THE IMPACT OF PINYON MORTALITY ON GROUND-DWELLING ARTHROPOD COMMUNITIES

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ABSTRACT

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Robert J. Delph

We documented the indirect impact of drought-induced mortality of pinyon pine (*Pinus edulis*) on ground-dwelling arthropod communities. Tree mortality alters microhabitats utilized by ground-dwelling arthropods through increased solar radiation, dead woody debris, and understory vegetation. Our major objectives were to determine if there were differences in species composition, richness and abundance of ground dwelling-arthropods associated with environments experiencing high or low pinyon mortality and whether specific microhabitats could account for differences. We predicted significant impacts on arthropod community dynamics due to the increased complexity of micro-habitats from both standing and fallen trees. Despite only moderate increases in the amount of area that experienced new microhabitats, there were significant differences in arthropod community composition between high and low pinyon mortality environments. Overall, 22% (51 taxa) of the arthropod community were identified as being indicators of high or low pinyon mortality. Thus, our study supported the notion that arthropods are responsive to disturbance events that lead to even moderate changes in the environment. However, areas of high tree mortality also contained lower tree densities, allowing for the possibility that intrinsic differences in woodlands that vary in susceptibility to drought-induced mortality plays a significant role in structuring ground-dwelling arthropod communities.

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Preface

This thesis was written for publication and will be submitted to Ecological Entomology. Sections of this thesis regarding fallen woody debris and ground vegetation will be used in other publications.

INTRODUCTION

Pinyon-Juniper Woodlands &Regional Drought

Pinyon-juniper woodlands are one of the most extensive vegetation types in western North America and cover approximately 19 million hectares (Evans 1988). *Pinus edulis* exists as a co-dominant with *Juniperus monosperma* throughout New Mexico. Within our study region pinyons comprise 55% of woodland canopy cover. Pinyons are a major food and habitat source for many vertebrate and invertebrate species; a decrease of this vegetation type could have dramatic consequences on species occurring in pinyon-juniper woodlands.

Since 1996, at least some areas of the southwestern US have experienced drought. The drought that occurred in 2002 was considered the worst drought in the western United States in 500 years (USGS 2004). Aerial surveys and ground studies in pinyon-juniper woodlands throughout the Southwest have shown regional death of pinyons from 2002-2003 (Breshears et al. 2005, Shaw et al. 2005) as a result of bark beetle outbreaks. Droughts can lead to increased frequency of insect herbivore pest outbreaks (Logan et al. 2003, Breshears et al. 2005) leading to altered forest ecosystems at local to regional scales (Ogle 2000, Breshears et al 2005), as a result of dominant plant mortality and major shifts in overall plant composition, distribution and abundance (Stephenson 1990). Pinyon pine grow regularly in arid climates and are known to be drought tolerant, however the drought in 2002-2003 was warmer than previous droughts in the 1950's (Breshears et al. 2005, Seager et al 2007) which lead to large scale pinyon mortality mostly driven by population outbreaks of bark beetles. Warmer summers and shortened

winters changes the phrenology of bark beetle life cycles allowing more generations to occur more rapidly in a single season leading to population outbreaks (Logan et al. 2003). The pinyon ips (*Ips confusus* (LeConte)) is a pinyon-specific bark beetle that bores through the bark and feeds on the cambium layer (Paine et al. 1997, Negron and Wilson 2003). Most conifers produce defensive resins, which normally prevents beetle attack under regular precipitation conditions. However, in drought conditions, resin production is reduced in conifers, enabling bark beetles to colonize trees.

Semi-arid systems, which are prevalent in the southwestern United States, are thought to be especially sensitive to drought (Allen and Breshears 1998, Hanson 2000, Mueller et al. 2005). Such systems have been known to tolerate low baseline water levels and may be particularly sensitive to climate changes (Risser 1995). Brown et al. (2001) suggest that these arid and semi-arid systems could serve as indicators of change that may later occur in other ecosystems. According to recent global climate change models, projected increases in temperature will lead to increased frequency and intensity of drought (Seager et al 2007, Easterling et al. 2000, Intergovernmental Panel on Climate Change 2001, Hoerling and Kumar 2004).

Ground-Dwelling Arthropod Communities

Arthropod communities can be highly responsive to temporal and spatial environmental changes, including climate (Larocque et al. 2001), habitat alteration (Intachat et al.1997, Ellis et al. 2001), topography, soil type, fire, and plant quality (Parmenter et al. 1989). Arthropods respond more quickly to environmental changes and management decisions than do larger, longer-living organisms. Small size, rapid

population growth, short life cycle, and high mobility make arthropods useful in detecting fine-scale spatial variation and short temporal changes. In assessing habitat quality, arthropod species often serve as indicators of both undisturbed (Morrison and Marcot 1995) and disturbed ecosystems (González-Megías et al. 2004), and can be surrogates of environmental gradients (Agosti and Alonso 2000).

Previous studies have been conducted on how stand structure (Breshears et al. 2005), and birds (Gottfried 2004, Wiggins 2005) have been affected by the large-scale pinyon mortality. There have been several studies showing the impacts of tree-stress on insect herbivores directly associated with pinyons (Cobb et al. 1997, Trotter et al., 2008), but very little work on the ground-dwelling arthropod community, which is indirectly associated with pinyons. Ground-dwelling arthropods constitute a large portion of arthropod communities in many habitats (Leather 2005) and are highly responsive to changes in microhabitat characteristics (Intachat et al.1997, Ellis et al. 2001). Ground-dwelling arthropods are comprised primarily by taxa represented by generalists, predators, and scavengers, dominated by ants, beetles, and spiders. Ants alone have been found to turn more soil than earthworms (Lyford 1963), while 35% of all herbaceous plants are dependent on ants to have their seeds dispersed (Beattie 1985). In addition to ants, other ground-dwelling arthropods such as Carabid beetles (Haila et al. 1994), Tenebrionid beetles (Parmenter et al. 1989), grasshoppers (Parmenter et al. 1991), and ground-spiders comprise the majority of ground-dwelling organisms and thus are considered indicator species of habitat quality (Willett 2001).

Objectives of the Study

Within our study region pinyons comprise 55% of woodland canopy cover. We therefore proposed that the die-off of pinyon would alter ground-dwelling arthropod abundance, species richness and community composition due to the conversion of live to dead pinyon crowns and increase complexity of micro-habitats from fallen woody debris and dead pinyons. The three major objectives were to; **1)** determine differences in species composition, relative abundances and species richness of ground dwelling-arthropods associated with environments experiencing high pinyon mortality and environments experiencing low pinyon mortality, **2)** identify arthropod species that were indicators of microhabitats characteristic of high- and low-mortality habitats, and **3)** Correlate habitat variables that distinguish high- and low-mortality habitats within the pinyon-juniper woodland that could account for differences in arthropod communities.

METHODS

Study Area

We selected six study sites in throughout the Middle Rio Grande Basin (MRGB) of New Mexico. The six sites were located in three areas of the MRGB that represented the north, central, and south portions of the basin (**Figure 1**). For each area the paired sites were comprised of a "high-mortality" site and a "low-mortality" site". The distance between areas was 80.4 km from south to central and 32.1 km between central and north. Paired sites were less than 10 km from each other. The low pinyon mortality sites were chosen based on visual observation where no more than 10% of pinyons within a 100 x

200 meter area were dead. The high pinyon mortality sites were chosen based on visual observation where more than 10% of the pinyons within a 100 x 200 meter area were dead.

Regional Weather

All study sites within the MRGB have experienced intense drought, causing high levels of pinyon mortality from an ensuing bark beetle infestation (Clifford et al. 2008, Floyed et al. 2007, Floyed et al. 2009). In 2002, pinyon-juniper woodlands throughout the region have experienced a 100-year drought. Interpolated PRISM (Parameter-elevation Regressions on Independent Slopes Model Parameter-elevation Regressions on Independent Slopes Model) data (Daly 2002) showed precipitation levels in the MRGB significantly ($P<0.001$) decreased 34% in 2002-2003 from pre-drought (1976-2001) conditions, then increased 35% during post-drought (2004 -2007) conditions (**Figure 2**). The reduced precipitation and concomitant pinyon mortality agree with the conclusion that drought-induced tree mortality occurred in the MRGB as it did regionally (Breshears et al. 2005). The resumption of normal precipitation in 2004 suggests that differences in arthropod communities between high-and low-mortality sites were likely due to primarily to tree mortality and not direct effects of drought on arthropods.

For each site we measured a number of habitat and stand structure traits to characterize high- and low- mortality sites. These included tree density, community composition of ground vegetation and arthropods between high and low levels of pinyon mortality.

Stand Structure

To determine if there were differences in tree density between high and low pinyon mortality areas, numbers of trees, tree species and status (e.g., alive or dead) were recorded in each control site (low mortality) and death site (high mortality). At each control and death site, sixteen 100 m^2 plots were chosen on a uniform grid. Pit-fall traps (n=32) were used as reference points for the grid and a single pitfall trap was designated as the center of each 100 m^2 plot (see methods below on pit-fall traps). In each plot, numbers of trees, tree species and tree status were recorded. Tree status was based on observation, whether the tree was dead or alive. On dead pinyons, percent foliage was measured to estimate how long the tree had been dead. Foliage density measurements are widely used as indicators of forest condition (Innes 1993) and have been used to assess impacts of climatic factors (Innes 1988), nutrient deficiencies (Hunter et al. 1991), insect herbivory (Sutton 1981, Lansberg 1989) and mammalian herbivory (Meads 1976, Leutert 1988, Payton et al. 1997) in forest systems. At least two observers would calculate percent foliage by assessing the degree of background light silhouetted by the canopy of the individual tree (Frampton 2000) then subtracting the amount of needles (foliage) present and subtracting it from the amount of bare trunk and stem visible, the average of these two estimates was recorded. This system also applies to the Kerns et al. (2005) method for estimating age of dead pinyons, which was also used for each dead pinyon in this study. Age of death was determined by giving each dead pinyon a classification A – G, where class "A" signified the least amount of time (~5 years) the tree has been dead, class "F" signified the most amount of time (~16 years) the tree has been dead and class "G" was given to trees that were too old to be dated accurately (See Kerns and Jacobi,

2005 method). In addition, the basal trunk diameter (BTD) was also measured for each tree to estimate stand age between sites and tree volume. Basal trunk diameter was measured where the trunk meets the roots just above the ground also known as the root collar diameter (RCD).

To test differences in ground cover, canopy height and width were measured in meters with the use of a meter pole. Canopy width was measured twice, one measurement perpendicular to the first measurement to get an accurate measurement of total width. At each site sixteen, 100 m^2 plots were measured for stand structure. A spherical densitometer device was used at every 100 m^2 plot, which has been used in many studies to accurately estimate forest overstory density (Lemmon 1956). Litter depth was also measured for each tree to obtain an estimate of overall ground cover beneath the canopy of each tree. Stand data was also taken in the intensive microhabitat plots in each region for each pit-fall trap to determine if tree type, architecture of the tree, and litter depth had direct affects on ground-dwelling arthropod abundance and community dynamics.

Understory and Intercanopy Ground Cover

To understand habitat characteristics that may explain differences in arthropod communities we measured five classes of ground cover; shrub, grasses, forbs, litter, and bare ground. Ground cover estimates have been used as a key indicator for rangeland health (USDI-BLM 1997). In each site, all 32 plots were measured for these five ground cover classes. Each plot was divided into four 25 m^2 sections. A 1 m^2 quadrat frame was randomly placed in three of these sections. Ground cover was estimated in each quadrat

by measuring the amount of area taken up by shrubs, grasses, forbs, leaf litter, rock, soil and other elements such as dead wood, moss and dung, then averaged to estimate total cover in each 100 m² plot (Oosting 1956, Cook & Stubbedieck 1986, ITT 1996). Plant specimens were collected and pressed for identification purposes along with digital photos taken of each plant species.

Dead & Down Woody Debris

To test the hypothesis that ground-dwelling arthropods would respond to the increase in habitat complexity from fallen woody debris in high pinyon mortality areas, numbers of dead, fallen branches, twigs and logs, along with the overall volume were recorded (Brown 1974). We estimated fallen woody debris using the plane-intercept method (Kershaw 1973, Brown 1974, Grieg-Smith 1983). 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 length, small diameter, large diameter and percent decay. Small diameter was the smallest part of the woody debris and the large diameter was the largest part of the woody debris. Percent decay was estimated by the degree of breakability (Brown 1974) and the amount of bark still on the branch or twig. In addition, two litter depth measurements were also taken 2 meters north and 2 meters south from the center of the 10 m line to obtain an estimate of decomposition. A modified Brown (1974) fuel loads classification by diameter (cm) of woody debris was used. Each piece of woody debris measured was placed in fuels classification (1 hour – 1000 hour) based on diameter (cm) of the woody debris. Thus the following fuel burn time for different measurement classes was used for quantifying dead and down woody

material (adapted from Huffman): 1 hr = <0.64 cm, 10 hr = 0.64 – 2.54 cm, 100 hr = 2.54 – 7.62 cm and 1000 hr = >7.62 cm.

Comparing Ground-Dwelling Arthropod Community Structure in High-Mortality and Low-Mortality Habitats

To test the differences in ground-dwelling arthropod community dynamics between high and low levels of pinyon mortality, pit-fall traps were used to capture arthropods. Pitfall trapping has been shown to obtain satisfactory abundance estimates for all ground-dwelling arthropods (Thomas and Sleeper 1977). For trapping arthropods, we used Borsilicate glass test tubes with a 2.5 cm diameter opening and 15 cm in length. Glass containers seem to be the most effective at preventing arthropods from escaping (Luff 1975, Obeng-Ofori 1993). Test tubes are encased by SDR 35 material PVC pipe complete with a PVC lid to detour rain and debris from falling in the trap.

There have been many arthropod studies that utilize pitfall traps to quantitatively sample ground-dwelling arthropods however there does not seem to be a consistent trap design or size diameter preference among these studies. Therefore, an array of larger pitfall traps were used to determine if the smaller pitfall traps had any biased sampling to specific types or groups of arthropods. For example larger arthropods such as desert hairy scorpions, adult tarantulas and lubber grasshoppers can be quite common in arid and semi-arid ecosystems, which may not fit into a 2.5 cm diameter opening of our small pitfall traps and thus will not be sufficiently sampled. We used plastic Dixie® brand cups, which had a 9.5 cm diameter opening. One cup was placed within the other to create a sleeve for the collecting cup. Small puncture holes were made in the outer cup to

prevent rain water from collecting and pushing the inner cup out and large ABC pipe lids were nailed into the ground covering each cup to detour rain and other debris. Each test tube and Dixie® cup was filled with a 1:1 dilution of water and propylene glycol. Propylene glycol appears to be the best preserving/killing agent for use in pit-fall traps, since it preserves arthropods for long periods of time without evaporating and is less toxic than ethylene glycol (e.g., Hall 1991, Digweed et al. 1995, Dennis et al. 1997). In some cases pitfall traps can be ineffective at capturing a random number of arthropods if there is bait or some type of attractant in the trap. Ants can pose a problem especially if a trap is near an ant nest. Many foraging ants will leave chemicals trails for other ants within the colony to follow. If a scouting ant leaves a chemical trail to a pitfall trap, then numerous individuals could fall into the trap, thus biasing the random sample. Therefore, samples that had more than 500 individuals of a species of ant were considered outliers in our data and were removed then analyzed again. We established 100 x 200 meter grids within each sample area, where thirty two 2.5 cm diameter pitfall traps were deployed on a uniform grid at 35 meter intervals and ten 9.5 cm diameter pitfall traps were placed 60 meters apart embedded in the grid.

In order to compare the results of arthropod efficacy sampling between small (2.5 cm) diameter and large (9.5 cm) diameter pitfall traps we had to standardize for trap perimeter differences. Therefore, every 4 adjacent small pitfall traps for each site were summed together to equal the perimeter of one large pitfall trap thus creating 8 small (scaled perimeter) sample units per site to represent the sample size perimeter of 10 large traps in each site.

Microhabitat Study

To determine if specific microhabitat characteristics of pinyon-juniper woodlands could account for differences between high and low mortality sites, pitfall traps were placed in different microhabitats near high pinyon mortality areas. Another intensive study site was chosen in each area adjacent to the high pinyon mortality sites, where comparable live and dead pinyons could be found to compare microhabitat characteristics. Microhabitats such as pinyon pine and one-seeded juniper, and grassy intercanopy areas comprise the pinyon-juniper woodlands, but because of recent pinyon mortality dead pinyons occur more frequently and loss of canopy cover increases intercanopy area allowing more open areas in this system. Thus four habitat types were sampled: live pinyon, live juniper, dead pinyon and open areas.

A total of 120 pitfall traps were placed within a 100 x 200 meter area adjacent to each high pinyon mortality site. In this area ground-dwelling arthropods were sampled from four microhabitat types indicative of a high mortality habitat. Since high pinyon mortality habitats will have more dead pinyons this should also reflect the decrease in the amount of canopy cover, thus open areas will also be an important habitat characteristic of the high mortality habitats, where as live pinyons and live junipers are characteristics of low pinyon mortality habitats. Kearns et al. (2005) describe these microhabitats as the current habitat status of the pinyon-juniper woodlands. A single pitfall trap was placed under each of 30 dead pinyons, 30 live pinyons, 30 live junipers and 30 open areas. Traps were placed in the ground between the base of the trunk and the edge of the canopy leaf litter. All trees selected were of comparable heights and widths. The microhabitats were selected as triplets where a single dead pinyon, live pinyon and live juniper of

comparable sizes were relatively close to each other but not close enough to severely affect the leaf litter composition of the other. Traps placed in open areas were chosen at least 1 meter distance from the canopy width of any nearby dead pinyon, live pinyon and live juniper triplet, thus making a single quadruplet unit (1 dead pinyon, 1 live pinyon, 1 live juniper and 1 open area).

Arthropod Sampling Schedule & Sample Processing

Arthropods were sampled each summer (July 14 –August 3) for three years (2005-2007). For each sampling period the uniform traps were left open for a period of 21 days, and collected. Arthropod sampling for the microhabitat plots occurred only in year 2005 (July 16 – August 5). After the traps were collected, all specimens were removed from the propylene glycol and stored in 70% ethanol. Our primary focus was ground-dwelling arthropods that have important roles in semi-arid systems as detritivores, herbivores and predators (Crawford 1988, Whitford et al.1986, Polis 1991).

One consistent problem with arthropod studies is that arthropod communities are hyper-diverse, especially terrestrial ground-dwelling communities (Basset et al 2004). Many studies often observe only a subset of the terrestrial arthropod community excluding most flying insect (e.g. Lightfoot et al. 2008 Uetz and Unzicker 1976, Thomas and Sleeper 1977, Adis 1979) or observe specific groups within the ground-dwelling community such as spiders (e.g. Buddle 2001, Clark & Grant 1968, Huhta 1971, McIver et al 1992, Pajunen et al 1995, Uetz 1976), mites (e.g. Johnston & Crossley 1996), ants (e.g. Anderson & Sparling 1997, Cerda & Retana 1994, Punttila et al 1994) and ground-beetles (e.g. Dennis et al 1997, Digweed et al 1995, Obeng-Ofori 1993, Parmenter et al

1989, Thomas & Sleeper 1977). Pitfall traps yield large numbers of arthropods, many of which are often discarded since they are not considered true ground-dwelling arthropods (Lightfoot et al. 2008). Insects in arid climates such as flies, bees, and small butterflies are often attracted to liquid and will occasionally fall into pitfall traps (Hammond 1990, Holopainen & Varis 1986).

In this study we wanted to be inclusive but not include arthropods that did not spend a significant amount of their life history on or near the ground. We therefore restricted analyses to what we operationally defined as the "surface-dwelling" community, which included all ground-dwelling arthropods and some flying insects that occasionally forage, feed or have part of their life-cycle on the ground that could have some relationship to the ground-dwelling community including species that are restricted ground-dwelling foragers and predators and are appropriately sampled by pitfall traps (Uetz and Unzicker 1976, Thomas and Sleeper 1977, Adis 1979). The surface-dwelling community included all ground-dwelling arthropods such as: spiders, ants, bristletails, crickets, beetles, scorpions, centipedes, and millipedes as well as other taxa that may have indirect associations with the ground-dwelling arthropod community such as: grasshoppers, true bugs, and parasitic wasps.

A subset of the arthropods collected were prepared as museum-quality specimens and deposited in the Colorado Plateau Museum of Arthropod Biodiversity at Northern Arizona University. Operational Taxonomic Units, which were considered to be species, were used to produce a synoptic reference collection of all taxa collected from all sites in the MRGB. Specimens were identified to genus and species level when possible. Unidentified specimens were sent to taxonomists (S.L. Brantley and D.C. Lightfoot,

Museum of Southwestern Biology, Division of Arthropods, University of New Mexico, Albuquerque) for identification confirmations at the genus and species level.

Statistical Analyses

We examined differences in canopy area, tree density, and percent vegetation cover and vegetation abundance between high and low mortality environments. One-way ANOVA univariate analysis was used to compare means of tree density, canopy area, and percent vegetation cover and vegetation abundance between high and low mortality environments.

Measurements of downed woody debris were sorted into fuel burn time classifications based on cm diameter then calculated to estimate total volume of each measurement. Means of volumes for each fuels load classification were compared between high and low mortality areas using a one-way univariate ANOVA. All significant values were accepted at the 0.05 probability level, using statistical program SPSS (Version 16.0 2007).

To determine efficacy sampling between small (2.5 cm) diameter and large (9.5 cm) diameter pitfall traps we had to standardize for trap perimeter differences. Four adjacent small pitfall traps for each site were summed together to equal the perimeter of one large pitfall trap thus creating 8 small (scaled perimeter) sample units per site to represent the sample size perimeter of 10 large traps in each site.

Species accumulation analysis using the UGE curve (Ugland et al. 2003) was used to determine efficacy of sampling using pitfall traps to sample the surface-dwelling

community in each site each year. We examined differences in arthropod community dynamics between high and low pinyon mortality sites.

We performed both parametric and non-parametric analyses to assess the arthropod communities and habitat characteristics for the high- and low-mortality comparisons. A one way ANOVA univariate analysis of variance (Levene's Test of Equality Error Variances) and an independent sample t-test were used to compare means of habitat variables, arthropod abundance, and arthropod species richness between large and small pitfall traps and between high and low pinyon mortality sites. In addition we compared the means of specific feeding guilds and major arthropod groups within each site to determine if there were specific groups that showed significant differences between trap types and mortality sites. All significant values were accepted at the 0.05 probability level, using statistical program SPSS (Version 16.0 2007). Additional statistics programs, PCORD (Version 5.10 2006) and Primer (Version 6 2006) were used to run community analyses, species indicator analyses, and species accumulations of all arthropods collected in different trap types and high and low pinyon mortality sites for each area and each year. We used a multi-response permutation procedure (MRPP) as quantitative measure to explain arthropod community difference between mortality sites. A non-metric multi dimensional scaling (NMS) scatter plot (Clarke 1993) was used as a descriptive method to examine similarities of arthropod species assemblages between trap types, mortality sites and habitat types, based on Bray-Curtis distance (Beals 1984, McCune and Beals 1993). Species indicator analysis determined if specific arthropod taxa were found in certain habitat types or habitat characteristics, using a Monte Carlo Test of significance. A regression analysis was used to determine which indicators taxa

were correlated with certain habitat characteristics that characterize mortality habitats. We operationally define strong mortality indicators based on the criteria that they were positively correlated with at least one habitat characteristic of high or low pinyon mortality.

RESULTS

Stand Structure

Pinyon mortality was significantly (16n, $P<0.001$) higher in the high pinyon mortality sites in all three areas (**Figure 3**). The north and central regions had greater than 20% pinyon death in the high mortality sites, whereas the southern area had the least amount of pinyon mortality with only 8% pinyon death, which did not meet our original criteria (>10%) of a high mortality habitat. In all high mortality sites only 25% of the dead trees were downed trees, (Class D) while 75% of the dead trees were still standing, (Class A) (Kearns et al. 2005).

There were no significant differences in tree density of pinyons or junipers between high and low pinyon mortality habitats. However, canopy cover for all tree species combined were significantly (16n, $P=0.001$) higher in the low pinyon mortality habitats for each of the three study regions and was driven mostly by pinyons (**Figure 4d**). Juniper canopy cover was variable between sites showing no significant (16n, $P=0.200$) differences and little to no canopy loss (**Figure 4b**). Ponderosa canopy cover was significantly (16n, $P=0.043$) higher in the low mortality habitats for north and central sites (**Figure 4c**). Pinyon canopy cover was significantly (16n, $P=0.001$) higher in the low pinyon mortality habitats for all sites and overall canopy loss was correlated with

pinyon death, which was significantly (16n, P=0.009) higher in the high pinyon mortality habitats (**Figure 4a**).

Understory Vegetation

Of all the understory cover classes, grasses were the primary vegetation cover for all sites (**Table 1a**). Percent ground cover by grasses was significantly (32n, P= 0.007) higher in the high mortality habitats, which shows a positive correlation with pinyon mortality. Blue grama grass (*Bouteloua gracilis*) was the most common species that occurred in our study areas. This species was significantly (32n, P= 0.040) more abundant in the high mortality habitats and was found in all sites. Western wheat grass (*Pascopyrum smithii*) was significantly (32n, P= 0.005) more abundant in the low mortality environments. However this species only occurred in the central and north sites and was very scarce in the high mortality environments.

Dead and Down Woody Debris

We hypothesized that habitat complexity from fallen woody debris of dead pinyons would be greater in the high mortality sites. Thus fuel loads would change with the increase in dead pinyons. Overall total volume of woody debris was significantly (32n, P=0.003) higher in the high mortality habitats which supports this hypothesis and was driven by woody debris in the 100 and 1000 hour fuels classification (**Table 1b**). Majority of woody debris in the 100 and 1000 hour fuels classification averaged 4.9 cm in diameter and was significantly (100 hr, P<0.001 and 100 hr, P=0.010, 32n) more abundant in the high mortality habitats, thus increasing the overall volume of woody

debris. Other fuel load classifications, such as, 1 hour (32n, P= 0.923) and 10 hour (32n, P= 0.359) fuels were not found to be significantly different between high and low mortality habitats. The 1 hour and 10 hour fuels are small twigs, which are usually abundant in most conifer forested areas.

Determining Efficacy of Sampling

There were two issues we wanted to resolve with efficacy of sampling 1) trap size and 2) weather we adequately sampled the community. After combining the sums of four adjacent small (2.5 cm) diameter pitfall traps to equal the perimeter of one large (9.5 cm) diameter pitfall trap, we compared arthropod species richness and abundance between trap types and found significantly (32n, $P<0.001$) more species and individuals in the small (scaled perimeter) pitfall traps. All feeding guilds and major ground-dwelling arthropod groups were also significantly (32n, $P<0.001$ – $P=0.014$) more abundant in the small (scaled perimeter) pitfall traps (**Table 2**). There were no significant differences in arthropod community composition between trap types and there were no arthropod indicator species of mortality that were restricted to only large traps. Comparisons of several analyses between high and low mortality habitats yielded similar results for each trap type. We used 32 small pitfall traps at each site to sample the surface-dwelling arthropod community, which proved to be a sufficient number to collect a satisfactory representation of the surface-dwelling arthropod community (**Figure 5**).

Ground Dwelling Arthropod Community Responses

A total of 564 taxa (38,871 individuals) were collected from pitfall traps and identified to family level with more than 80% of the taxa identified to species level. Of the 564 taxa collected, we only used 225 taxa (36,627 individuals) in our analysis that were defined as our surface-dwelling community. In response to our hypothesis that ground-dwelling arthropods will favor areas with high pinyon mortality, we found no significant (P= 0.398) differences in arthropod abundance between low and high pinyon mortality habitats from 2005 - 2006. However, there were significantly (32n, P=0.052) more arthropods in the high mortality habitats in 2007 for all three regions. Arthropod abundance was variable between sites and years in 2005 – 2006, but showed a consistent pattern in all three regions in 2007. Species richness was not significantly (32n, P = 0.702) different between high and low mortality habitats in 2005 and 2007, but was significantly (32n, P=0.018) higher in the low mortality habitat in 2006 (**Table 3**). Despite the significance in 2006 species richness was variable between sites and between years, showing no consistent trend. In 2006 species richness was higher in the low mortality habitats, but only for the north and south region, which was opposite in the central region.

Arthropod feeding guilds of predators and omnivores/detritivores showed no consistent patterns between high and low mortality habitats. Herbivores were significantly (32n, P<0.001) more abundant in high mortality for all years except 2005. In 2005 herbivore abundance was higher in all high mortality habitats but not at a significant level (32n, P=0.063). Some groups of arthropod taxa that specifically characterize the ground-dwelling arthropod community showed consistent differences between high and low mortality habitats. Darkling-beetles (Family: Tenebrionidae) and

ants (Family: Formicidae) were the most abundant omnivore/detritivores but only darkling beetles were significantly (32n, P=0.027) more abundant in the high pinyon mortality habitats in 2007. Predaceous ground beetles (Family: Carabidae) were also significantly (32n, P<0.001) more abundant in the high mortality in 2007. Arachnids were the most abundant predators and were significantly (32n, P<0.001) more abundant in the low mortality habitats for all three years and were consistent for each site (**Table 4**). Significant (32n, P<0.001) abundances of arachnids were driven by ground-mites (Family: Erythraeidae).

Community analysis of ground-dwelling arthropods showed ground-dwelling arthropod community composition to be significantly (R=0.112, P<0.001) different between high and low mortality habitats from 2005-2007 (**Figure 6**). Analysis of each site independently showed a consistent trend in community composition of ground dwelling arthropods to be fundamentally different between mortality habitats for all sites (**Figure 7**).

Arthropods and Microhabitat Characteristics

Analysis of four microhabitats within the pinyon-juniper woodlands showed ground-dwelling arthropods to be significantly (30n, P<0.001) more abundant under live pinyons than any other microhabitat type and least abundant in open areas. However, the community composition between these microhabitat were showed open areas to be significantly (R=0.177, P<0.001) different from the other three microhabitats. Community differences between live pinyons and dead pinyons were significantly (R=0.004, P=0.027) different when all sites were grouped together but seemed to

deteriorate when separated. Open areas had the strongest amount of community differences between microhabitat types and were consistent for each site (**Figure 8**). Arthropod communities under live junipers seemed to show a consistent pattern with live pinyons.

Arthropod Indicators

Arthropod indicator taxa in our study are defined as taxa that occurred significantly more frequent and abundant in one site more than the other (McCune & Grace 2002). Of the 225 surface-dwelling taxa 22% (51 species) of them were indicators of either high or low pinyon mortality habitats. There were 28 species that were indicators of high pinyon mortality and 23 species were indicators of low pinyon mortality. We operationally define strong arthropod indicator species as taxa that were both frequent and abundant in a site as well as having a strong correlation with specific habitat characteristics that characterize high or low pinyon mortality sites. A regression analysis of all mortality indicator species on specific habitat characteristics which characterize high or low mortality habitats showed only 6% (14 species) of them to be strong indicators of pinyon mortality (3% high and 3% low).

Forty nine percent (51 species) of the 104 microhabitat surface dwelling taxa were indicators of specific microhabitats (5=dead pinyons, 11 =live pinyons, 5=live junipers and 30=open areas) and 20% (21 species) of them were also indicators of high or low pinyon mortality. We amalgamated dead pinyons and open areas as characteristics of high pinyon mortality, while live pinyons and live junipers were considered characteristics of low pinyon mortality. We selected 30 of the microhabitat taxa that had

the highest indicator values and found 16 of them were also mortality indicators (9 high mortality and 7 low mortality). Of those 16 mortality indicators 14 of them were correlated with a habitat type that is a characteristic of high or low pinyon mortality. At least 10 of the microhabitat indicators were defined as strong mortality indicators that were correlated with a habitat characteristic that characterizes high or low pinyon mortality sites.

Thus a total of 14 species were indicators for high mortality habitats and were habitat specialists under dead pinyons and open areas, while 7 species were indicators for low mortality habitats and specialists under live pinyons and live junipers. Of those 14 species, 4 of them were considered strong indicators of high pinyon mortality and 4 of them were strong indicators of low pinyon mortality (**Table 5**). Comparison of the microhabitat arthropod community and mortality arthropod community show an overlap between arthropods occurring in high mortality sites and open areas (**Figure 9**) suggesting that arthropod communities in high mortality habitats resemble arthropod communities in open habitats.

DISCUSSION

Arthropod Community Responses

Arthropod community composition was significantly different between high pinyon mortality sites and low pinyon mortality sites despite the lack of differences in species richness or abundance between high and low mortality environments. This was due to suites of species that were more abundant in either high- or low-mortality habitats,

resulting in offsetting each other and leading to the overall equal diversity and abundance. Twenty-two percent of the surface-dwelling arthropods were indicator species that responded to either high- or low-mortality sites. Also 49% of the surface-dwelling arthropods were habitat specialists occurring in specific habitat types indicative of high or low mortality habitats. Arthropod community dynamics were different between mortality sites which were strongly correlated with intrinsic differences in canopy cover that existed prior to the drought in 2002-2003. However, differences in fallen woody debris as a result of the drought may have contributed to differences in arthropod community dynamics.

An increase in precipitation and fallen woody debris may explain why arthropod abundance was higher in high mortality habitats in 2007. Precipitation significantly ($P<0.001$) increased in 2006 which may have resulted in increased habitat complexity in vegetation combined with increased decay of large amounts of woody debris. There may have also been an increase in fallen woody debris from 2005 -2007 in the high mortality habitats, thus increasing the amount of habitat complexity and refugia for ground-dwelling arthropods. The intense drought in 2002 caused dramatic landscape changes with the mortality of pinyon pine. However, these changes may not have an immediate affect on the ground-dwelling arthropod community, until centuries later. It may take a considerable amount of time for the ground-dwelling arthropod communities to have a strong response to the increase in habitat complexity from fallen trees and woody debris. Most ground-dwelling arthropods seek shelter beneath large woody debris that touches the soil and has had time to decay (Varady-Szabo et al. 2006). Many of the trees that died were still standing when pitfall traps were deployed in August of 2005. Many of the

trees that were dead fell under Kearns et al. (2005) class "A", meaning the tree had only been dead for 5 years or less. In 2007 many of the dead trees and fallen branches had at least 5 years or more time to decay. However, dead trees usually do not fall to the ground until after 10 years of death (Kearns et al. 2005), which means the peak of the arthropod response may not occur until 2013 – 2019.

Significant grass cover in the high mortality sites could account for the significant differences in herbivore abundance. Many of the herbivores found were seed bugs, and leaf hoppers, which may be feeding on the juices of blue gramma grass which was more abundant in high pinyon mortality habitats. Predator abundance often parallels herbivore abundance due to the increase in prey availability (Hassell 1978). However, overall differences in predator abundance were not significant (P=0.202). There were two major predator groups that were found in opposite habitat types, arachnids (spiders & mites) were found in low pinyon mortality habitats while predaceous-ground beetles (Family: Carabidae) were found in high pinyon mortality habitats, which explains why there was not a significant (32n, P=0.202) difference in predator abundance between mortality habitats.

Arachnids are one of the most abundant predators in most terrestrial environments and are indicators of habitat quality (Majer 1997). Studies have shown that spider abundance is associated with vegetatively heterogeneous habitats and tend to be highest in late serial stages (Uetz 1990), thus they are linked to herbivore, omnivore/detritivore and microbial communities and influence growth patterns in food webs, which influence plant growth, succession and recovery after disturbance (Crossley 1977; Peterson and Luxton 1982). Though herbivores were more abundant in low mortality habitats

predators are not limited by prey availability since they are capable of switching from one prey to another depending on availability (Hassell 1978). Spiders can switch prey base and are cannibalistic, therefore they can feed on other spiders (Moya-Laraño 2003 and Hallander 1970). Spiders can represent the majority of an entire predator feeding guild and can be used as indicators of microhabitats or ecological processes (Majer 1997). For example, litter spider communities are directly affected by habitat structure and prey abundance and thus can be used to infer variations in quality and quantity of litter microhabitats (Clarke and Grant 1968; Huhta 1971; Uetz 1976, McIver et al. 1992; Simmonds et al. 1994; Pajunen et al. 1995; Petersson et al. 1995; Halaj et al. 1998).

Litter depth was significantly (32n, $P<0.001$) higher in low pinyon mortality habitats in our study which could reflect an increase in soil litter arthropods. However pitfall traps alone may not be efficient enough to account for the dearth of this group. Berlease funnel traps have been known to collect satisfactory representations of soil and leaf litter arthropod communities (eg.Brown and Gange 1990). Small arthropods such as springtails and mites may not have been accurately rough sorted since they are difficult to see with the human eye. Some micro arthropods such as ground-mites were large enough to see even without a microscope and thus were well represented in the sample.

Ground-mites (Family: Erythraeidae) were the most abundant arachnids and were significantly (32n, $P<0.001$) more abundant in the low pinyon mortality habitats in all three regions of the MRGB, suggesting these arthropods may be indicators of healthy pinyon-juniper woodlands. Ground-mites are predators of many soil-dwelling organisms such as springtails and other mites. Soil-dwelling arthropods such as mites and springtails might be the most important constituents of soil microbiota (Lattin and

Moldenke 1990). They play a major role in the decomposition and cycling of soil nutrients, and are essential in the establishment of mycorrhizal fungi on roots (Crossley 1977, Peterson and Luxton 1982). Studies have shown that up to 50 to 90% of primary production takes place below-ground (Brown and Gange 1990), a process which is greatly regulated by microarthropods (Reichle 1977, Peterson and Luxton 1982). In fact, many researchers agree that due to their importance in decomposition and soil nutrient cycling, microarthropods should be included in forest management assessments (Lattin and Moldenke 1990, Kremen et al. 1993).

Ground beetles are also important indicators of habitat quality in semi-arid environments (Haila et al. 1994). Darkling beetles and predacious ground beetles are both considered ground beetles. These beetles typically seek shelter under rocks and woody debris. The fact that these groups were most abundant in high pinyon mortality habitats suggests that it may be utilizing the high amount of woody debris in the high mortality habitats as refugia, thus ground beetles could be indicators of disturbed pinyon-juniper woodlands. The larvae of darkling beetles often feed on rotten woody debris and the predacious ground beetles often feed on their larvae. It has been noted that many ground beetles have a positive attraction to a variety of solutions (Woodcock 2005) including propylene glycol (Holopainen and Varis 1986, Hammond 1990) which was used as a preserving killing agent in our study. However, propylene glycol was used in all pitfall traps at all sites, therefore it is highly unlikely that the attraction ground-beetles have to this solution would bias sampling in some sites more than others.

Ants are among the most abundant ground-dwelling arthropods, and occupy a diversity of roles as predators, herbivores, commensals, and movers of soil. They are

particularly notable for their impacts on their biotic surroundings (Holldobler and Wilson 1990). Specifically, harvester ants are a conspicuous component of many desert and grassland ecosystems (Brown and Davidston 1977; Davidson 1977; Holldobler and Wilson 1990), and scrublands (Willott et al. 2000). They are the main seed predators in these environments (Lopez et al. 1993; Cerda and Retana 1994). Harvester ants are also the most dominant and conspicuous group throughout arid portions of the southwestern United States and northern Mexico, which includes ~ 75 species (Johnson 2001). Ant abundance was variable between sites and years, but this variability could have been due to due to over sampling of specific species in certain traps that may have been near ant colonies. There were pitfall traps in our study sites that contained numerous individuals of the same species at times accumulating more than 1000 ants. However, even by removing samples that had more than 500 individuals and analyzing the data again, our results did not change. Many ant species specifically harvester ants (*Pogonomyrmex sp*.) will make a clearing of grasses and debris for their nests and are commonly found in open areas (Crist and Wiens 1994, McIntyre 1999). Harvester ants, *P. occidentalis* and *P. rugosus* were the two most common species of harvester ants collected in our study sites and were significantly (32n, $P<0.001$) more abundant in the high pinyon mortality habitats. Harvester ants may be responding to the increase in openness in high mortality habitats. Other ant species such as acrobat ants (*Crematogaster sp*.) and big-headed ants (*Pheidole sp*.) were also abundant in the high pinyon mortality habitats and have been known to have positive correlations with environmental disturbances, even though they make poor indicators of environmental stress (Whiteford et al. 1999). Other ant species such as carpenter ants (*Camponotus sp*.) were more abundant in the low mortality

habitats, which were most likely feeding on nectar from aphids and other pinyon herbivores.

Arthropod Community Response

Arthropod community composition did show annual and regional differences; however the differences were not consistent and varied from year to year for certain areas. Despite the large scale mortality of pinyons in the MRGB, canopy understory and habitat complexity from fallen trees only accounts for 5% of the change in habitat structure for high mortality habitats yet ground-dwelling arthropod composition was still different between mortality sites for all three years (2005-2007) and in all three regions (North, Central and South), which may have been due to intrinsic differences in canopy cover that existed prior to the 2002-2003 drought.

The open areas in the high pinyon mortality habitats are analogous to the vegetation characteristics of grasslands that often border pinyon-juniper woodlands. Lightfoot et al. (2008) conducted a study on ecoregional differences in ground-dwelling arthropod community composition and found little differences between grasslands and pinyon-juniper woodlands, most likely because woodland canopy cover ranges from 5-60% and so even in dense woodlands intercanopy areas dominate. In our study sites intrinsic differences between canopy cover were noted and canopy loss from dead pinyons only increased the amount of openness already present in our sites. However, as a result of drought habitat characteristics that once described the pinyon-juniper woodlands before 2002 may increasingly becoming a grassland-juniper dominated ecosystem. Thus

ground-dwelling arthropod communities in high mortality habitats will be similar to the grassland arthropod communities and may be changing as a result of drought.

Arthropods as Indicators for Climate Change

Terrestrial, ground-dwelling arthropods constitute a large portion of arid and semi-arid ecosystems (Greenberg and McGrane 1996). These arthropods respond quickly to variations such as climate change and environmental stresses brought on by droughts. In addition to these ecological roles, terrestrial arthropods serve as an important food source for many vertebrate and invertebrate species (Peterson and Luxton 1982, Van Home and Bader 1990). Ground-dwelling arthropods represent food sources for specific targeted species (Williams 1993, Haila et al. 1994), which implies the presence of prey (Adams and Morrison 1993, Morrison and Marcot 1995) and denotes specific habitat structures such as fallen logs (Okland 1996) and tree hollows (Gellman and Zielinski 1996). For example, many families of ground-dwelling, terrestrial arthropods were found to be the main food source for many vertebrate species living in arid and semi-arid environments (Fallaci et al. 1992). Their key role in food webs makes arthropod assemblages an essential indicator when assessing the impacts of forest management practices on ecosystem function (Kremen et al. 1993) and developing evidence of habitat stability (Lattin and Moldenke 1990).

Arthropods are enormously diverse (Ehrlich and Wilson 1991) and represent a substantial portion of all terrestrial biodiversity, thus their responses to environmental changes are very important (Basset et al. 2004). In addition, insects are an ideal organism for study because of their relatively short life-cycles and sensitivity to environmental

changes (Young 1994, Evans and Bellamy 1996). Therefore insects can be used as an indicator species for climate change (Goehring et al. 2002). By understanding how arthropods are affected by drought we can use them as a model for determining how global climate change will affect species at higher trophic levels.

CONCLUSION

Pinyon pine mortality was extensive throughout the Middle Rio Grande Basin averaging 41%, whereas juniper mortality was only 3% (Clifford et al unpublished). This mortality has changed the arthropod composition between high and low mortality areas from the resulting reduction in canopy cover, increased solar radiation, and decomposing woody material. A more drought tolerant species of grass, *B. gracilis*, was observed in all high pinyon mortality sites which may have been due to intrinsic differences in canopy cover. Fallen woody debris biomass changed in the 100 and 1000 hr fuels classification, thus increasing total amount of woody debris in high mortality sites, which was evident from the significant amount of pinyon mortality. While overall arthropod species richness and abundance was not significant between mortality sites until 2007, 22% of the surface-dwelling arthropods were indicator species that responded to pinyon mortality, both positively and negatively, showing several arthropod abundances did change. Also 49% of the surface-dwelling arthropods were habitat specialists, specifically in open intercanopy areas, which were indicative of high pinyon mortality sites based on canopy cover. Arthropod community composition in open areas resembled the arthropod community of high pinyon mortality sites. It is possible that these differences may have been due to intrinsic differences in canopy cover that existed prior

to the 2002-2003 drought. However fallen woody debris was the only difference that was directly associated with drought induced mortality of pinyons and could also account for arthropod community differences between sites. It is clear there have been many ecological impacts of drought induced mortality on pinyon-juniper woodlands from the stand level to the landscape level, showing the importance of studying these semi-arid systems for monitoring current and future climate change.

Tables and Figures:

Table 1. Mean values (standard error) of habitat characteristics that characterize high and low mortality sites. Results of ANOVA tests are given as P-values. Average percent grass cover was significantly (32n, P=0.007) higher in all high mortality sites. High mortality sites also had a significantly (32n, P=0.003) higher volume of fallen woody debris, which was largely driven by 100 hour and 1000 hour fuels.

a

Average % Ground Cover	High Mortality		Low Mortality		
	Mean	Std. Error	Mean	Std. Error	P-Value
Shrub Cover	7.45	0.92	8.31	1.04	0.0805
Grass Cover	12.08	1.04	8.89	0.80	0.0065
Forb Cover	11.63	0.89	10.26	0.85	0.3299
Litter Cover	32.26	2.22	34.57	2.03	0.7917
Bare Ground Cover	32.04	1.93	30.71	1.72	0.5698

b

Dead & Down Woody Debris (cm3)	High Mortality		Low Mortality		
	Mean	Std. Error	Mean	Std. Error	P-Value
Total Volume	49,498.10	15,766.72	11,424.18	4,668.79	0.0031
1 Hour Fuels	13.17	4.03	13.53	4.83	0.9230
10 Hour Fuels	951.98	185.44	781.73	235.45	0.3588
100 Hour Fuels	9,167.46	2,273.55	3,642.35	1,140.70	0.0004
1000 Hour Fuels	39,365.50	15,133.67	6,986.57	4,338.23	0.0102

Table 2. Mean values (standard error) of arthropod differences between trap types. Results of ANOVA tests are given as P-values. There were significantly (32n, P<0.001) more arthropod species and individuals in the small (scaled perimeter) pitfall traps than large ones. All arthropod feeding guilds and major groups were also significantly (32n, P<0.001-P=0.0141) more abundant in the small (scaled perimeter) pitfall traps.

	Small Scaled Pitfall Traps		Large Pitfall Traps		
	Mean	Std. Error	Mean	Std. Error	P-Value
Species Richness	89.688	3.526	55.002	3.824	0.0000
Total Abundance	764.531	118.593	329.372	66.598	0.0000

	Small Scaled Pitfall Traps		Large Pitfall Traps		
Feeding Guilds	Mean	Std. Error	Mean	Std. Error	P-Value
Predators	117.000	27.709	50.131	16.821	0.0008
Herbivores	141.188	45.987	45.462	12.121	0.0015
Omnivore/Detritivore	506.344	86.842	233.779	53.592	0.0000
	Small Scaled Pitfall Traps		**Large Pitfall Traps**		
Major Groups	Mean	Std. Error	Mean	Std. Error	P-Value
Grasshoppers	33.500	5.532	17.402	3.240	0.0002
Carabid Beetles	8.219	2.159	4.029	1.008	0.0141
Ground Beetles	5.938	1.258	2.293	0.602	0.0001
Ants	481.938	106.606	119.139	21.310	0.0000
Arachnids	81.906	13.641	39.690	15.869	0.0022

Table 3. Mean values (standard error) for arthropod species richness and abundance between mortality sites from 2005-2007. Results of ANOVA tests are given as P-values. There were no significant (32n, P=0.703) differences in arthropod species richness in 2005 and 2007 between high and low pinyon mortality sites. However there were significantly (32n, P=0.018) more species in the low pinyon mortality site in 2006, but only for the south site. Arthropod abundance was not significantly (32n, P=0.399) different between high and low pinyon mortality sites from 2005-2006, but was significantly (32n, P=0.052) higher in the high mortality sites in 2007 for all sites.

	High Mortality		Low Mortality		
Species Richness	Mean	Std Error	Mean	Std Error	P-Value
All Years	37.92	1.35	38.33	1.23	0.7027
2005	39.37	2.18	38.87	2.20	0.7821
2006	30.44	2.18	34.32	1.77	0.0182
2007	44.05	1.89	41.72	2.02	0.1490

	High Mortality		Low Mortality		
Total Abundance	Mean	Std Error	Mean	Std Error	P-Value
All Years	209.25	32.88	183.44	29.45	0.3989
2005	198.54	48.25	194.70	63.79	0.9505
2006	149.20	36.07	179.26	53.36	0.5027
2007	279.58	76.37	178.42	19.14	0.0528

Table 4. Mean values (standard error) for arthropod feeding guilds and major groups between mortality sites. Results of ANOVA tests are given as P-values. Herbivores were significantly (32n, P<0.001) more abundant in the high mortality sites in 2006-2007. Other feeding guilds were not significantly different between high and low pinyon mortality sites. Three major groups of arthropods showed significant (darkling beetles 32n, P=0.029 high, ground beetles P<0.001 high, arachnids P<0.001 low) differences between high and low mortality sites.

Feeding Guilds	High Mortality		Low Mortality		
	Mean	Std Error	Mean	Std Error	P-Value
Predator Abundance	24.30	5.90	31.28	4.64	0.2015
Herbivore Abundance	53.53	16.03	11.57	1.42	0.0003
Omnivore/Detritivore Abundance	130.41	18.67	140.13	28.33	0.6941

Major Groups	High Mortality		Low Mortality		
	Mean	Std Error	Mean	Std Error	P-Value
Grasshoppers	7.773	1.159	9.619	1.075	0.0754
Darkling Beetle Abundance	3.13	0.47	2.27	0.41	0.0286
Ground-Beetle Abundance	2.56	0.59	0.75	0.23	0.0004
Ant Abundance	138.09	30.81	104.35	25.19	0.2475
Arachnid Abundance	13.10	1.62	25.47	3.40	0.0000

Table 5. Strong indicator species between mortality sites that are associated with microhabitats. Results of Monte Carlo tests are given as P-values. Twenty two percent (12% high & 10% low) of the 225 surface dwelling arthropod community were indicators of either high or low pinyon mortality habitats. Only 6% (3% high & 3% low) of the community was considered strong indicators that were correlated with habitat characteristics of high or low pinyon mortality. The numbers under years represent how many years the taxa were present.

High Mortality Indicators	Years	North	Central	South	Indicator Value	P-Value
Hoplosphyrum boreale	2	Absent	Present	Absent	14.4	0.0002
Dasymutilla vestita	3	Present	Present	Present	26.4	0.0002
Crematogaster depilis	2	Present	Present	Present	32.3	0.0002
Pheidole hyatti	3	Absent	Present	Present	40.8	0.0002
Pogonomyrmex rugosus	3	Absent	Present	Absent	15.6	0.0002
Forelius pruinosus	2	Present	Absent	Absent	14.6	0.0002
Liometopum apiculatum	3	Absent	Present	Absent	25.7	0.0002

Low Mortality Indicators	Years	North	Central	South	Indicator Value	P-Value
Styracosceles neomexicanus	2	Present	Present	Present	21.1	0.0002
Dallasiellus descrepans	2	Absent	Absent	Present	17.6	0.0076
Myrmica sp.	1	Present	Absent	Absent	7.5	0.0002
Solenopsis molesta	2	Present	Absent	Present	22.3	0.0014
Camponotus acutirostris	3	Present	Absent	Absent	17.2	0.0002
Phoridae	2	Absent	Absent	Present	17.2	0.016
Erythraeidae	3	Present	Present	Present	50.1	0.0002

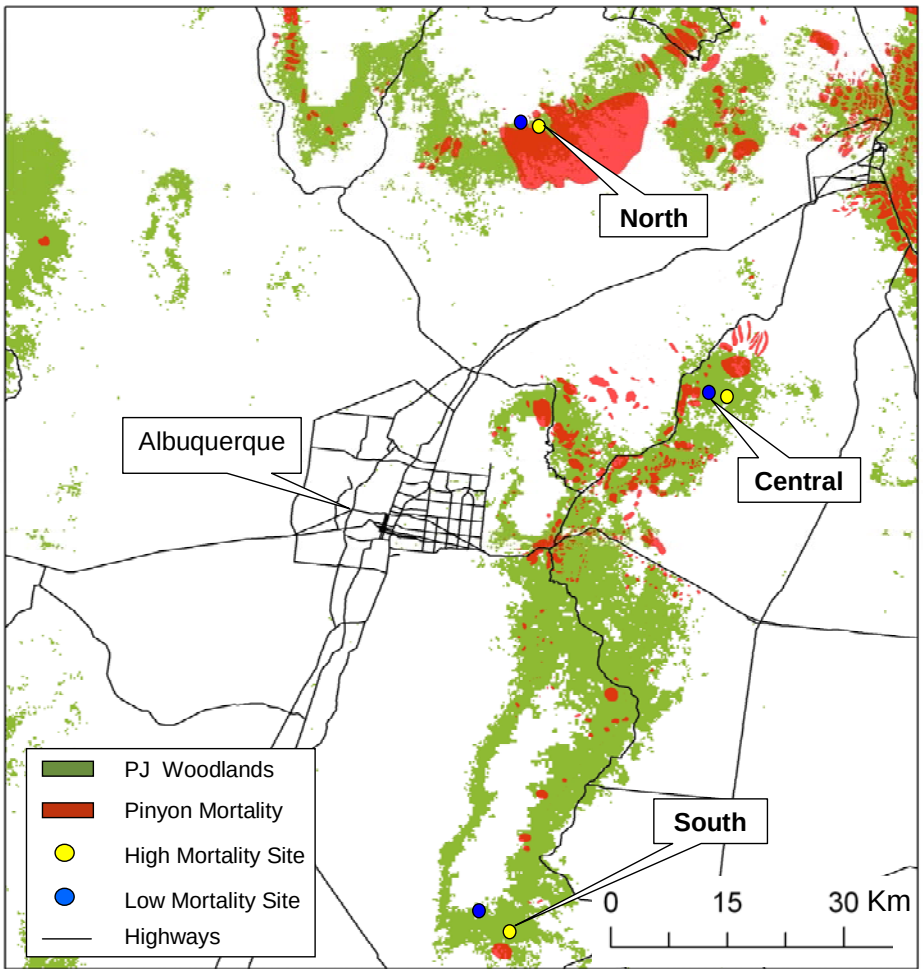

Figure 1. Map of the Middle Rio Grande Basin study area along the showing the three sets of paired study sites (circles). Areas of high pinyon mortality were obtained from USFS Forest Enterprise Team.

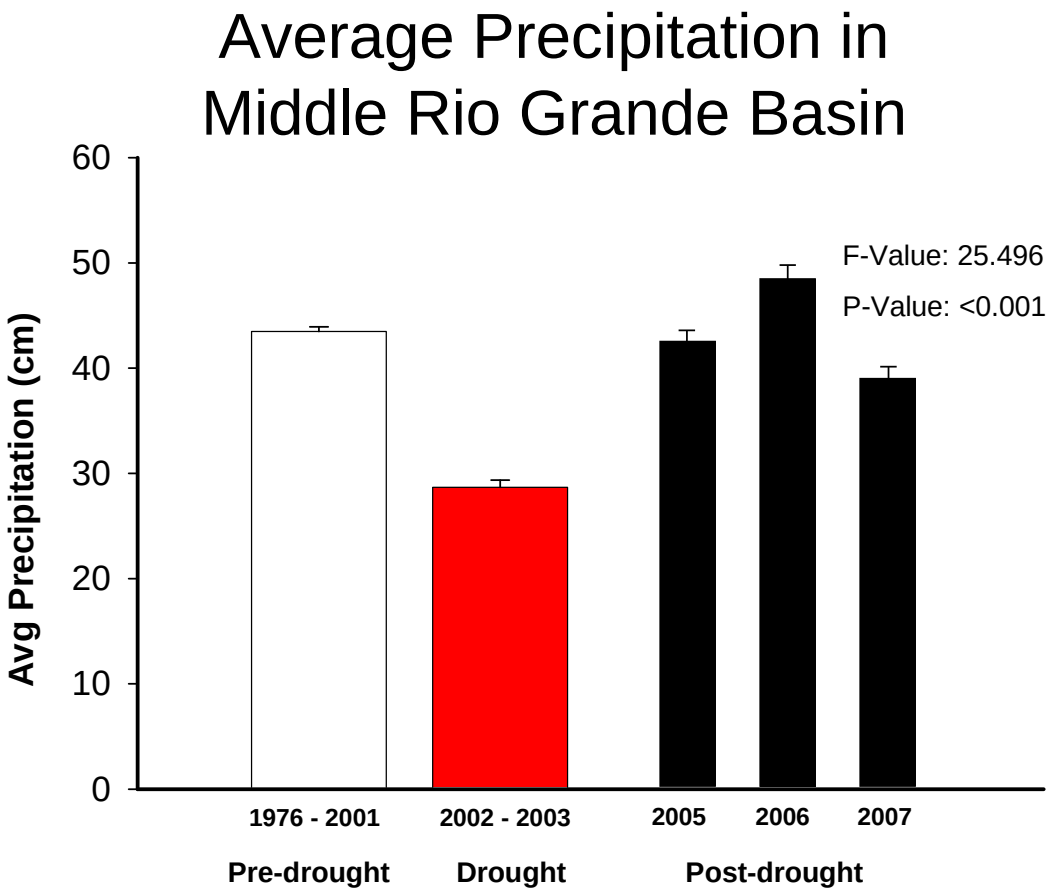

Figure 2. Average precipitation (cm) in the Middle Rio Grande Basin for three time periods (bars) from 1978-2007. Average precipitation during pre-drought (1976-2001) conditions significantly ($P<0.001$) dropped 34% during the drought (2002-2003) then increased 35% during post-drought (2005 -2007) conditions. In 2006 average precipitation was significantly ($P<0.001$) higher than 2005 and 2007.

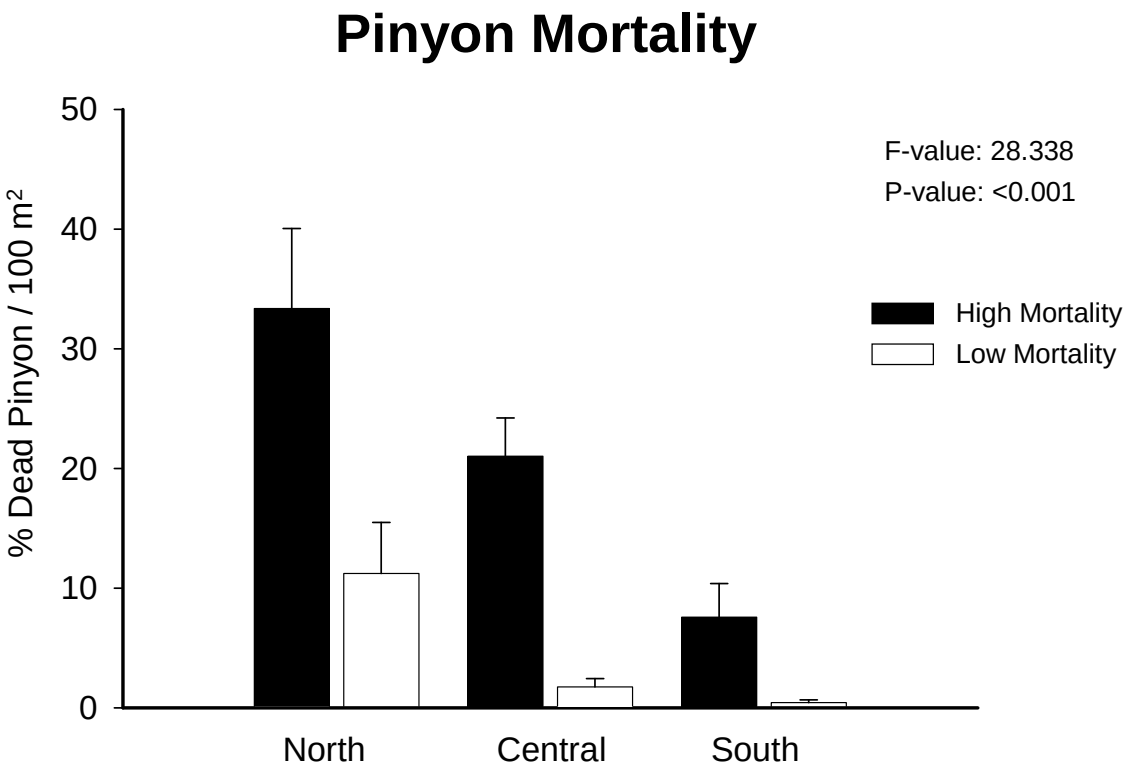

Figure 3. Average percent pinyon mortality. Differences in pinyon mortality were significant (16n, P<0.001) between mortality sites. North and central areas had absolute differences between mortality, while the south area had a relative difference. Percent pinyon mortality for each site (bars), which was designated high or low mortality based on percent of dead pinyons.

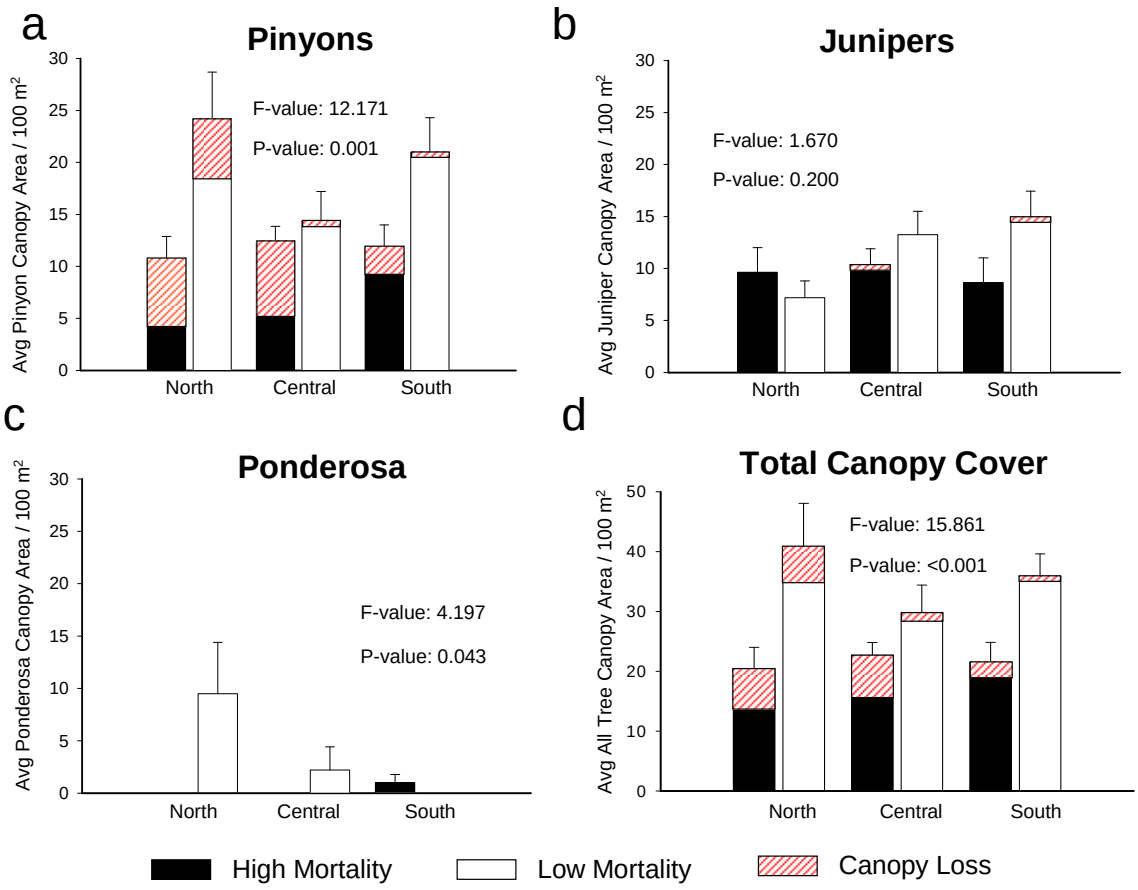

Figure 4a-d. Mean canopy area (m^2) at each site (bars) for each tree type: (a) pinyon pine, (b) juniper, (c) ponderosa and (d) all trees. Canopy cover was significantly (16n, P<0.001) higher in the low pinyon mortality habitats for all trees except for junipers (16n, P=0.200) in the north site. Canopy loss was significantly (16n, P=0.009) higher in the high pinyon mortality sites and was driven by the death of pinyon pine, *Pinus edulis*.

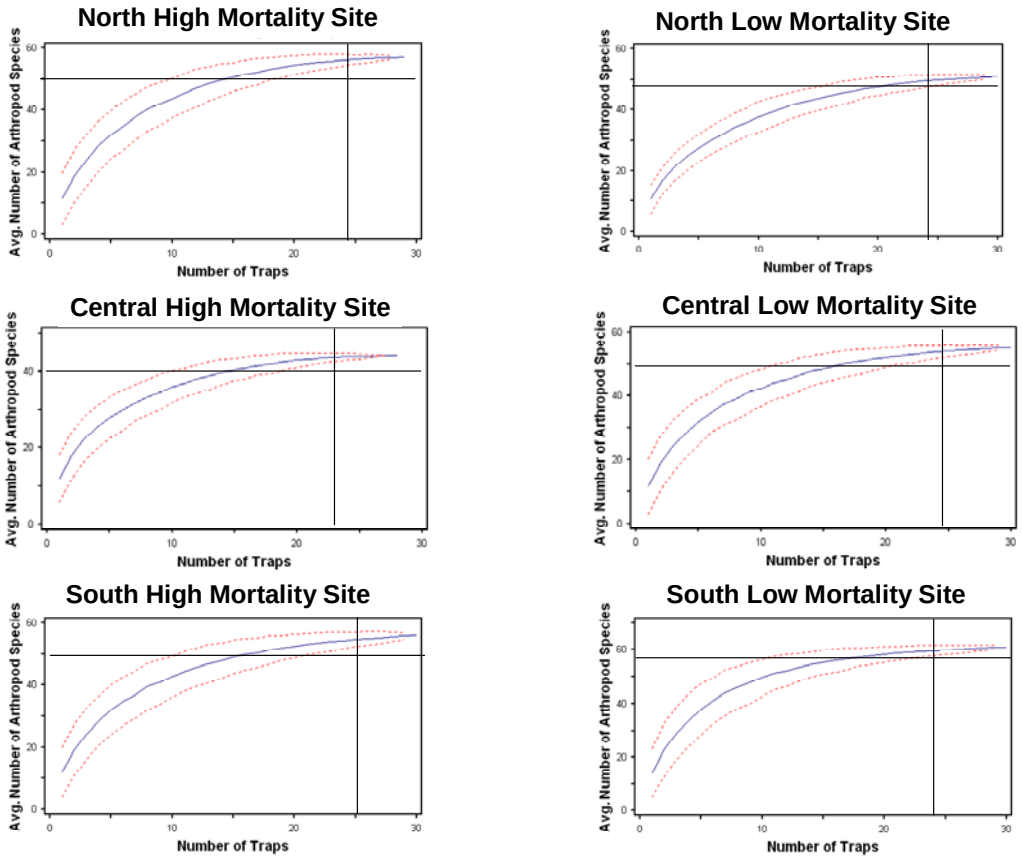

Figure 5. Arthropod species accumulations for each site. At each site ~25 small (25 mm diameter) pitfall traps set in a uniform grid 32 meters apart is sufficient enough to collect a satisfactory representation of the surface-dwelling arthropod community.

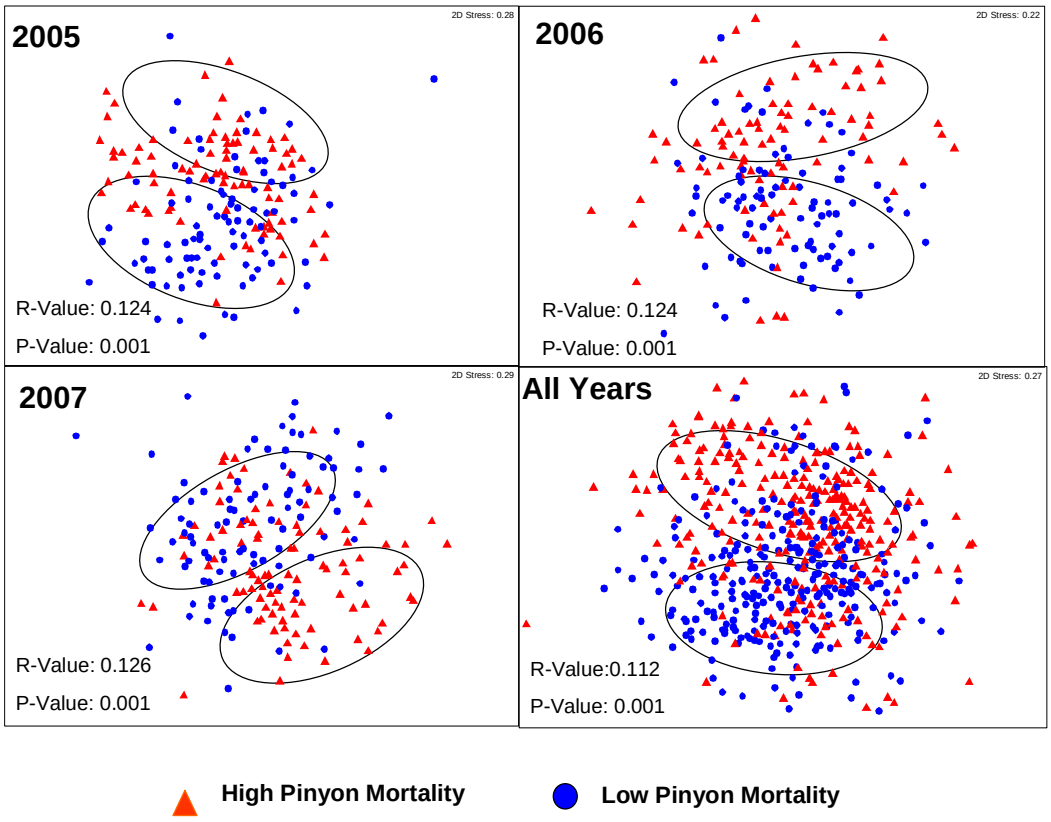

Figure 6. Scatter plot showing arthropod community differences between mortality sites from 2005 – 2007. Red triangles represent arthropod community from high mortality sites while blue circles indicate arthropod communities from low mortality sites. Results from MRPP are given as R and P-values. Arthropod community composition was significantly ($P<0.001$) different between high and low pinyon mortality habitats from 2005-2007.

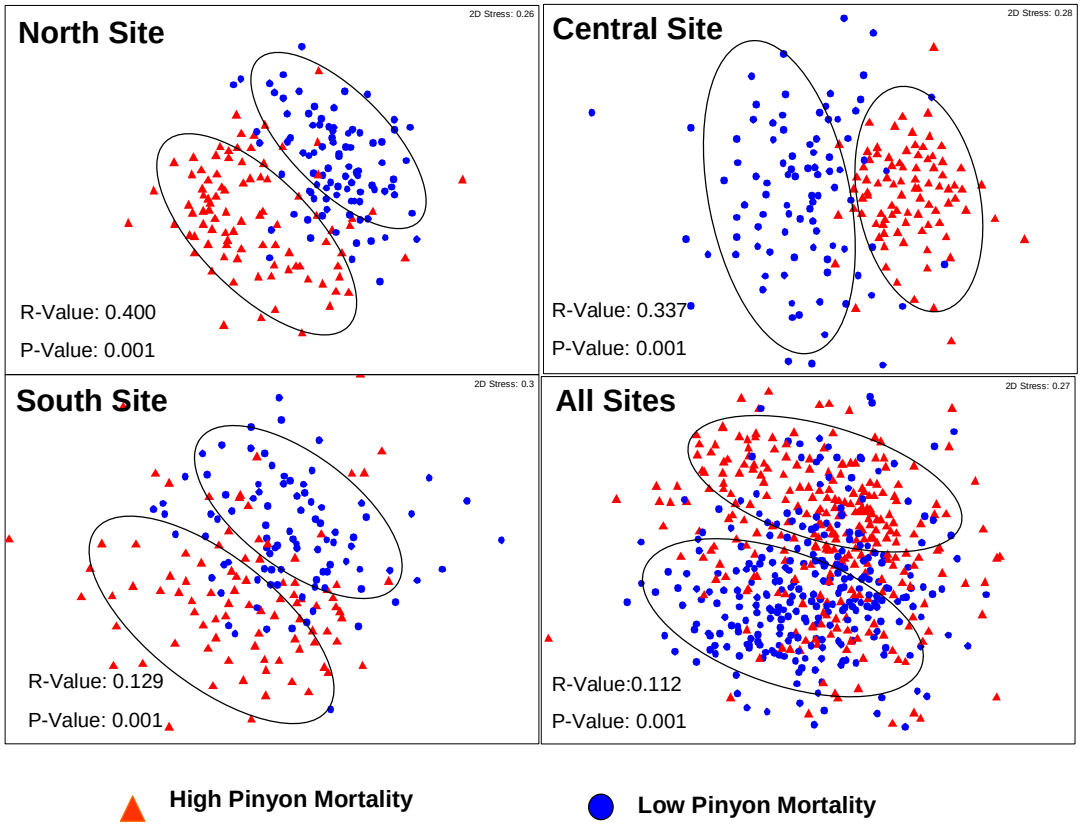

Figure 7. Scatter plot showing arthropod community differences between mortality sites in each region. Red triangles represent arthropod community from high mortality sites while blue circles indicate arthropod communities from low mortality sites. Results from MRPP are given as R and P-values. Arthropod community composition was significantly ($P<0.001$) different between high and low pinyon mortality habitats in all three regions.

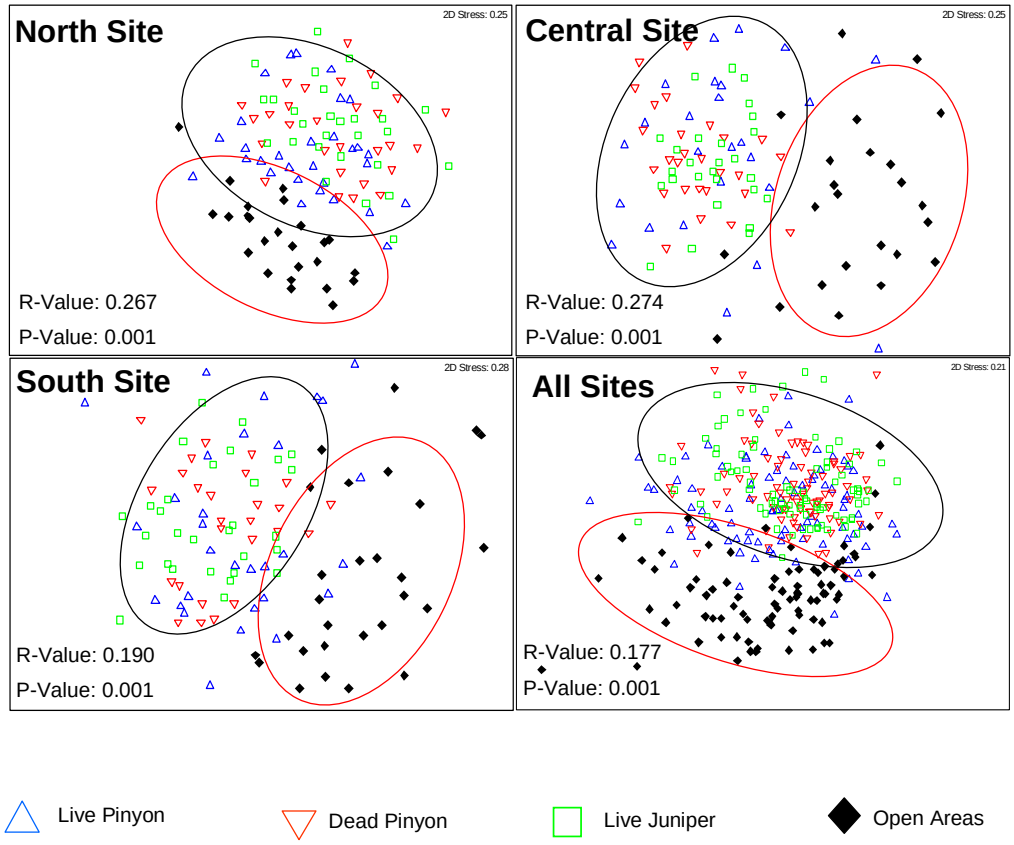

Figure 8. Scatter plot showing arthropod community differences between microhabitat characteristics in each region. Blue triangles represent arthropod community from live pinyons, red triangles = dead pinyon arthropod community, green squares = live juniper arthropod community and black diamonds = open area arthropod community. Results from MRPP are given as R and P-values. Arthropod community composition in open areas were significantly ($P<0.001$) different from arthropod communities occurring under live pinyons, dead pinyons and live junipers.

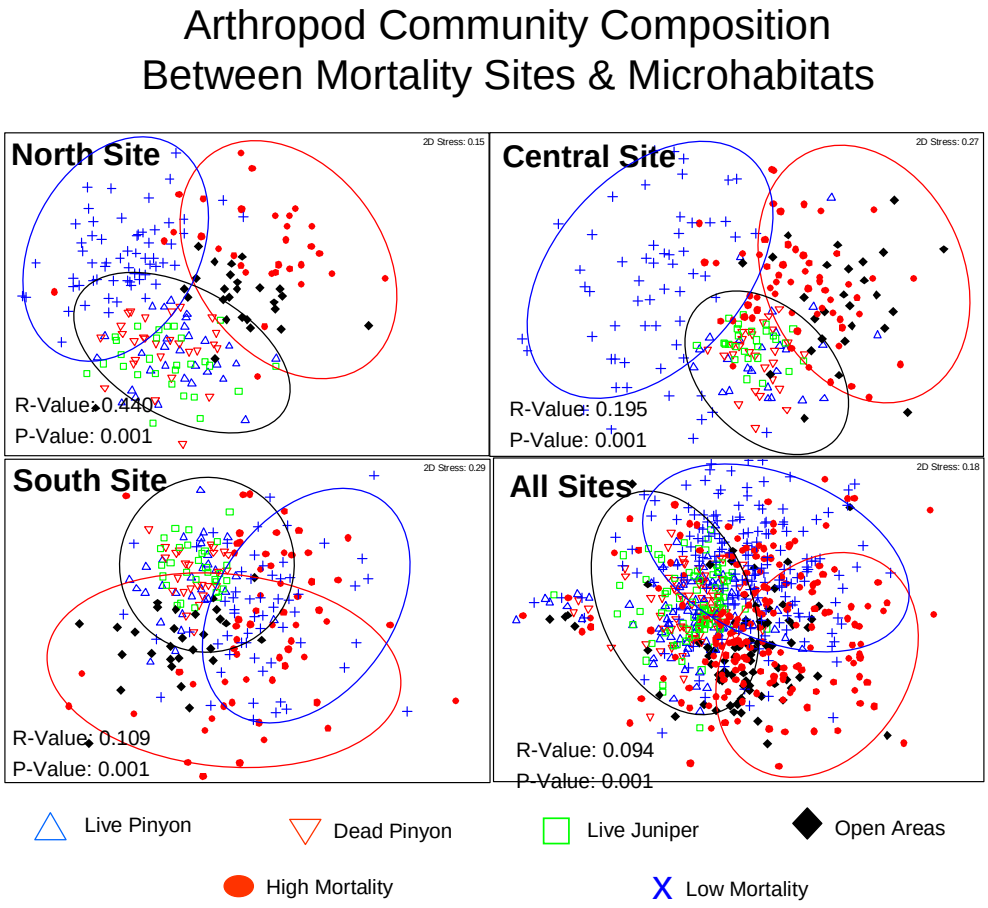

Figure 9. Scatter plot showing arthropod community differences between microhabitat characteristics and mortality sites in each region. Blue triangles represent arthropod community from live pinyons, red triangles = dead pinyon arthropod community, green squares = live juniper arthropod community, black diamonds = open area arthropod community, red circles = high mortality arthropods and blue X = low mortality arthropods. Results from MRPP are given as R and P-values. Arthropod community composition in high mortality habitats resembles arthropod community composition in open areas.

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