Relationships Between Forest Age and Soil Macroinvertebrate Biodiversity

University of Michigan Biological Station

Ian Bernstein

Rachael Gingerich

Stason Schafer

Catherine Tait

Abstract

Succession is a process describing directional, continuous and non-seasonal changes in the species richness and abundance of ecological communities. Fire disturbance in six burn plots spanning a 102-year period has spurred secondary succession in tree communities and macroinvertebrate communities, providing a burn chronosequence along which links between these communities can be characterized. In this study, we aimed to address the following questions: 1. Does soil macroinvertebrate diversity change with forest age? 2. Is there a relationship between macroinvertebrate community diversity and tree community diversity? 3. Are there correlations between tree species and soil macroinvertebrate orders, and how do these potential relationships change over time?. Soil macroinvertebrates were sampled four times from four pitfall traps in each of the six burn plots (years: 1911, 1936, 1948,1954, 1980, and 1998), along with concurrent measurements of overstory and understory plant species abundance.. Soil macroinvertebrates diversity did not increase with forest age. Tree species succession in the burn plots conformed to the Intermediate Disturbance Hypothesis (diversity was lowest immediately following fire disturbance [1911 – 1948], increase to a climax at its midpoint [1954], and decreased thereafter). Macroinvertebrate diversity did not follow this pattern. Chi-Square analysis revealed significant short-term and long-term changes in soil macroinvertebrate communities. We found significant positive correlations between larvae and bigtooth aspen, millipedes and red oak, spiders and red oak, beetles and white pine, and a negative correlation between beetles and bigtooth aspen. Further research needs to be conducted to explore underlying factors affecting soil macroinvertebrate community change after disturbance events.

<u>Introduction</u>

Succession is a process describing directional, continuous and non-seasonal changes in the species richness and abundance of ecological communities (Johnson et al. 1995). Shifts in physical and chemical properties of the environment (e.g., nutrients availability and soil stability) during primary and secondary succession, can also influence the subsequent establishment of other species (i.e. facilitation). Secondary succession is the process of ecological communities changing following a disturbance such as a fire, where the substrate maintains vegetation from previous communities. In forests, this process moves from conditions favoring species that require high amounts of sun to conditions favoring species that are less light dependent, as the canopy cover grows (Johnson & Miyanishi 2007).

Controlled burning is a process in which large sections of forests are intentionally burned, often for different reasons. These burns disrupt the established ecological communities and spur successional events. A successional event is any event that brings a forest to a uniform starting point and allows for new forest growth and an increase in species richness (Everett & Ward 1984). In northern temperate forests of the upper Great Lakes region, *Populus grandidentata* (bigtooth aspen) are the first tree species to sprout and dominate following a disturbance, but are gradually replaced by *Acer rubrum* (red maple) and *Pinus strobus* (American white pine) (Scheiner & Teeri, 1981). As forests recover from disturbance, the growth contributes in the form of increasingly carbon rich topsoil (Scheu & Schulz, 1996). Additionally, older forests should show an increase in accumulation of leaf litter, although the annual rate of accumulation may not change (Persson & Malmer & Wallen, 1987). In terms of soil composition, there tends to be an increase in NH_4-N immediately after burning; one year later, the soil NH_4-N decreases, mostly due to transformation from NH_4-N to NO_3-N (Covington & Sackett 1992). All of these changes allow for directional, continuous and non-seasonal changes in forest communities.

Johnson et al. (1995) found that older forests have more soil moisture, increased organic matter, and lower average temperatures, conditions that also affect soil invertebrate communities. The researchers found that soil macroinvertebrate species abundance, diversity, and biomass generally increase with forest age, and they hypothesized that the increased favorable conditions allowed for a greater number of species to thrive in older forests. Another important finding from this research was that every soil macroinvertebrate species found in the youngest forest was also

found in the oldest forest, indicating that species populations present in the soil immediately after a controlled burn are maintained as the forest ages (Johnson et al. 1995).

Plant communities aboveground and soil macroinvertebrate belowground are often part of complex systems that regulate one another, resulting in ecosystem functions that are dependent on both communities. Hunter and Price (1992) suggested that the soil macroinvertebrate community could influence plant communities by altering rates of soil nutrient cycling and availability. The photosynthetic and nutrient uptake capacity of plants (particularly for nitrogen uptake) directly influence belowground resource quantity and quality for soil macroinvertebrate communities. For example, earthworms, which act as environmental engineers, can indirectly alter primary production by modifying soil nitrogen availability (Huhta 2007). Furthermore, soil macroinvertebrates can increase plant species richness and affect forest community composition (Brown and Grange, 1992; Grange and Brown, 2002; De Deyn et al., 2007). What we can gain from these small interactions among plants and soil macroinvertebrates is that soil macroinvertebrates can influence and check the growth of plants and the growth of plants can influence diversity of macroinvertebrates., These complicated interactions are likely to change as forest succession progresses.

At the University of Michigan Biological Station, controlled burns of forest areas across 102 years are ideal locations to link soil macroinvertebrate and tree community species richness and abundance across forest successional stages. In this study, we aimed to address the following questions: *1. Does soil macroinvertebrate diversity change with forest age? 2. Is there a relationship between macroinvertebrate community diversity and tree community diversity? 3. Are there correlations between tree species and soil macroinvertebrate orders, and how do these potential relationships change over time?* We expect soil macroinvertebrate communities and tree communities to directly correlate in species richness and abundance with forest age. The increased accumulation of leaf litter, increasing soil carbon pool size, and the other increasing favorable conditions documented in the literature should increase habitat complexity and resource availability for soil macroinvertebrate communities in older forests. The abundance of positive growing conditions might create favorable environments in which more species of plants and macroinvertebrates can thrive, potentially leading to an increase both tree species and soil macroinvertebrate species richness and abundance. Accordingly, we have three alternate hypotheses. H_{a1} = *soil macroinvertebrate diversity will increase with forest age, H_{a2} = as forest*

age increases, tree community diversity and macroinvertebrate community diversity will both increase, and H_{a3} = there will be correlations between specific plant species and macroinvertebrate orders.

Materials and Methods

Site Description

      Our study was conducted in the University of Michigan Biological Station burn plots, located in Pellston, Michigan (Cheboygan County, 45.5528° N, 84.7839° W). These forest plots are approximately 100×100 m in size and were burned naturally in 1911 and experimentally in 1936, 1948, 1954, 1980, and 1998 (Figure 1). The plots provide a chronosequence of forest succession and differ in tree community composition and soil composition (UMBS Burn Plots).

      Heavy logging and fire in the mid-nineteenth and early twentieth centuries has lead to successional changes in the temperate forest communities across the UMBS burn plots. After these disturbances, an oak-maple community, with patches of white pine and bigtooth aspen, has replaced the original northern hardwood-pine community that existed prior to logging in Northern Michigan (Correia et al., 1994). Soil communities have also changed in response to fire and logging disturbances. The most recent glacial events left soils in the Pellston outwash plain sandy and nutrient-poor. Fire and logging lead to nutrient loss due to runoff and soil compaction as forests age and use available ammonia-nitrogen (Covington 1992). Forest communities across burn plots overlie nutrient-poor soils that are well-drained, acidic, and sandy in texture.

Soil Macroinvertebrate Diversity

      Soil macroinvertebrates included in this study are arthropods and gastropods larger than two millimeters in length, and include beetles, larvae, spiders, centipedes, millipedes, ants, earthworms, slugs, snails, and grasshoppers. To determine whether soil macroinvertebrate communities are related to forest age, we sampled soil macroinvertebrate communities across the burn plots using pitfall traps that were flush with ground level and filled with ethylene glycol (antifreeze). Plastic roofs supported by long toothpicks were installed above each trap to prevent rainwater from filling the cups. Sixteen pitfall traps were placed in each plot and four cups from each of these sixteen were sampled. In five out of the six burn plots, the traps were placed in 4×4 grids, each separated by ten meters, within a 40x40 meter plot. In these plots, the four traps

were collected diagonally across the grid from Southwest to Northeast (Figure 2). In the 1998 plot, sixteen traps were split between a 60x10 meter plot and a 50×20 m plot located on opposite sides of a fenced exclosure set up for other research, six traps separated by ten meters were placed in a straight line and the two center traps of the line were sampled. In the 50×20 m plot, ten traps separated by ten meters were placed in two parallel lines of five and the center trap from each row was sampled (Figure 3). Traps were collected twice a week over 12 days. The contents of each trap were emptied into a glass jar and macroinvertebrates subsequently transferred into archive jars containing 95% ethanol to prevent decomposition. Several salamanders, shrews and a mouse were also trapped over the course of the study but were not included in data analysis. The salamanders were transferred to ethanol along with all macroinvertebrates and the shrews and mouse were removed and frozen for other research on the burn plots. Using a dichotomous key for the macroinvertebrates, we identified the order of each macroinvertebrate specimen.

Successional Pairings Between Tree Species and Macroinvertebrate Communities

In order to determine relationships between tree species and macroinvertebrate species, we measured tree species richness at each pitfall trap using the point-center-quarter method. Traditionally this method involves splitting an area into four sections, hence point-center-*quarter*, and sampling the specimen in each section nearest the center. For a more representative sample, we chose to split the area in which we sampled into eight sections. A 1 m^2 constructed from PVC pipe was placed over the pitfall trap so that the trap was located in the center, and we divided the grid into eight equal sections using four lines of string originating from the midpoints and corners and intersecting at the center of the square. Using a transect tape, we measured the distance from the trap to the tree nearest the trap in each of the eight sections. The species of the selected tree was recorded and the diameter at breast height (DBH) was measured. To measure percent cover of understory plant species, we placed a 1 m^2 grid split into 25 sections constructed from PVC pipe and string directly over our pitfall trap. We took photographs of the area and later identified any plant that fell within one of the 25 grid sections.

Statistical Analysis

To characterize tree species richness and tree species diversity (number of species present and evenness of species), we utilized the Shannon-Wiener index (H' = $-\sum p_i lnp_i$). Chi Square analysis was used to determine changes in macroinvertebrate species with forest age. To investigate the relationship between tree species communities, understory plant species communities, and macroinvertebrate species with non-normally distributed data, Spearman rank correlation matrices were created to determine correlations (ρ, $n = 6$, $\alpha = 0.05$) across forest age classes. To examine relationships between the abundance of individual tree species and macroinvertebrate groups, we used regression analysis.

Results

Tree Species Diversity and Forest Age

Shannon-Wiener indices were calculated for tree species diversity in each burn plot. Relative tree species diversity increased between the 1911 and 1936 burn plots, and between the 1948 and 1954 burn plots. Relative tree species diversity decreased between the 1936 and 1948 burn plots;1954 and 1980 burn plots; and between the 1980 and 1998 burn plots (Shannon-Wiener Indices, Figure 4).

Soil Macroinvertebrate Community Diversity and Forest Age

A pitfall trap (#10) in the 1948 burn plot was excluded from our data analysis due to a relatively high number or Carrion beetles attracted to a decaying shrew that was caught in the pitfall trap in between collection periods, but not fully submerged in the ethylene glycol. Shannon-Wiener indices were also calculated for soil invertebrate community diversity in each burn plot. Soil macroinvertebrate diversity similar across all plots. There was a decrease in macroinvertebrate diversity between the 1936 and 1998 burn plots; and a relative increase in invertebrate diversity between the1936 to 1911 burn plots (Figure 5).

Soil macroinvertebrate community composition and the relative abundance of taxa differed significantly with forest age ($X^2 = 97.334$, d.f. = 8, p < .001; Table 1). However, no invertebrate group showed a non-random pattern of change with forest age. Beetles, spiders, and millipedes consistently comprised the largest percentage of individuals sampled, but their numbers did not show any specific patterns of growth or decline. To assess whether or not there were specific changes of growth or decline in specific macroinvertebrate groups, we ran a linear

regression to examine changes in soil macroinvertebrate abundance over time. The results indicated that no specific soil macroinvertebrate group exhibited significant, consistent patterns of change with forest age (p = 0.132) [Table 2].

Pair-wise comparison between successional burn plots revealed short-term changes in macroinvertebrate communities, indicating that these communities not only changed over the 102 years of forest succession, but they changed between each individual burn plot as well. Comparisons between the youngest two forests and the oldest two forests indicated the largest short-term changes (p < .001). Comparisons between the intermediate aged forests yielded smaller, but still significant short-term changes (p $\leq$ 0.05). In the youngest forests, soil macroinvertebrate communities showed significant changes in the 18 year transition from a 15-year-old forest burned in 1998 to a 33-year-old forest burned in 1980 (X^2 = 31.751, d.f. = 8, p < .001). Ants showed a large increase in this time period indicated by a high partial X^2 value (X^2 = 6.278). In the oldest two forests, soil macroinvertebrate communities showed significant changes in the 25-year transition from a 77-year-old forest burned in 1936 to a 102 year-old forest burned in 1911 (X^2 = 47.543, d.f. = 8, p < .001). Beetles exhibited the greatest change in this time period (partial X^2 = 16.6) and slugs showed considerable growth in this interval as well (partial X^2 = 12.012).

Correlations Between Macroinvertebrates, Undergrowth, Tree Species, and Biomass
To examine relationships between the abundance of individual tree species and macroinvertebrate groups, we used regression analysis. Because the data was not normally distributed, we chose to use the non-parametric Spearman rank correlation analysis. The analysis showed statistically significant positive relationships between three tree-macroinvertebrate pairs: larvae and bigtooth aspen (R^2 = 0.894, p = 0.041); millipedes and red oak (R^2 = 0.918, p = 0.028); beetles and white pine (R^2 = 0.975, p = 0.005) and spiders and red oak (R^2 = 0.894, p = 0.041). The analysis also showed a negative correlation between beetles and bigtooth aspen (R^2 = -0.883, p = 0.02), and a negative correlation between larvae and white pine (R^2 = -0.949, p = 0.051). Larvae had a statistically significant inverse correlation with biomass (R^2 = -0.894, p = 0.041). All other soil macroinvertebrate groups we studied did not show any significant relationship with tree biomass, and the abundance of no macroinvertebrate groups correlated with any understory plant species abundance.

Discussion

Invertebrate community diversity was found to decrease slightly from the 15 year-old forest to the 65 year-old forest (burned in 1948), after which invertebrate community diversity began to increase. We observed significant changes in macroinvertebrate community composition with forest age, although specific patterns of growth and decline were not observed for any specific species. Beetles, spiders and millipedes consistently comprised the largest percentages of individuals measured, but their compositions fluctuated rather than showing any specific patterns of growth or decline. Significant correlations were found between larvae and bigtooth aspen trees, between millipedes and red oak trees, between beetles and white pine trees, and between spiders and red oak trees.

Tree species diversity was found to increase from the 15-year-old forest (burned in 1998) to the 59-year-old forest (burned in 1954), after which species diversity began to decline (Figure 6). Previous research has indicated that diversity may be low immediately following a disturbance, but will increase to a climax at its midpoint. This climax is then directly followed by a sorting point characterized by a decrease to a sustained level of diversity due to the lack of available niches (Begon, et al. 1986). Other reasons for the decline in the sorting phase may also include increasing competition for nutrients and sunlight. This pattern of increase, climax, and decline is known as the Intermediate Disturbance Hypothesis (Begon, et al. 1986). After a fire, nutrients that were previously locked in the biomass are released and there is an increase in the availability of light due to the lack of canopy cover (Karowe, 2013). This means that light-intolerant plant species will be abundant at the start, and gradually decline as a canopy evolves, resulting in the highest diversity of plant life during the intermediate phases of forest succession. When we look at the data from each individual burn plot (Figure 7), we can see that tree species diversity is lowest in the youngest and oldest burn plots with only two species present in the 1998 burn plot and only three species present in the 1911 burn plot. When we examine the 1936 and 1948 plots, the number of tree species remains constant at four species present, but the evenness of those species changes markedly. These changes in species evenness could account for the observed decrease in the Shannon-Wiener Indices for tree species diversity (Figure 8). Furthermore, the data show an increase in both tree species and the Shannon-Wiener Index between the 1948 and 1954 burn plots, followed by a decline in both the index and species abundance. These results support the idea that the decrease in tree species diversity can be

attributed to a change in the evenness of tree species distribution rather than a decrease in species abundance. Therefore, our data lends support to the Intermediate Disturbance Hypothesis that as a forest ages, tree species diversity will increase until it reaches a peak that is followed closely by a decrease in species diversity (Karowe, 2013).

Previous research on invertebrate community composition in the UMBS burn plots have shown steady increases in soil macroinvertebrate diversity with forest age (Johnson et al., 1995). Contrary to these findings, we found soil invertebrate community richness to be highest in the youngest forests: the 1998 burn plot had the highest invertebrate diversity and the tree species consisted entirely of bigtooth and trembling aspen. The 1980 plot had a slightly lower soil invertebrate diversity index compared to the 1998 plot and consisted of bigtooth aspen (50%), trembling aspen (22%), white pine (16%), red maple (9%), red pine (3%), and red oak (3%). The higher tree species richness in the 1980 plot indicates that this plot is entering a relatively later successional stage, although it is still dominated by aspen species. The senescence of aspen in this plot could decrease food resources for the invertebrate communities that previously thrived in an aspen-dominated tree community, though soil invertebrate community sorting may lag behind tree community sorting. Soil macroinvertebrate diversity decreases from the 1954 plot to 1948 plot and tree diversity varies for each of these plots. The 1954 burn has a higher evenness and species richness than the 1948 burn, with higher percentages of white, red pine, and red oak. The 1948 plot is dominated by bigtooth aspen (68%). Soil macroinvertebrate diversity may be related to the increased variety of resources in the 1954 plot.Factors such as soil nutrients and light availability may have contributed to the high soil invertebrate diversity in these younger plots due to an increase in nutrient and light availability and decreased competition (Huston 1979).

While we would expect soil macroinvertebrate diversity to increase with forest age, our results do not follow this pattern. There are various environmental variables that we did not measure that could have caused our results to deviate from our predictions. Sampling the composition of the soil could help us compare resources for soil macroinvertebrates across all of the plots. Additionally, our study took place over a period of four weeks in the spring at UMBS. We therefore did not account for seasonal and longer-term temporal changes that could affect soil macroinvertebrate richness and abundance. Also, we did not account for soil macroinvertebrate dispersal between all burn plots, especially the adjacent plots.

Previous research can help us to understand some of the correlations we found between certain soil macroinvertebrates and tree species. The increase in white pine and increase in proportion of beetles in the 1911 plot may indicate that beetles flourish in this older forest community. We found a correlation between beetle abundance and white pine abundance that supports this relationship. Research by Christensen et al. (1951) showed that there are many species of beetles that chose the aspen leaves as a preferred choice of foraging; these beetles include *phytodecta americana, chrysomela scripta, C. interrupta,* and *C. tremulae*. Since these beetles preferred diet consists largely of aspen leaves, it follows that adult female beetles would select areas with higher concentrations of aspen trees to lay their eggs. A surprising result was the inverse correlation between beetles and bigtooth aspen trees. As mentioned above, research shows that many beetle species prefer aspen trees as a food source (Christensen et al., 1951). We would expect a positive correlation between aspen and beetles, especially given the positive correlation between beetle larvae and aspen trees. Something that could explain this unusual result is that beetles are highly mobile; they have the ability to fly and can therefore disperse across all of the plots, which are very closely located to one another. The fact that beetles have mobility that the plant community do not have added noise the data comparing plant diversity to soil macroinvertebrate order diversity.

Significant relationships between tree species and macroinvertebrate taxa were also observed for beetle larvae, millipedes, and spiders. The majority of the larvae we sampled were likely beetle larvae, though we recorded them simply as "larvae" in our data as soil macroinvertebrate larvae can be very challenging to identify. However, many of the larvae found matched or very closely resembled the descriptions and images of beetle larvae in our identification key. Given this assumption, we can pose a plausible explanation for the positive correlation found between larvae and bigtooth aspen trees. The positive correlation observed between millipedes and red oak trees is also supported by previous research. Past research on millipedes has revealed that acorn radicals (the elongated part of a germinating oak tree) are an important food source to millipedes, and that millipedes have even been considered a pest for oak trees (Galford et al.1992). These results lend support to the positive correlation we found between millipedes and red oak trees. Given that millipedes rely on oak acorns as a food sources, it makes sense that an increase in oak communities in a plot would correlate with an increase in millipedes.In agreement with our results, previous studies investigating Michigan forests with

heavy beech-maple communities and forests with heavy oak communities have shown a greater abundance of spiders in the beech-maple forests and a greater variety of spider species in the oak dominated forests (Bultman et al. 1982). This research did not have a proposed mechanism to explain the higher diversity and thus it does not explain the correlation we found between red oak abundance and spider abundance, but the higher spider species diversity typical of the oak dominated forests supports our finding a high number of spiders in burn plots with greater oak tree abundance.

We predicted soil macroinvertebrate abundance to increase as tree biomass, and therefore leaf litter, increased. Excluding an inverse correlation with larvae, tree biomass had no significant effect on the abundance of soil macroinvertebrates. Despite no research or studies available with which to compare our results, we can speculate as to the reasons for the lack of a relationship between tree biomass and soil macroinvertebrates. An increase in tree biomass should produce an increased amount of leaf litter, which can serve as both food and a habitat for soil macroinvertebrates. Because there was not a significant relationship between biomass and soil macroinvertebrate abundance for almost any of the classes studied, the data suggests the soil macroinvertebrate populations are well below carrying capacity (Karowe, 2013).

There are several sources of error for our results, the first of which is the attraction of soil macroinvertebrates to organic matter decomposition. Most macroinvertebrates use their olfactory systems to navigate, and we know that this affected our sampling in the case of a decomposing shrew. One shrew that we captured was not completely submerged in the antifreeze, and it let out a very distinct smell as it decomposed. As a result, we captured nearly 50 carrion beetles in that one trap alone. This single cup was almost certainly responsible for the overwhelming abundance of beetles in 1948 and that change in evenness originally resulted in a large decrease in the Shannon-Wiener index for macroinvertebrates in the 1948 burn. Accordingly, we were compelled to exclude that point from our analysis. Second, the spacing and timing of our sampling could also have influenced our results. We made every effort to collect evenly from each plot, but the 1998 burn plot was structured very differently from the rest of the plots. The unusual orientation of the traps could have affected the species we captured, possibly explaining why our macroinvertebrate diversity was highest in the youngest forest. We only collected samples over the course of two weeks in the beginning of a particularly cold spring season. Furthermore, we do not know if there are temporal differences in soil macroinvertebrate

community composition. Seasonal comparisons would provide future researchers with a much stronger representation of the soil macroinvertebrate communities.

Future work on forest succession and macroinvertebrate diversity should seek to improve upon our methods by collecting more samples of macroinvertebrate communities across forests that span a wider age range. The samples we collected covered 102 years of forest succession, which is a relatively short period of time in the life of a forest. The Intermediate Disturbance Hypothesis suggests that in general, species diversity will increase until it reaches a climax community and then begin to decline because the forest can no longer support all species. The macroinvertebrate communities in these forests may be following this pattern, but a higher number of sampling replicates and longer observation period may be needed to observe this pattern. Accordingly, our 102-year-old forest may be relatively young, still experiencing a stage of steady growth prior to climax, and the fluctuations we observe may be nothing more than natural variation during an overall period of increasing diversity. Having more burn plots from a wider range of years would provide us with a wider variety of macroinvertebrate and tree diversity samples, allowing us to construct a more complete forest succession timeline.

References

Begon, M. et al., 1986. Ecology: individuals, populations, and communities. *Ecology*, 67, 1698-1699

Brown, V.K. & Gange, A.C. (1992) Secondary plant succession: how is it modified by insect herbivory? *Vegetatio,* 101, 3-13.

Bultman, T. L., Uetz, G. W., & Brady, A. R. (1982). A comparison of cursorial spider communities along a successional gradient. *Journal of Arachnology*, 23-33.

Correia, S., Dooskin, N., Freedman, Z., & Varda, D. (1994) Forest succession: a study of biotic and abiotic factors in the UMBS burn plots. 2 Retrieved from the Deep Blue database.

Christensen, C. M., Anderson, R. L., Hodson, A. C., & Rudolf, P. O. (1951). Enemies of aspen. *Lake St. Aspen Rep.*, (22).

Covington, W. W., & Sackett, S. S. (1992). Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *Forest Ecology and Management*, *54*(1), 175-191.

De Deyn, G.B. van Ruijven, J., Raaijmakers, C.E., de Ruiter, P.C. & van der Putten, W.H. (2007) Above- and belowground insect herbivores differentially affect soil nematode communities in species-rich plant communities. *Oikos,* 116, 923-930

Everett, R. L., & Ward, K. (1984). Early plant succession on pinyon-juniper controlled burns. Northwest Science, 58(1), 57-68.

Gange , A.C. & Brown, V.K. (2002) Soil food web components affect plant community structure during early succession. *Ecological Letters,* 17, 217-227.

Galford, J. R., Auchmoody, L. R., Walters, R. S., & Smith, H. C. (1992).*Millipede damage to germinating acorns of northern red oak*. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.

Huston, M. (1979). A general hypothesis of species diversity. *American naturalist*, 81-101.

Huhta, V. (2007) The role of soil fauna in ecosystems: a historical review. *Pedobiologia,* 50, 489-495.

Hunter, M.D. & Price , P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73, 724-732.

Johnson, J., Kruszewski, Z., Malvitz, M., & Simons, J. (1995). A comparison of soil arthropod communities in successional forest plots. 2-19. Retrieved from the Deep Blue database.

Karowe, D. (2013). *Biodiversity.* General ecology course lecture (EEB 381), University of Michigan Biological Station. Pellston, MI.

Karowe, D. (2013). *Carrying Capacity.* General ecology course lecture (EEB 381), University of Michigan Biological Station. Pellston, MI.

Karowe, D. (2013). *Ecological Succession.* General ecology course lecture (EEB 381), University of Michigan Biological Station. Pellston, MI.

Persson, S., Malmer, N., & Wallén, B. (1987). Leaf litter fall and soil acidity during half a century of secondary succession in a temperate deciduous forest.*Vegetation*, 73(1), 31-45.

Scheiner, S.M. and J.A. Teeri. 1981. A 53-year record of forest succession following fire in northern lower Michigan. *Michigan Botanist*. 20:3-14.

Scheu, S., & Schulz, E. (1996). Secondary succession, soil formation and development of a diverse community of oribatids and saprophagous soil macro-invertebrates. *Biodiversity & Conservation*, 5(2), 235-250.

UMBS Burn Plots. University of Michigan Biological Station. Retrieved June 13, 2013, from umbs.lsa.umich.edu.

Tables:

[Table 1] Partial chi-square X^2 values for each invertebrate order by burn plot year (1911, 1936, 1948, 1954, 1980, and 1998). The chi-square statistic and critical value (d.f. = 8) are also given.

Species	P1911	P1936	P1948	P1954	P1980	P1998
Ants	1.270286	2.910281	0.02688	1.765229	7.156554587	2.559866
Beetles	7.201153	2.106788	24.19801	2.735512	5.862686369	6.613188
Larvae	0.191854	0.005371	2.90631	0.334823	0.288614364	1.267788
Millipedes	0.067318	0.00848	6.963974	0.217287	0.225873	4.627083
Opilionids	1.467098	0.464491	0.064921	0.029746	0.006847704	7.28E-05
Slugs	15.4329	0.834156	3.814532	0.951511	0.004108622	4.37E-05
Snails	0.680688	0.718929	0.726577	0.083706	0.550669216	10.26361
Spiders	6.381185	0.655389	4.758761	3.718832	1.351387303	0.916299
Worms	0.664268	0.048468	0.172713	1.004235	1.789674952	0.691937
					Chi Statistic	139.759
					Critical Value	26.125

[Table 2] Linear regression modeling soil macroinvertebrate abundance over time.

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	63.730	1	63.730	2.293	.132[b]
	Residual	4419.127	159	27.793		
	Total	4482.857	160			

ANOVA[a]

a. Dependent Variable: Abundance

b. Predictors: (Constant), Year
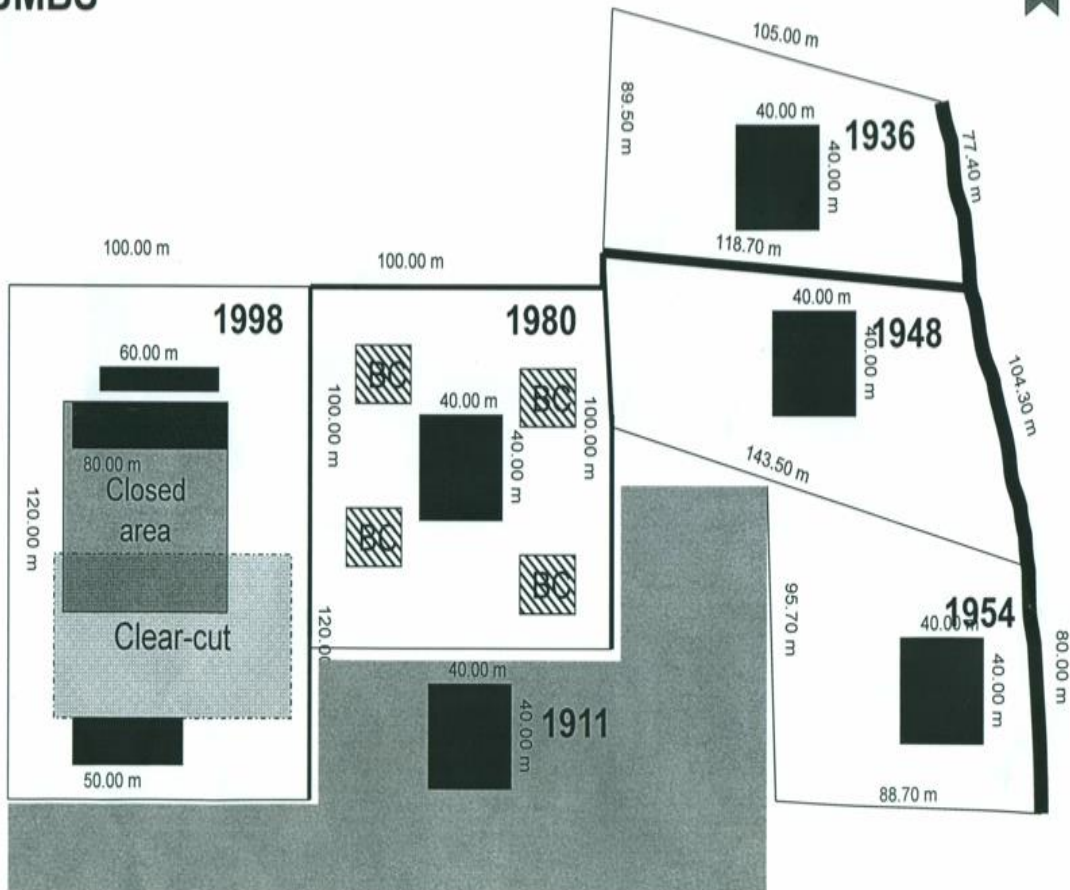
[Figure 1]. Map showing the UMBS burn plots. Study areas are 40x40m squares within larger 100 ×100 m plots burned in the following years: 1911, 1936, 1948, 1954, and 1980. Study area dimensions of the 1998 burn plot are 60 ×10 m and 50 × 20 m.
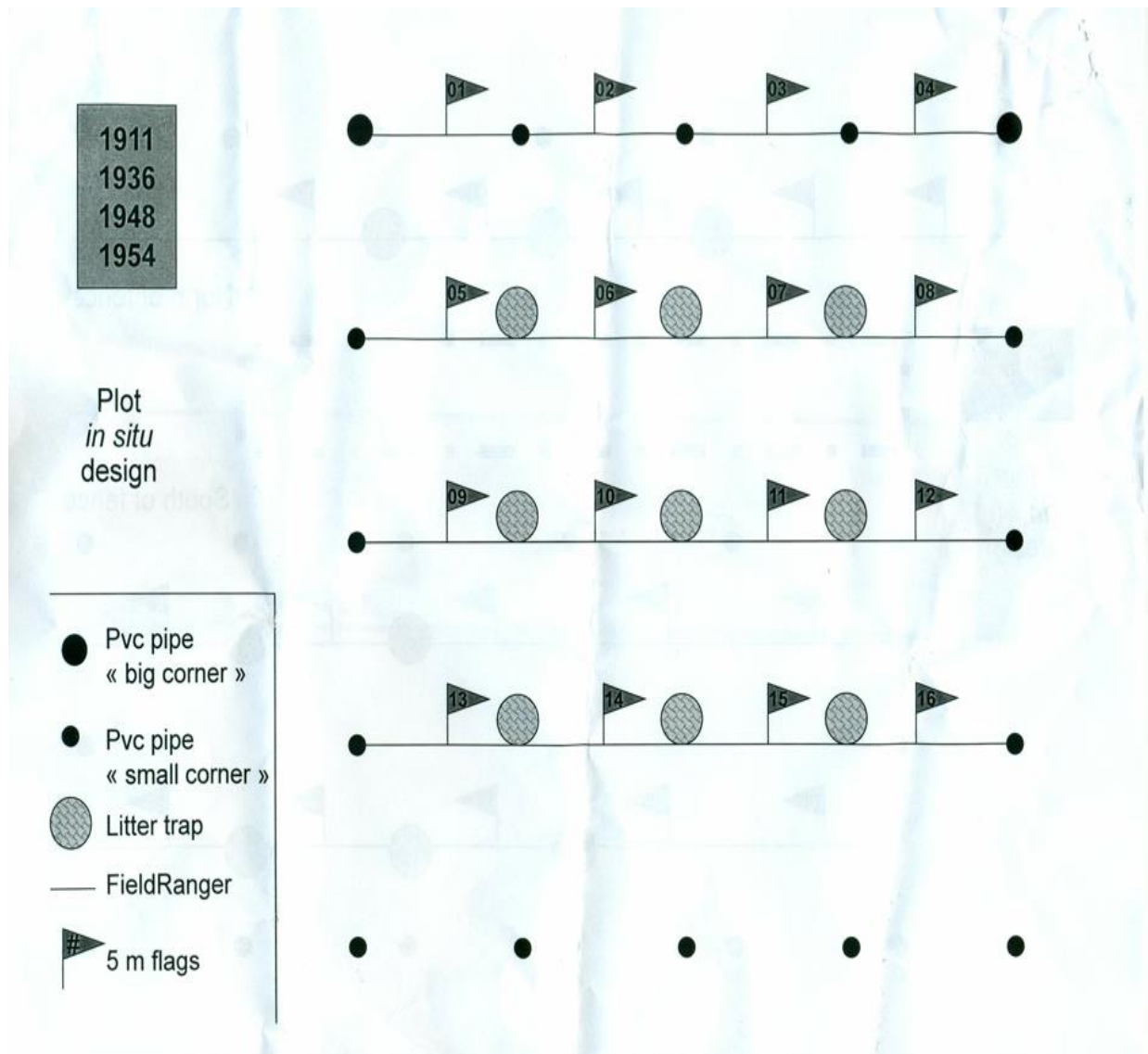
[Figure 2.] Representation of 1911, 1936, 1948, 1954 and 1980 pitfall trap setup with flags marking pitfall trap locations within 40 × 40m plots. Traps were sampled on a diagonal from Southwest to Northeast (bottom left to top right).
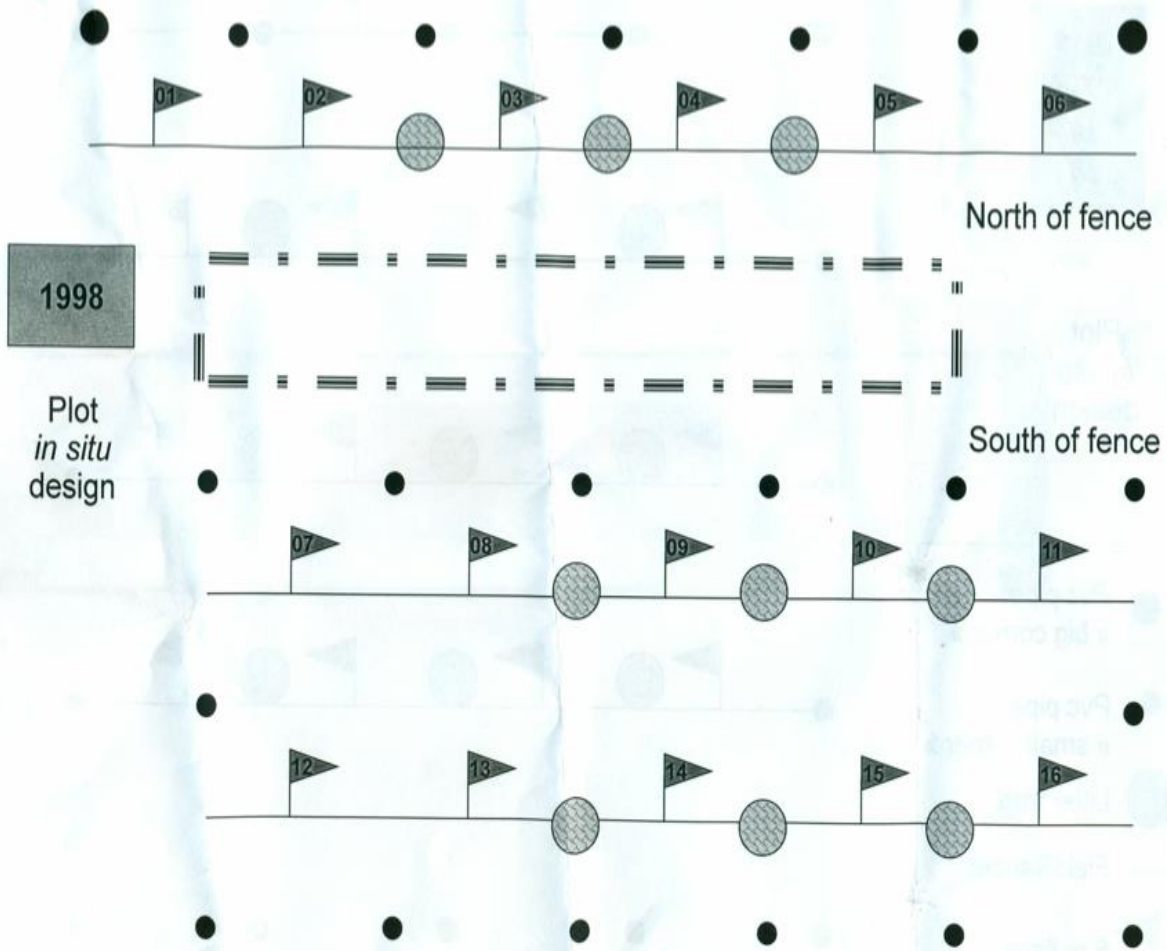
[Figure 3.] Representation of 1998 burn plot setup. Flags represent pitfall trap locations. Sampled traps include the two center traps on the north of the fenced area (dashed line) and the center trap from each row on the south of the fence.
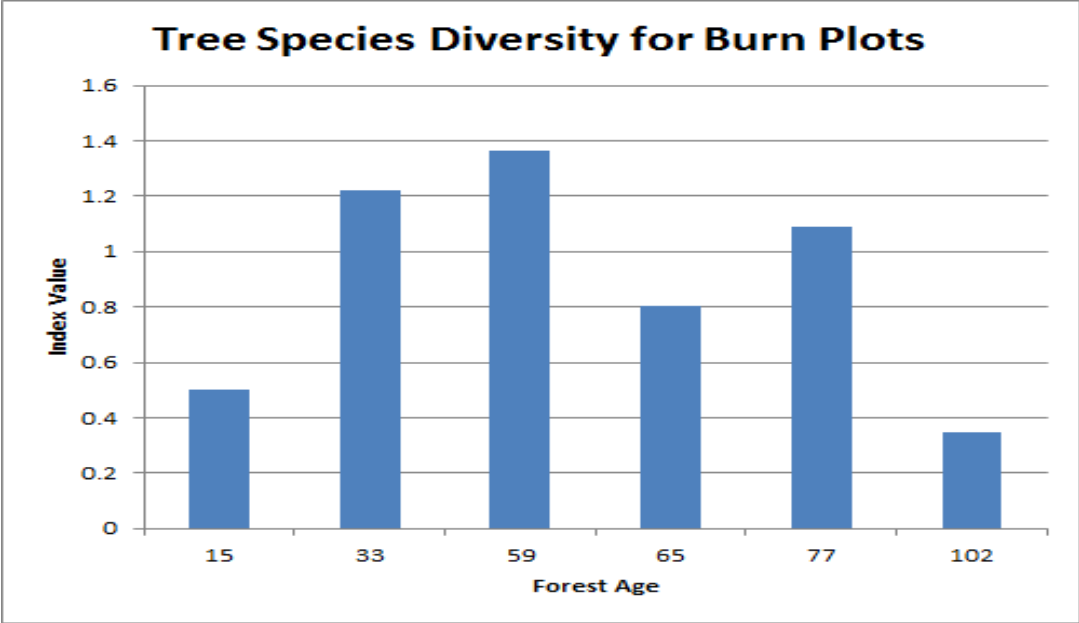
[Figure 4.] Shannon-Wiener index for tree species diversity over forest age.
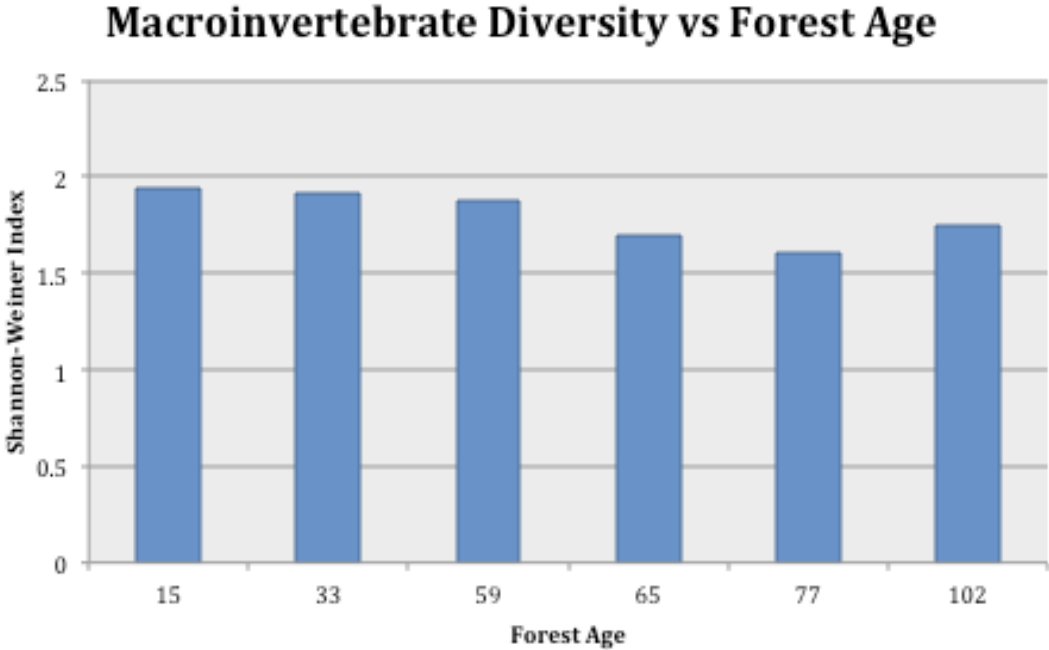
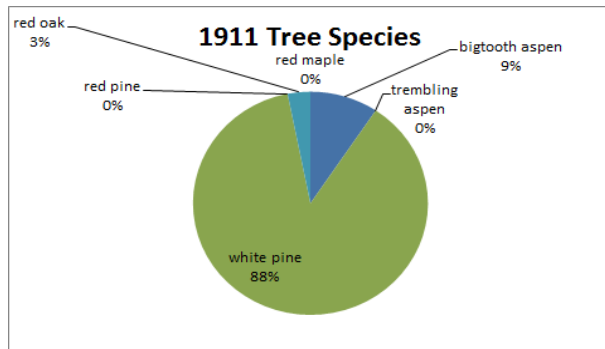[Figure 5.] Shannon-Wiener index for macroinvertebrate diversity over forest age.
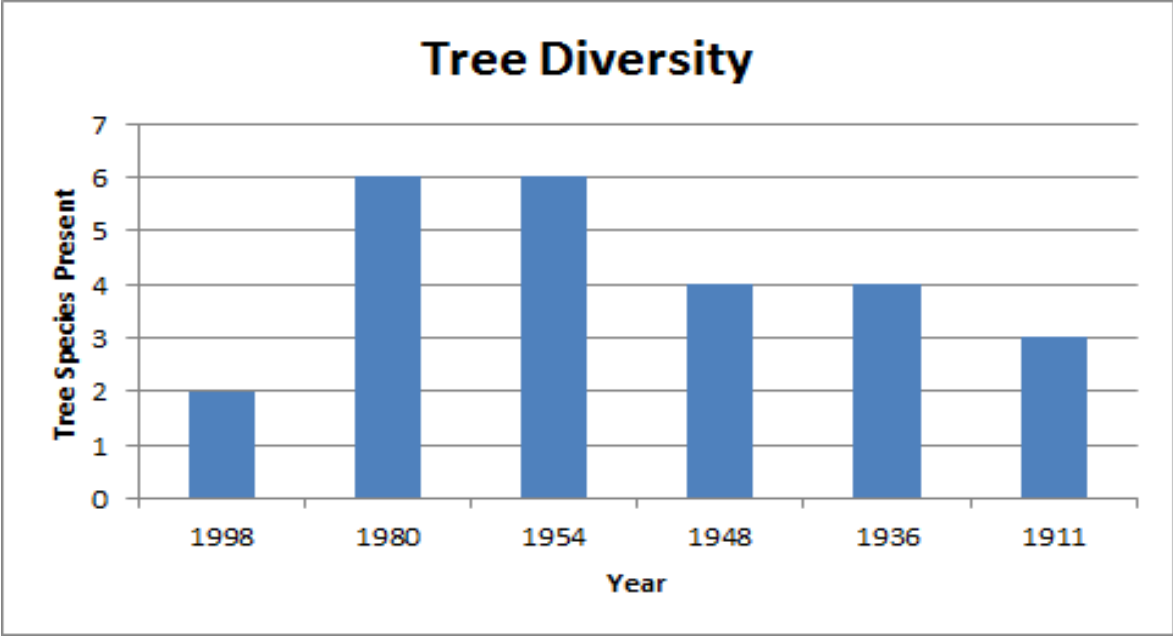
[Figure 6.] Tree species richness over year of forest burn.
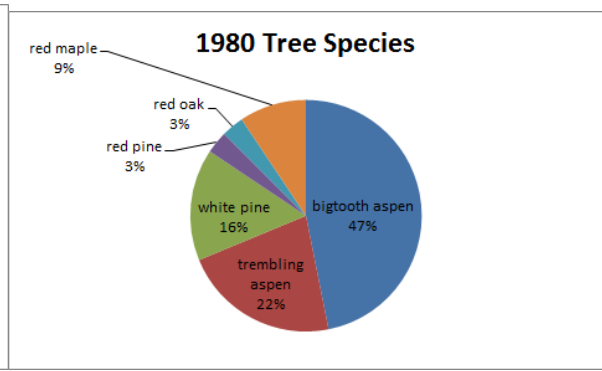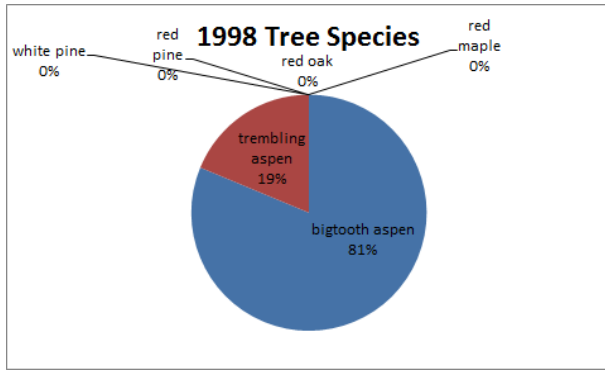
[Figure 7A.] Tree species relative abundance,1998 burn   [Figure 7B.] Tree species relative abundance; 1980 burn
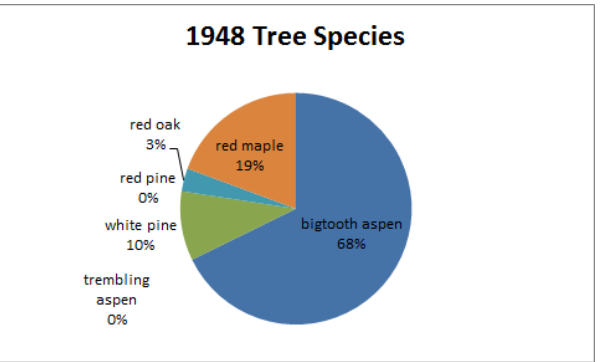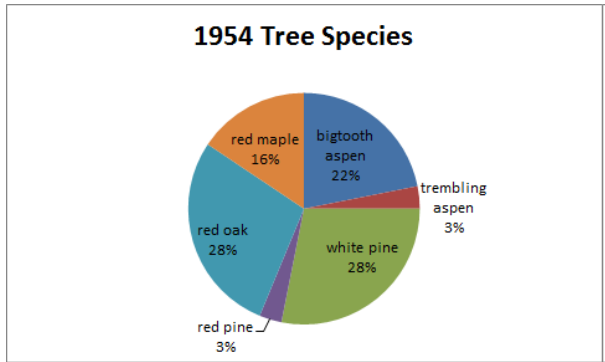
[Figure 7C.] Tree species relative abundance; 1954 burn   [Figure 7D.] Tree species relative abundance; 1948 burn
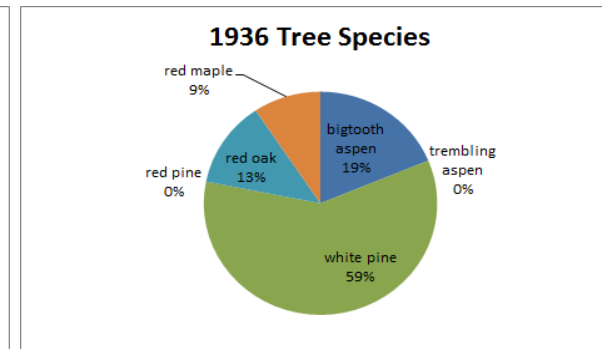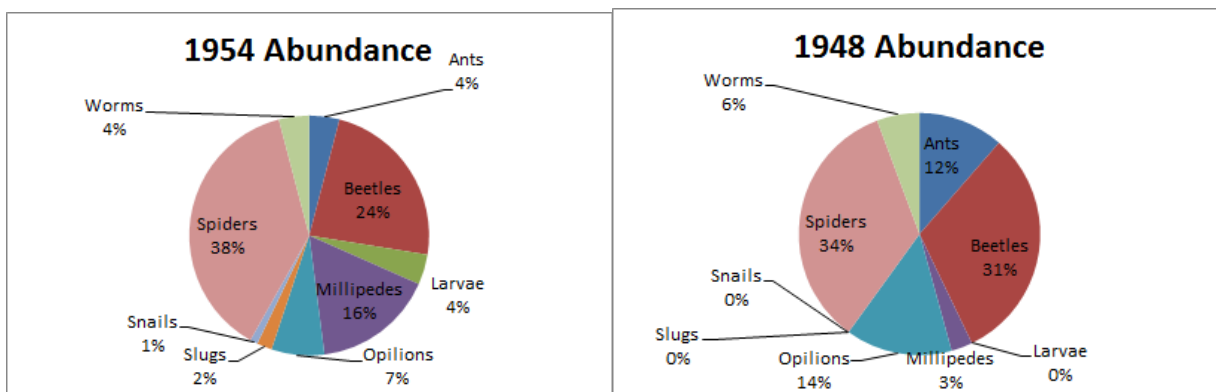
[Figure 7E] Tree species relative abundance, 1911 burn   [Figure 7F] Tree species relative abundance; 1936 burn

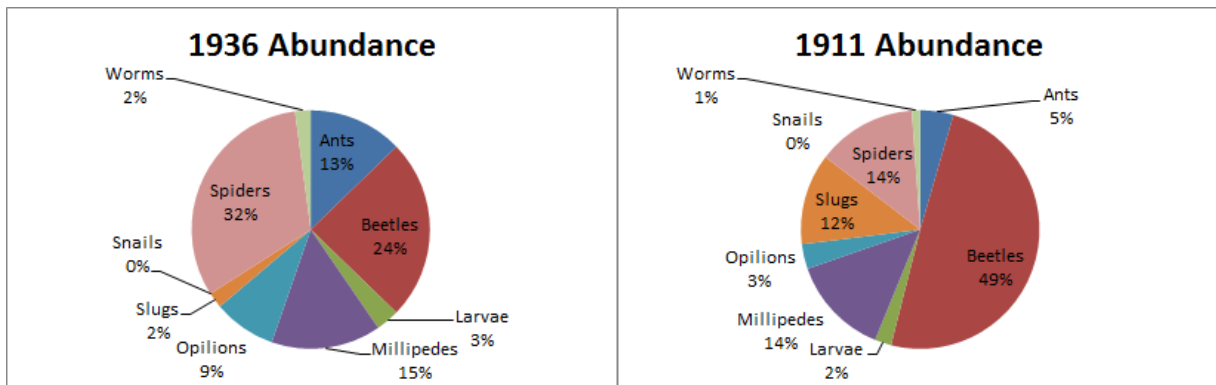[Figure 7.] Pie charts showing relative tree species abundance by forest burn plot.
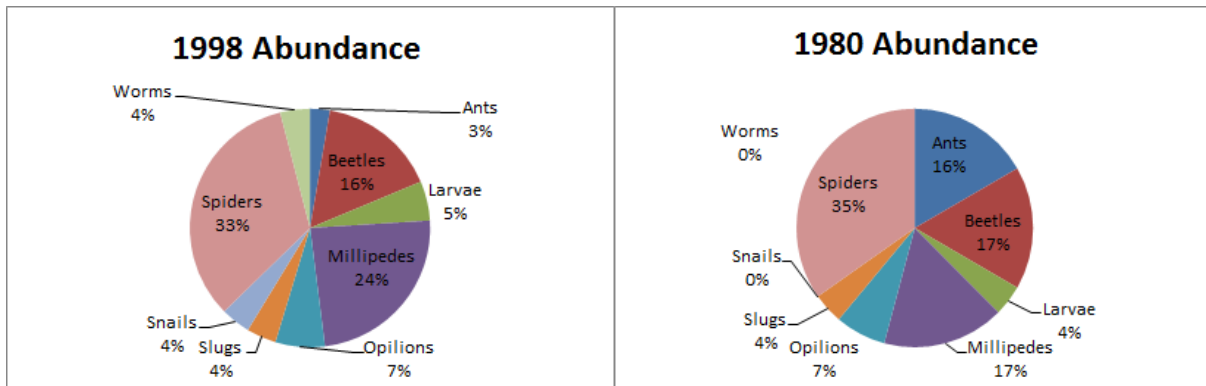
[Figure 8A.] Invertebrate relative abundance; 1998 burn   [Figure 8B.] Invertebrate relative abundance; 1980

[Figure 8C.] Invertebrate relative abundance; 1954 burn   [Figure 8D] Invertebrate relative abundance; 1948 burn

[Figure 8E.] Invertebrate relative abundance; 1936 burn   [Figure 8F] Invertebrate relative abundance; 1911 burn

[Figure 8.] Pie charts showing relative macroinvertebrate abundance by forest burn plot.