepidopteran, detritivore and predator abundances decreased while sap-sucking insect abundances increased in response to canopy-opening disturbances such as hurricanes and timber harvesting (Schowalter 1994; 1995). Grasshopper (Kerstyn & Stiling 1999; Nagel 1973), leaf miner (Kerstyn & Stiling 1999) and herpetofaunal (Mushinsky & Gibson 1991; Halstead 2007) abundances were found to be higher in the more frequently burned plots at this study site. Friend (1996) found that the overall composition of assemblages were often resilient to fire, even if substantial changes in arthropod abundances at the species level occurred.

Differing time since the last fire, which is known to affect species diversity, could be attributed to the mixed results found (Gibson & Hulbert 1987; Mehlman 1992). It has been found that fire intervals of 2 to 3 years do not affect species richness or composition. Most populations, especially those arthropod populations that are common in an area, have been found to recover within a growing season, although some may take up to 2 years or more (Hanula 2003; Panzer, 2002). Uncommon species recovery time may take longer or not occur at all (Bess et al. 2002). With the exception of mites, every order increased in abundance from November 2004 to November 2005. This may suggest that post-fire recolonization may still have been occurring. As noted earlier, however, these increases in abundance may be a result of annual environmental variation.

Leaf litter mass increased with increasing time since the last fire, but was not correlated with diversity. Perhaps time since the last fire has an indirect effect on diversity. The amount of time since the last fire affects leaf litter mass, which then affects diversity. In January 2005, it had been 14 months since the last fire. This meant that leaf litter was allowed to accumulate during that time. In April, even more time had passed, allowing more leaf litter to accumulate. Perhaps this affected the arthropod community.

It is not known why diversity in November 2004 was not affected by the amount of time since the last fire. Because the November 2004 sampling occasion was closest to the most recent burn date, one might expect differences in diversity to be stronger and lessen as plots became more similar in successional stage. However, it is also possible that because different arthropods are active at different times of the year, arthropod community composition may be more sensitive to the amount of leaf litter in January and April than in August and November.

Studies have been inconsistent in determining the relationship between fire and diversity. The relationship between arthropod abundance, diversity and community composition and fire could be too subtle to detect with the experimental design used, or there could have been low power attributed to the relatively small number of replicated treatments and the short sampling period of the study. Although not possible in the site where the research was conducted, additional replication beyond that of east and west would be a way to increase sample size.

Sampling only occurred over a 12 month period. A longer period of sampling would have increased the sample size and decreased any variation attributed to sampling. For reasons beyond my control, the prescribed fire that was intended for 2005 never occurred, therefore, immediate responses after a fire were not able to be observed. If there had been a longer sampling period, perhaps sampling would have occurred just before and after the next prescribed fire to detect more immediate changes in the arthropod communities. Data collection also didn't begin until a year after the most recent fire. Immediate effects of fire are probably strongest and they were probably missed.

In a study of prescribed burning effects on spider and carabid beetles, it was found that the effects of burning can differ within taxonomic families (Niwa & Peck 2002). The level of taxonomic classification needed to understand the patterns of a community can differ among organisms (Hirst 2006). Although not possible in this study because of lack of funding, identifying arthropods to a finer taxonomic resolution than order may have been more effective for understanding the patterns of diversity, arthropod abundance and community composition in the sandhill community that was studied. Organisms within taxonomic families such as coleoptera differ so much in their environmental requirements, and tolerances that genus level identification may be necessary for this analysis. It is likely, given the large number of species within orders and the broad range of ecological responses of individual species, that species-specific responses may be hidden by the broad taxonomic level.

It does seem important for conservation of soil arthropods in fragmented habitats for land managers to provide for the various needs of the different arthropods in a habitat. It is also important to include different intensities and timing of prescribed burns and to include areas without burns to allow for recruitment (Hanula 2003; Howe 1994; Panzer 2002; Swengel 1996). Perhaps the optimal fire frequency of 3 years found for many prairie-inhabiting birds (Swengel 1996) could be compatible with that of arthropods on fragmented land as well (Panzer 2002).



Arthropods in the sandhill habitat of the USF ecological research areas seem to respond more strongly to seasonality than to fire frequency. Fire frequency may be important but likely it may be more important at certain types of year or to certain groups of arthropods. A lot of the response to fire may have been masked by the low taxonomic resolution, low replication, short sampling period and length of time passed between the last fire and the beginning of sampling.

Further study should include a longer sampling period including periods immediately before and after a fire. This would allow for observation of seasonal effects and immediate effects of fire. It would also allow for separation of the time since the last fire and fire frequency treatments, something that was unable to be done in this study because all the recently burned plots were also the most frequent burn treatments. Analysis of pitfall and leaf litter traps separately would also be helpful because they seemed to target different compositions of arthropods.

Arthropods should also be identified to at least the family level and maybe even the genus level if possible. There is almost as much diversity in several of the larger families of beetles as is found in the entirety of most of the other arthropod orders (Arnett 2000). To conserve time and resources, perhaps beetles could be used as a subset of the arthropods present to test for differences at a higher taxonomic resolution. Replication which includes other areas of sandhill habitat would also help to increase the power of the study. If these changes were included in the next study, perhaps the response of sandhill soil and leaf litter dwelling arthropods to fire may be better understood.

A quote by Friend (1996) seems to sum up this study most eloquently, “invertebrate populations are so variable in time and space, being largely driven by environmental factors, that the impacts of fire may be largely over-ridden and almost impossible to predict. This is particularly the case where a broad level of taxonomic resolution is adopted.”

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## **APPENDICES**



## APPENDIX A: DATES OF PRESCRIBED BURNS AT THE USF ECO AREA

Before 1976, burns were inconsistent and may have been natural fires. Data were obtained by inspection of maps by Bruce Williamson. Check marks indicate intended prescribed burn schedule. Date of fire indicates when the actual fire occurred.

1968 2W burned 4/4

1971 2W burned 5/4

1976 5E, 5W, 7W burned 1/15

1979 1E, 2E burned 5/3

	1E	1W	2E	2W	5E	5W	7E	7W	Date of Fire
1979	✓		✓						5/3
1980	✓								5/29
1981	✓		✓		✓	✓	✓		6/10
1982	✓								5/15
1983	✓	✓	✓	✓				✓	5/27
1984	✓								5/29
1985	✓		✓						5/16
1986	✓	✓		✓	✓	✓			5/27
1987	✓	✓	✓	✓					6/25
1988	✓	✓							6/15
1989	✓	✓	✓	✓					6/16
1990	✓	✓					✓	✓	7/12
1991	✓	✓	✓	✓	✓	✓			7/18
1992	✓	✓							6/30
1993	✓	✓	✓	✓					7/20
1994	✓	✓							None
1995	✓	✓	✓	✓					None
1996	✓	✓			✓	✓			8/2
1997	✓	✓	✓	✓			✓	✓	None
1998	✓	✓	✓	✓			✓	✓	8/20 – 2 and 7 yr burned a year late
1999	✓	✓							8/28
2000	✓	✓	✓	✓					None
2001	✓	✓	✓	✓	✓	✓			None
2002	✓	✓							None
2003	✓	✓	✓	✓	✓	✓			10/27 – 1 yr plots burned 3 years late & 11/24 – 2 & 5 yr plots burned 3 and 2 years late, respectively
2004	✓	✓							None
2005	✓	✓	✓	✓			✓	✓	None

Revised from (Schmidt, 2005). Compiled September 1998, Updated March 2006

**APPENDIX B: DISPERSION WEIGHTED AND SQUARE ROOT TRANSFORMED SIMILARITY  
MATRIX**

Bray-Curtis Similarity Between Plots										
	CE	CW	1E	1W	2E	2W	5E	5W	7E	7W
CE										
CW	88.43									
1E	87.89	80.72								
1W	89.36	83.57	88.35							
2E	80.81	74.39	85.93	84.04						
2W	83.97	75.54	86.40	86.19	90.10					
5E	79.24	73.16	86.27	82.27	89.99	87.78				
5W	79.75	70.56	87.53	83.07	89.90	89.44	90.01			
7E	88.31	90.61	85.20	88.00	79.33	79.02	76.22	74.98		
7W	87.79	86.38	85.20	89.59	80.90	83.13	82.54	79.99	91.03	