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## Soil moisture, fire, and tree community structure

William Patrick White

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SOIL MOISTURE, FIRE, AND DIFFERENCES IN  
TREE COMMUNITY STRUCTURE

A thesis submitted in partial fulfillment  
of the requirements for the degree of  
Master of Science

By

WILLIAM PATRICK WHITE

B.S., SHAWNEE STATE UNIVERSITY, 2008

2011  
Wright State University

WRIGHT STATE UNIVERSITY  
SCHOOL OF GRADUATE STUDIES

January 27<sup>th</sup> 2011

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY William Patrick White ENTITLED Soil moisture, fire, and differences in tree community structure BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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## ABSTRACT

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Soil Moisture, Fire, and Differences in Tree Community Structure.

My study was conducted to understand tree community structure and how soil moisture and fire frequency influence them. Eighteen plots were placed in the Edge of Appalachia Nature Preserve of unglaciated southern Ohio: nine within a prescribed burn site and nine control sites outside the burn. Sites were stratified in triplicate across GIS-derived integrated soil moisture index (IMI) classes. Burning was done in 1996. Overstory species dbh and sapling species were sampled 1997, 2001, and 2008. Overstory stems were located in 2009 using range finders. Stem locations were loaded into GIS using novel techniques to quantify individual stem IMI values.

Nonmetric multi-dimensional scaling identified greater heterogeneity among intermediate and mesic sites than xeric sites. Multi-response permutation procedures did not detect community differences between burned and unburned sites, but did detect strong ( $A=0.3$  to  $0.2$ ,  $T=-3.6$  to  $-4.1$ ) distinct community differences that were statistically significant ( $P < 0.05$ ) among xeric, intermediate, and mesic IMI classes. Analysis of variance identified significant initial effects of burning on *Carya* saplings and overstory *Sassafras albidum* stems, as well as lasting effects significant on *Carpinus caroliniana*.

ANOVA detected significant differences across all sampling years in sapling relative number for *Acer rubrum*, *Sassafras albidum*, and *Carpinus caroliniana* saplings, as well as *Quercus prinus*, and *Liriodendron tulipifera* overstory stems between IMI classes. Bonferroni adjusted Kolmogorov-Smirnov tests were used to identify and quantify IMI habitat restrictions of species. *Quercus prinus* dominated xeric sites (IMI quartiles 18-24), *Carya* occupied intermediate sites (IMI quartiles 22-44), *Acer saccharum* occupied intermediate to mesic sites (IMI quartiles 33-44), *Sassafras albidum* (IMI quartiles 20-40, IMI median 43) and *Liriodendron tulipifera* (IMI quartiles 39-45) were restricted to mesic sites. My results suggest that greater

than one prescribed burn is needed to influence tree community structure; however, some species can be affected by a single burn. Tree communities within a continuous forest region appear to segregate along an IMI gradient. Xeric regions present greater homogeneity than intermediate or mesic regions. However, my results also suggest that specialization does not occur just at the extremes of the gradient, but also in intermediate sites. This finding presents interesting avenues for future research of potential species-specific landscape genetic structures that would be reflective of moisture regimes within a continuous forest. One other possible future application is the use of these novel techniques to resolve and quantify environmental and spatial variables for individual stems with a high degree of accuracy in other study systems.

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## **Introduction-**

### **Understanding Tree Species Community Structure-**

This study seeks to understand the tree community structure of the Appalachian forests of southern Ohio and how soil moisture and fire frequency influence them. To understand the dynamics of change in a forest ecosystem, long term studies are needed due to the long maturation time of the canopy trees and complexities of interactions with environmental and biological factors.

Many factors working together determine tree communities: deer browse (Rooney 2001, Côté 2004), disease (Runkle 2007), logging, land use history (Abrams and Norwacki 1992), and topography (Boerner 2007), among others. Two factors of special concern in forests of southern Ohio and other parts of Appalachia are topographically-influenced soil moisture (Wolfe et al. 1949) and fire (Cottam 1949). My study focuses on the effects of a single prescribed burn, and also seeks to quantify the role of topographically influenced soil moisture.

## Fire frequency dependent community structure-

In the Eastern Deciduous Forest of the United States (Braun 1950) a disconnect has been observed between overstory and understory tree community structure. The overstory is more often made up of an oak-hickory dominated community, whereas the understory is composed of far fewer oak and hickory species and individuals and many more shade-tolerant species and individuals (Drury and Runkle 2005). As the understory matures understory composition eventually changes overstory composition. This change in composition is driven by changes in environmental conditions such as changes in fire frequency (Drury and Runkle 2005). Norwacki and Abrams have called this process mesophication (2008).

Our modern forests have changed extensively from pre-European settlement forests in which *Acer rubrum* was a minor constituent to its present dominance, with one factor (of many) being a change in fire regime. *Acer rubrum* though favored by many other characteristics has a greater sensitivity to fire than many other species. Periodic burning from Native American practices, lightning strikes, and European settler activities kept red maple populations

low prior to 1900 (Abrams 1998). Later this regime changed, thus presumably causing changes in the importance of red maple. Suppression of forest fire during this century has resulted in increase of *Acer rubrum* in eastern forests as a later successional component (Abrams 1998).

Disturbances shape the structure of a community. One primary disturbance is fire. Boerner (2006) includes disturbance extensively in his synthesis of influences on tree community structure. Of particular interest for the current discussion is the role of fire. When the previous frequency of fire on the landscape has been high, species adaptations and ecosystem properties are determined more by fire than by extreme weather events or sporadic insect outbreaks (Boerner, 2006). The role of fire in eastern North American forests has been extensively studied (Abrams 1992, Abrams and Norwacki 1992, Abrams 1998, Blankenship and Arthur 1999, Iverson and Hutchinson 2002, Boerner *et al* 2004, Hutchinson, Sutherland, and Yaussy 2005, Norwacki and Abrams 2008). Fires increase the mortality of seedlings and saplings of shade tolerant species (Hutchinson Sutherland and Yaussy 2005) and can alter soil conditions favoring drier, more xeric, species (Blankenship and Arthur 1999, Boerner *et al.* 2004).

Abrams (1992) examined the prevalence of *Quercus* species in the Eastern United States both past and present. He noted the propensity for *Quercus* species to exhibit physiological adaptations that favor survival on sites exposed to periods of fire and drought such as thick bark, sprouting ability, resistance to rotting after scarring, etc. He also noted the role of fire in development of *Quercus* forests by keeping *Acer rubrum* and *Acer saccharum* seedlings in lower numbers due to their low tolerance to fire. Abrams (1992) concludes that if current factors antagonistic to oak regeneration (such as a lack of fire) persist into the 21<sup>st</sup> century retrenchment of oak dominance seems inevitable.

Investigation of reintroduction of fire into these forests remains difficult. One reason is that the impact of fire potentially varies with topography. The species rich tree flora of the region tends to follow complex topographically influenced patterns.

#### **Topographic soil moisture-based community structure-**

In the Neotoma Valley, Wolfe *et al.* (1949) deduced that micro-climate patterns influenced by topography are the primary factors that determine the tree species

community. As related in an extensive review by Boerner (2006), the primary early work of Wolfe *et al.* (1949) in the Neotoma Valley area of Ohio described in detail the relationship of aspect and topographic position to tree communities as was first proposed by Geiger (1927). Wolfe *et al.* (1949) concluded that only edaphic extremes, fire, flood, tornado, and clearing supersede micro-climatic controls on tree species community composition. They go further stating that even in disturbance situations an organized pattern of community structure controlled by micro-climate inevitably returns from the seedling level up (Wolfe *et al.* 1949).

Micro-climate determines the tree species community by affecting soil moisture in a variety of ways. In Athens County of southern Ohio McCarthy *et al.* (1984) found slope aspect was a good indicator of species abundances. This relationship suggests that the importance within the community of specific species changes with respect to slope-dependent micro-climate. In the Blue Ridge Mountains, Racine (1971) found a similar pattern, with the addition that seedlings were more broadly distributed. McCarthy *et al.* (1987) studying Hawk Woods, an old growth forest in southeastern Ohio, found a continuum of vegetation that can be characterized into three classes across a topographic

gradient, but these classes have more to do with moisture than with soil type or parent material. McCarthy *et al.* (1987) further speculate that soil moisture is closely tied to soil texture, slope position, and aspect. Other factors complicate the situation. Anderson and Vankat (1978) found that parent material substrate was the key factor in explaining the variation in the tree assemblage. Their study was conducted in Abner's Hollow a few miles from the site of the current study. They did however also find that within each parent material group the vegetation gradient was best explained first by soil moisture and then by human interactions. Their parent material groups were arranged along a topographic gradient.

Soil moisture is the main factor by which the tree species community is distributed in each of these studies. Aspect determines temperature fluctuations and drying, affecting community structure (Wolfe *et al.* 1949). Slope position determines water accumulation which has been shown to affect community structure (McCarthy 1987). Soil material determines water retention capacity which has been shown to also affect community structure (Anderson and Vankat 1978).

A model that was predictive of soil moisture could be expected to be predictive of tree community structure.

Iverson *et al.* (1997) used GIS analysis to predict soil moisture in terms of water retention capacity, topography, and solar incidence with the aim of understanding tree species distribution. Topographic data were used to determine aspect, hill shading, flow accumulation, and curvature, which were then combined with soil water retention data. These factors were weighted by Iverson *et al.* (1997) (Hillshade 40%, Flow Accumulation 30% Curvature 10%, and Total water holding capacity 20%) to produce a GIS-derived model called Integrated Moisture Index (IMI) for predicting relative soil moisture. Iverson and Prasad (2003) classified sites by IMI according to the following rankings: Xeric IMI = 0-35.0, Intermediate IMI = 35.0-50.6, and Mesic IMI = 50.6-100. One impediment to studying topographic relationships has been the lack of a way to quantify species relationships to landscape moisture features. An aim of this study was to use IMI as a tool to do so.

### **Where is my study within this context?**

One difficulty in understanding the drivers of tree community structure in a topographically and vegetationally complex area is quantifying the position of tree species across landscape gradients. In my study I chose to

investigate the distribution of species over the landscape and the impact of prescribed fire at the Edge of Appalachia reserve in Adams County, south-central Ohio.

In 1996, a prescribed burn was performed on a portion of the Edge of Appalachia Preserve. Permanent plots were established by the Nature Conservancy staff and sampled before and after the burn. It was the intent of the experiment not only to examine the long term effects between burn and unburned plots, but to examine how relationships might vary among topographic soil moisture regimes.

The study area is situated on the Appalachian Escarpment in the Western Allegheny Plateau. Elevations in this region vary from 182.9 to 390.1 meters (Braun 1928). The study area is within the Richard and Lucile Durrell Edge of Appalachia Preserve, which is approximately 5261 hectares in size. It is predominately forested land, but also contains some prairie openings. It is maintained jointly by the Nature Conservancy and the Cincinnati Museum. Central to the preserve is the town of Lynx, Ohio (UTM 290370 Easting, 4294358 Northing, Zone 17N), (Cipollini, Maruyama, and Zimmerman 2005).

Using GIS analysis Norwacki and Abrams (2008) modeled both current and past vegetation types and fire regimes for the eastern United States. The current study site falls within the pre-settlement vegetation type of Oak-Hickory and has shifted to Oak-Mesic Hardwoods as the current vegetation. The fire regime grouping of the Edge of Appalachia site has shifted from a pre-settlement group I (frequent fire frequency with low percentage top kill) to currently a transition zone between group III and group V (group III - infrequent fires with low and mixed percentage top kill, and group V - rare fire frequency). Thus it can be expected that the tree species community in the area is undergoing changes in composition concurrent with changes in fire frequency.

## **Hypotheses**

The specific null hypotheses for this study are:

The areas of prescribed burning will be indistinguishable in tree community composition from unburnt areas.

The IMI classes will be indistinguishable in tree community structure from each other.

Mortality will not be distinguishable between burn classes, IMI classes, or the interaction of the two.

Each tree species does not vary in a distinguishable way in relative importance value in the overstory, or relative number in the sapling layer between burn classes, IMI classes, or the interaction of the two.

When location is resolved for individual stems:

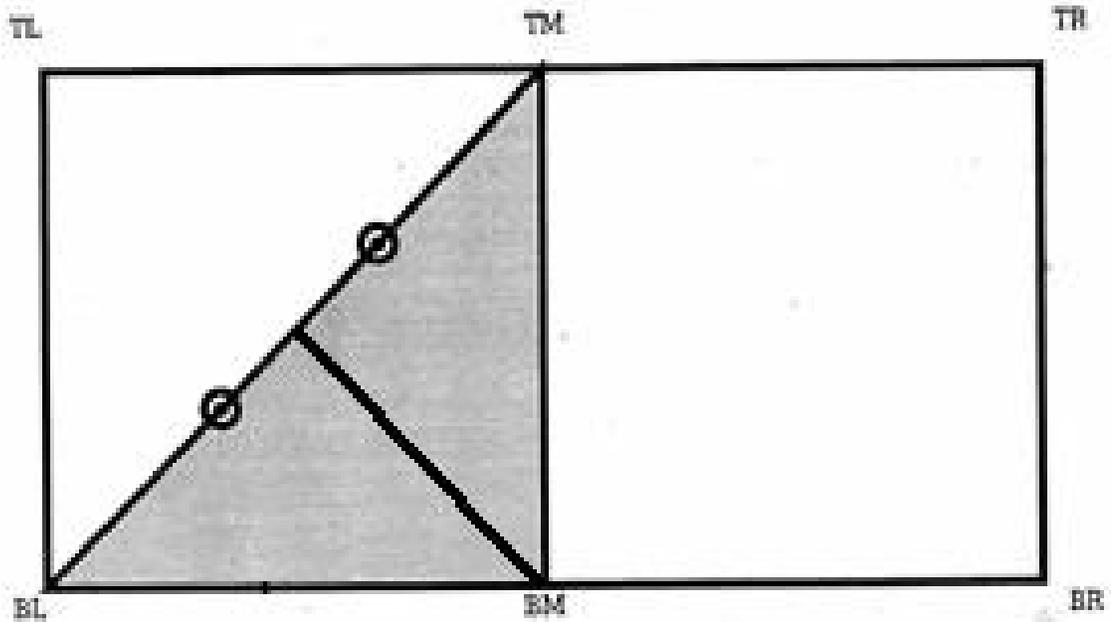
The IMI quantified distribution of each species individually will be indistinguishable from all species taken together, implying that the IMI niche of each species is the same.

## **Materials and Methods**

### **Plot set up and stratification**

In 1996, prior to a prescribed burn, eighteen plots with dimensions of 25 by 50 meters were established in mixed oak forest within the Edge of Appalachia Preserve. Nine of these plots would lie within a prospective burn area and the remaining nine plots would lie exterior to the burn area as control sites. Plot sites were selected based upon stratification across three IMI classes: xeric for IMI less than 35, intermediate for IMI 35 - 50, and mesic for IMI 50 - 67. Each IMI class interior and exterior to the burn would contain three replicates. . Six other plots were situated on limestone barren communities: three within and three outside the burn; they were not included in my study.

Each plot was further sub-divided into two 25 by 25 meter sub-plots, one for analysis of the sapling layer. The sapling sample plots were triangular subdivisions of the 25 by 25 meter half plot. Saplings were sampled across half of one of these 25 by 25 meter plots, or in some cases where their numbers were too large for this to be measured they were sampled in one quarter of the region (Fig. 1). My analysis contains information from the 25 by 50 meter plots for trees and the sapling sub-plots.



**Figure 1. Plot Design.** TL, TR, BL, and Br are plot corners. Tm and Bm are plot midpoints. Horizontal distance is 50 meters, vertical distance is 25 meters. Grey triangles are for sapling plots. When sapling abundance was very high only triangle closest to mid-line was sampled. Figure is adapted from Edge of Appalachia provided document.

## **Sampling of plots**

### **Overstory diameter and species sampling**

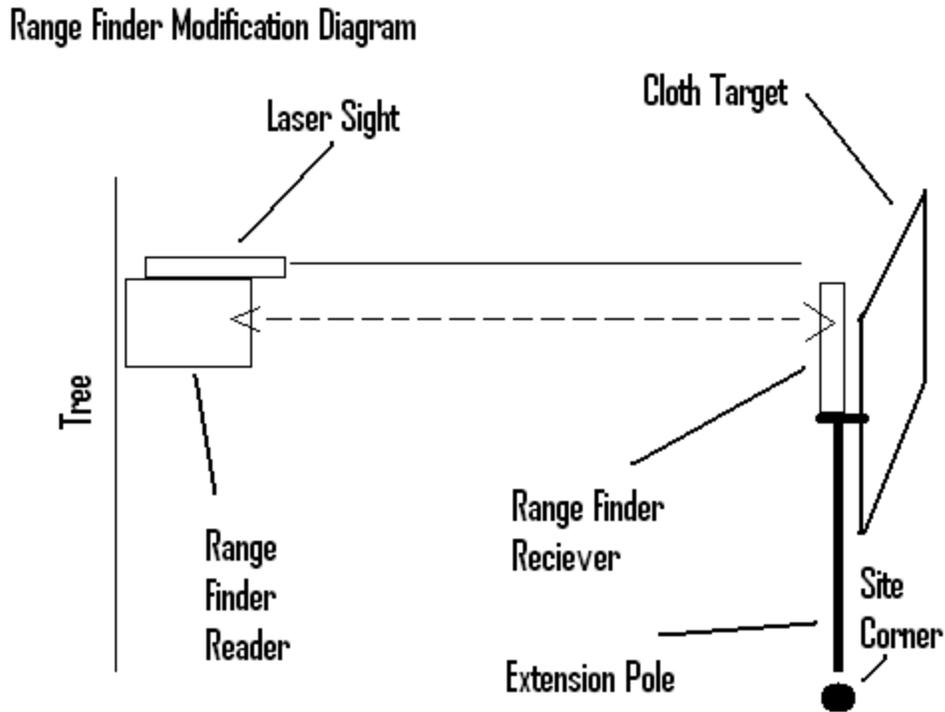
For the canopy layer, defined as trees  $\geq 10$ cm diameter at breast height (hereafter dbh), each canopy tree over each whole plot of 25 x 50 meters was measured. Canopy trees were identified to species except *Carya* and *Pinus* which were identified to genus. Trees were then identified as living or dead and their dbh measured.

### **Overstory tree spatial sampling**

Position estimates for the locations of overstory trees relative to the corners of the plots were recorded in 2001. In 2008, the latitude and longitude of each of the corners of each plot were recorded from a handheld GPS unit. In 2009, accurate position information on the canopy layer trees was collected using a set of Sonin Combo Pro range finders modified using a pole, target, and sight set up as in Figure 2 to allow for accurate sighting through or above foliage. Distance from each tree to two plot corners or mid-points were measured, forming a triangle of points from which the tree's position could be derived. When a mid-point was used the side of the mid-line on which the tree was located was recorded. In the case of blockages by

foliage or hill curvature, a point lying along the same line between the tree and the corner or midpoint was measured, and then the remaining distance was measured.

**Figure 2. Diagram of Rangefinder Modification Apparatus**



### **Sapling diameter class and species sampling**

Saplings were defined as stems less than 10 cm dbh and greater than 1.3 meters tall. They were classed into three size classes: less than 3 cm dbh, 3-6 cm dbh, and 6-10 cm dbh. Saplings were identified to species except *Carya* and *Pinus* which were identified to genus.

### **Plot Soil Sampling**

Four soil cores were collected for each plot. After the last tree was measured ten paces were taken from that point in a haphazard direction and a soil core was taken. After that sample an angle was chosen and ten more paces taken, after which a soil core was taken. This process was repeated until there were four soil cores for each plot. Sand, silt, and clay percentages were derived using the Rooney Lab Soil Texture Protocol, which is a modified version of Brian McCarthy's Soil Texture Protocol (Sheldrick and Wang 1993).

### **Chronology of sampling**

In 1996, pre-treatment sampling was completed by the Nature Conservancy staff. From 1997 to 1999 they completed post-treatment sampling of the herbaceous layer. The canopy was sampled in 1996, 1997, and 2001. The sapling layer was sampled in 1997, 1998, 1999, and 2001. Sampling before 2001 was undertaken by the Nature Conservancy staff, 2001 sampling was accomplished by Dr. James Runkle. These data were collected prior to my involvement. In July of 2008 I completed sampling the canopy and sapling layers. I then compiled canopy data from 1997, 2001, and 2008 and sapling

data from 1997, 1998, 1999, 2001, and 2008 into a Microsoft Excel data sheet. The overstory position data were collected between summer 2009 and winter 2010.

### **Variables for understanding the role of a species**

For the purposes of this study a P value of  $\leq 0.05$  will be considered statistically significant for rejection of a null hypothesis. I have used several calculated values in my analysis to characterize a tree species within the assemblage. These parameters are defined below.

Total or Species Basal Area = Number of Stems  $\times \pi \times \text{dbh} \times \text{dbh} / 4$

(Runkle 1990, 2000, 2007, McCarthy et al. 1984, McCarthy 1987)

Relative Number of stems = Number of stems of species / Total number of stems (Runkle 2007)

Relative Basal area = Basal area of species / Total Basal Area (Runkle 2007)

Relative species importance value = (Relative Basal Area + Relative Number) / 2  
(McCarthy et al. 1984, McCarthy 1987)

Mortality as exponential decay

Avg annual mortality = where:

S = number of survivors

No = Original number

Y = number of years between samples

(Runkle 1990, 2000, 2007)

## **Ordination**

### **Nonmetric multi-dimensional scaling**

Ordination procedures were run to detect community composition differences. Ordination was run in PC-Ord version 4.41. Nonmetric multidimensional scaling (hereafter NMS) was the chosen ordination procedure. Mather (1976) and Kruskal (1964) describe the method. Bray-Curtis (aka Sorensen) distance was used as the distance measure. The starting point was randomly chosen. There were 40 runs with real data. Dimensionality was assessed using a Scree plot comparison to 50 Monte Carlo randomized runs. PC-Ord ordination runs of NMS settled on two axes for saplings and three for the overstory. Axes are added until a further increase in the number of axes does not decrease stress in real data more than it does for Monte Carlo randomized data. There were 3 dimensions in the final solution run for overstory plots and 2 dimensions in the final solution run for the sapling plots. Stability was assessed based upon stress level stability vs. iteration.

## **Class-level Statistical Analyses**

### **Multivariate**

Multivariate class-level data were analyzed using PC-Ord version 4.41. Multi-response Permutation Procedures (hereafter MRPP), a non-parametric permutation based analysis was used as described in the appendix of Biondini et al. (1985). Bray-Curtis distance (aka Sorensen distance) was used as the distance measure, both in MRPP, and in NMS. Rank transformation (as in McCune et al. 2001) was chosen as a correction for any loss of distance measure sensitivity with heterogeneous communities. Groups were weighted as  $N/\sum(n)$ , the weighting option recommended by Mielke (1984). MRPP was used as above to compare plot overstory relative importance values and sapling plot relative number for each species by IMI class groupings and by burn class groupings. MRPP was also used to compare the overstory grouping generated by NMS. The test was run for all years taken together (pseudoreplication relaxed) and each year taken separately (true replicates). The aim here was to evaluate the presence/absence/magnitude of community level differences across classes.

## **Single Variable**

Univariate class-level data were analyzed using SAS version 9.2. SAS was used to derive and analyze values for total mortality, total basal area, total number of stems, and relative species importance values (overstory), relative number (saplings) for each species. Each was compared using analysis of variance (hereafter ANOVA) with classes burn, moisture index class, and burn\*moisture index class.

## **GIS Map Construction**

For individual stem analyses, a GIS map of the study area was constructed with the aim of resolving environmental variables for each stem. ArcMap was used to construct an IMI map of the study area at very high resolution using 1/3 arc second topographic maps available on Seamless Data Server (Gesch et al. 2002), and SSURGO soil maps compiled by US Department of Agriculture, Natural Resources Conservation Service available through Soil Data Mart (Soil Survey Staff). The same data can be used to create maps of very low or very high resolution by adjustment of only a few variables at several steps in this

process. As a consequence a detailed method description is included in the appendix.

The resultant IMI map consists of a combination of several GIS derived features weighted together to be predictive of relative soil moisture. The weighting of features, as in Iverson et al. (1997), is as follows: Hillshade 20%, Flow accumulataion 30%, Curvature 10% and Total soil water capacity 20%.

#### **Plot Location and Orientation Determination**

The Nature Conservancy provided a field navigation topographic map that was used for locating the plots in the field. This map was not used to directly derive the plot corners in the GIS map, but used as a check of approximate plot locations. This choice was made despite success in the field of using this map to locate plots without any detectable inconsistency. The reasons for not using the provided field map were that it lacked a depicted scale or projection, and the plot markers in most cases did not accurately depict the plot shapes. Thus direct importation into GIS would introduce great inaccuracy. Instead plot corner marker locations were directly measured in the

field, and checked for consistency with the field navigation map according to the following procedure.

Due to variable accuracies of corner measurements from the handheld GPS unit special steps were taken to ensure a high degree of accuracy of plot location importation into the constructed GIS map. The UTM Northing and Easting values for each plot corner were averaged (Northing A, B, C, and D together, and Easting A, B, C and D together) in order to derive a plot center value. This center value would be less skewed by inaccuracies of any individual sample measurement. This value was then compared to an overlay of topographic field navigation maps provided by the Nature Conservancy on which the position of each plot was labeled.

The criteria for acceptance of the derived plot center value were: each plot center must have the same aspect as center of plot marker on the Nature Conservancy field map, a matching distance up the slope, and must be located within the plot marker on the Nature Conservancy field map. If all criteria were not met, plot corners were derived from the Nature Conservancy field map using the center of marker as a centroid and the angle of orientation on the

map as the bearing from which to build the plot corner values. This was the case in one plot (A33).

The directional orientation of each plot was determined by similar averaging procedure as the plot center values excepting A33. The center of each short side of the plot was derived by averaging its corresponding two corners and a slope was taken between. Since GPS values were in UTM (a flat surface) slope is an acceptable alternative to bearing calculation. This directional orientation was then overlaid onto the plot center values and plot corners and midpoints were extrapolated according to the equations:

$A = \text{atan}(\text{slope})$	$N = H + (12.5 * (\cos(A)))$
$B = \text{atan}(1/\text{slope})$	$O = G + (-12.5 * (\sin(A)))$
$E = C + (25 * (\sin(A)))$	$P = H + (-12.5 * (\cos(A)))$
$F = D + (25 * (\cos(A)))$	$A = \text{Angle}$
$G = C + (-25 * (\sin(A)))$	$B = \text{Reciprocal of Angle}$
$H = D + (-25 * (\cos(A)))$	$C = \text{Centroid Easting}$
$I = E + (12.5 * (\sin(A)))$	$D = \text{Centroid Northing}$
$J = F + (12.5 * (\cos(A)))$	$E = \text{Side One Center Easting}$
$K = E + (-12.5 * (\sin(A)))$	$F = \text{Side One Center Northing}$
$L = F + (-12.5 * (\cos(A)))$	$G = \text{Side Two Center Easting}$
$M = G + (12.5 * (\sin(A)))$	$H = \text{Side Two Center Northing}$

I = Corner One Easting	Q = C+ (12.5(sin (B)))
J = Corner One Northing	R = D+ (12.5(cos (B)))
K = Corner Two Easting	S = C+ (-12.5(sin (B)))
L = Corner Two Northing	T = D+ (-12.5(cos (B)))
M = Corner Three Easting	Q = Midpoint One Easting
N = Corner Three Northing	R = Midpoint One Northing
O = Corner Four Easting	S = Midpoint Two Easting
P = Corner Four Northing	T = Midpoint Two Northing

This procedure produced a map of plot corners and midpoints that agreed with the locations of plots. It was also congruent with their orientation on the Nature Conservancy field map, while still exhibiting the high level of between corner distance accuracy that the plots exhibited when measured directly with optical range finders in the field. This accuracy of between corner distances was not true of Nature Conservancy field map.

### **Individual Overstory Tree IMI Derivation**

The overstory tree distances from plot corners, collected in the field from optical range finders, were used to triangulate the within-plot location to the nearest 0.1m (excepting fallen trees that were uprooted whose accuracy is roughly 1m). The following adapted trilateration procedure was used:

Distance to corner P = A

Distance to corner W = B

Px= Easting of P

Py = Northing of P

Wx = Easting of W

Wy = Northing of W

$\Delta x = Px - Wx$

$\Delta y = Py - Wy$

$\Delta^2 = \Delta x^2 + \Delta y^2$

$\Delta = \text{SQRT}(\Delta^2)$

$S = (\Delta^2 + A^2 - B^2) / (2 * \Delta)$

$Cx = Px + \Delta x * S / \Delta$

$Cy = Py + \Delta y * S / \Delta$

$U = \text{SQRT}(A^2 - S^2)$

$Dx = Cx - \Delta y * U / \Delta$

$Dy = Cy - \Delta x * U / \Delta$

$Ex = Cx + \Delta y * U / \Delta$

$Ey = Cy + \Delta x * U / \Delta$

Coordinates of Possibility 1 =

Dx, Dy

Coordinates of Possibility 2 =

Ex, Ey

Method from Kaminsky (2007).

Using the co-ordinates of the plot corners derived in the previous equation in place of corners P and W, the within-plot positions were determined. It is of special note that this equation produces two possible values. One value falls within the plot and one falls exterior. This location information, as well as species and corresponding basal area for each year, was then imported directly into ArcMap. The data for each overstory tree were then combined with the corresponding map values of IMI of the corresponding 1m<sup>2</sup> raster cell in which it is located. This information was then exported from the map into a spreadsheet containing the corresponding value of each variable above for every living overstory tree.

### **Individual Overstory Tree Species Analysis**

To test for IMI habitat restrictions of individual species the relative cumulative frequencies of IMI values for each species at a given IMI value were compared to the values for all stem locations in the study using the Kolmogorov-Smirnov test. Kolmogorov-Smirnov testing was run in SPSS (S-plus). This was done for only species that made up more than 1% of the sample. A Bonferroni correction was

then used to adjust the statistical significance to the number of tests. The Bonferroni adjusted p value was 0.03. The median, 2<sup>nd</sup> and 3<sup>rd</sup> quartile were calculated for the IMI distribution of each species that made up more than 1% of the stand based on frequency.

### **Limitations**

#### **Pseudoreplication of Burn (Hurlbert 1984)**

This study is of a single burn. Plots are true replicates for analyzing integrated soil moisture index trends but technically for analysis of burn/unburn they are pseudoreplicates. It is important to be aware that treating each burn plot as an independent replicate underestimates the true variability of prescribed burning. Fuel potential and weather conditions during the burn would be more similar amongst plots than if they were separated spatially. This may result in similarity of temperature or other factors related to this burn that may not be similar in all burns conducted in this locality. One benefit of a single burn locality is that the environmental variability between plots is decreased due to spatial as well as

temporal closeness amongst plots, therefore increasing the statistical power of the tests.

Relaxation of the stipulation of independence may be a proper course of action in the case of the burn. Even though the burn was a single event, each plot experienced it independently of each other. Variation among plots in total number of saplings and woody debris would suggest differences that would change the nature of the burn between plots because each plot would be subject to different localized burn conditions determined by just how much combustible material each plot contained, among other factors.

#### **Other relaxed stipulations and justification**

My analysis of GIS-derived variables for overstory trees treats each tree as an independent sample despite the non-random way in which the trees were sampled (organized into plots that were stratified beforehand evenly across a preset IMI range). This stipulation is relaxed because zero values for trees at a given IMI are more likely a result of unfavorable IMI than some other small scale spatially dependent disturbance. Two main lines of reasoning support

this choice. There is an even distribution of sampling effort across the entire IMI range within the study region (ignoring non forest areas). Also, the replication of each sampling block of IMI values (plot) multiple times across the study area lessens the probability of spatial dependence of one tree on another. Within each plot a high degree of IMI variation exists (Fig 20). Despite adjacency of cells, high local variation in IMI exists even between adjacent cells. Thus, I have relaxed the independence stipulation of the Kolmogorov-Smirnov test and am aware that as such, the statistical significance of the tests must be treated with caution.

### **Method Justification and Evaluation**

Since certain methods may not be standard, it is worthwhile to discuss the reasoning behind these choices. For univariate class level analysis ANOVA, a parametric test, was chosen because the distributions of individual species within plots were assumed to approximately fit normal distributions. Total basal area and stem number were not significantly different across classes when resolved at the whole plot level. The Kolmogorov-Smirnov test was chosen for analysis of IMI of individual stems. This non-

parametric test was chosen because it makes no assumptions about the distribution of values. IMI when resolved to the stem level does not follow a normal distribution, more stems occur in low and high IMIs than in intermediate values. Thus comparisons to all stem occurrences compare each species to a non-normally distributed curve.

Multivariate analysis was done using MRPP. MRPP makes no distributional assumptions, unlike discriminate analysis or MANOVA which assume multivariate normality and homogeneity of variance, which are seldom met for community data (McCune and Grace 2002). MRPP gives a test statistic (T) for the separation between groups, an effect size (A), and a measure of probable deviation from random (P). Each of these is a useful statistic for the aims of this study. The test statistic measures the distinctness of communities, the effect size measures the strength of the relationship, and the p-value demonstrates the likelihood of type I error. Rank transformation for MRPP was done to correct for any possible loss of sensitivity of distance measures for heterogeneous plots, (McCune 2000).  $N/\sum(n)$  was used to weight groups (Mielke 1984). For both MRPP and NMS Bray-Curtis distance was used as the distance measure.

This was done because Bray-Curtis is a semi-metric with a fixed maximum for sample units sharing no species (McCune and Grace 2002).

NMS was chosen as the ordination technique used in this study. NMS is based on ranked distances, and thus can be more effective at extracting information from nonlinear relationships (McCune and Grace 2002). Also, NMS does not exhibit a "zero truncation problem". NMS makes no assumptions of linear relationships among variables, which may or may not be the case with much of this data, (McCune and Grace 2002). NMS also performs well when gradient strength is unequal (Fasham 1977). Gradient strength is likely unequal in my data. Bray-Curtis ordination was not used because of the necessity for arbitrary choice of initial reference points. Subjective choice of end-points, though useful in many cases, would restrict interpretation of ordination to within the line of reasoning that justified the choice of endpoints. This choice would prevent a more general description of community structure. The reasons behind the choice of indirect gradient analysis over direct gradient analysis in this specific case are explained well by a quote from Beals (1984):

“Species differences between two samples do reflect their environmental differences, but in a highly integrated fashion, which includes differences in biotic interaction and in historical events. The environmental differences are automatically scaled according to overall species response. Therefore the ordination with the clearest species patterns reflects the environmental space the way the biotic community interprets it.”

De-trended Correspondence Analysis (DCA or DECORANA) was not chosen for two reasons. First, DCA rescaling of axes assumes all species have unimodal response curves with homogenous variances, and this may or may not be the case (Jackson and Somers, 1991). Second, there is a high potential instability associated with the selection of the number of axis segments with my number of sample sites (Jackson and Somers, 1991).

## **Results**

### **Overall Study Area**

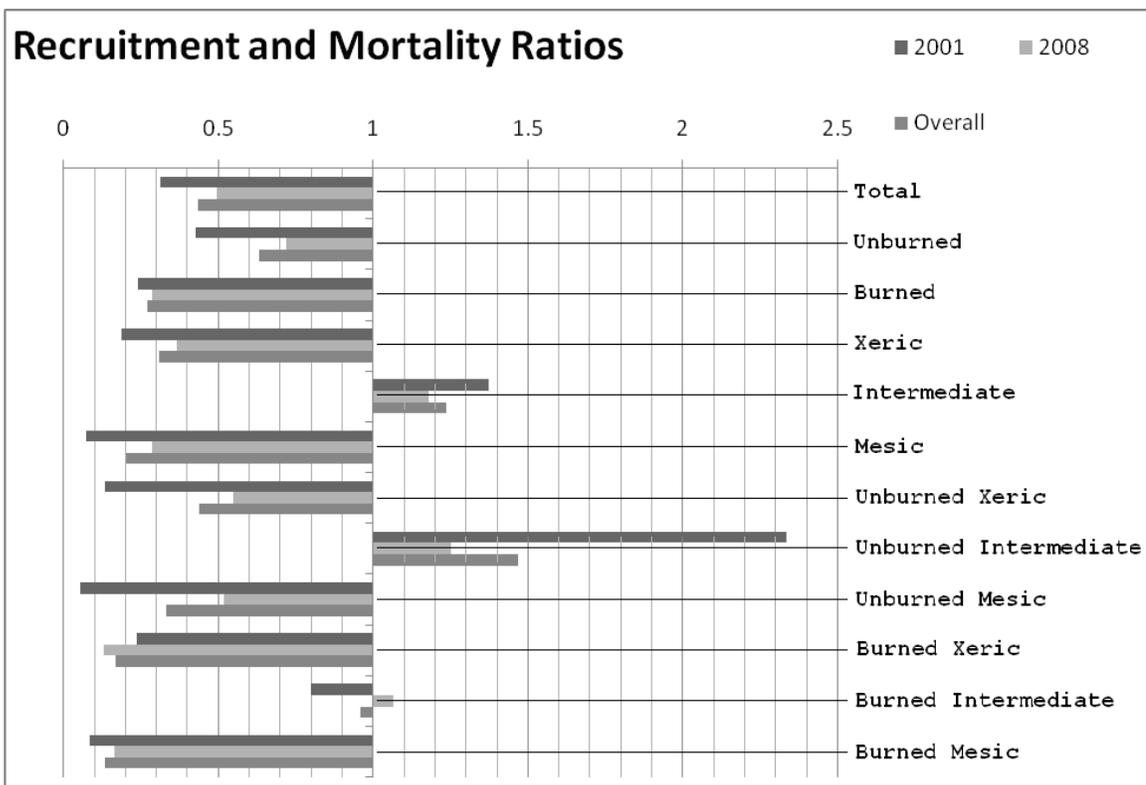
The total number of overstory stems contained within the study plots in 1997 was 987 (439 /ha); this decreased to 982 (436 /ha) in 2001, and increased to 1000 (444 /ha) in 2008. Total basal area of overstory stems increased from 26.51 m<sup>2</sup>/ha in 1997 to 28.09 m<sup>2</sup>/ha in 2001 to 31.45 m<sup>2</sup>/ha by 2008. The total number of sapling stems was 2228 in 1997, 1955 in 2001 and 2115 in 2008 .Altogether 35 species were found in the study plots as saplings or overstory stems (Table 1). Elevation varies from 138–386 m (Fig 4). Soil moisture index ranges from 2 – 80 IMI (Fig 5).

For overstory stems the study area presented an overall annual mortality of 2.83% from 1997 to 2001. From 2001–2008 annual mortality was 2.78%. Recruitment was greater than mortality with the exception of intermediate plots (Fig 3). Mortality differences between burn treatments, IMI classes and interactions were not significantly different according to ANOVA.

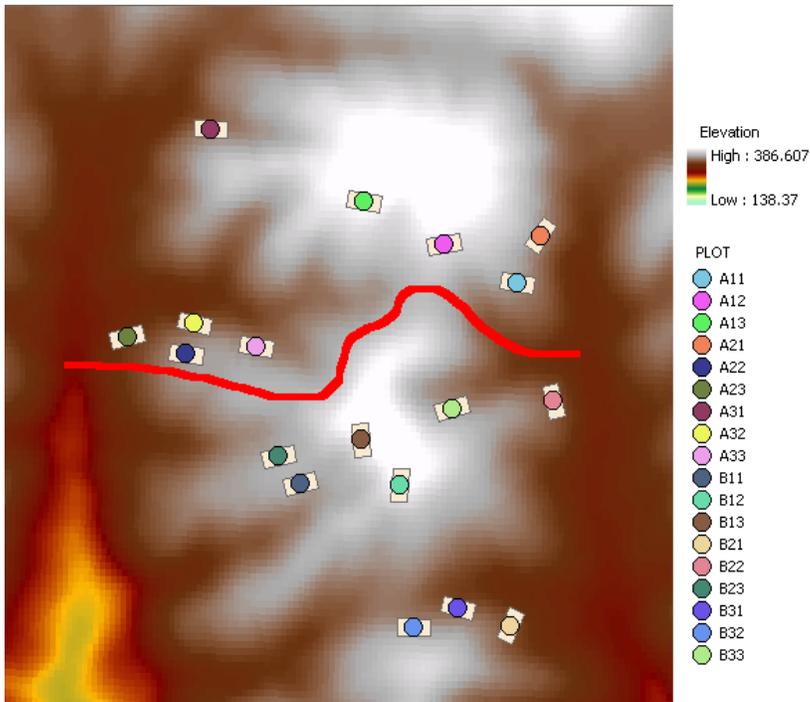
**Table 1. List of identified tree species occurring within study area.**

**Species List**

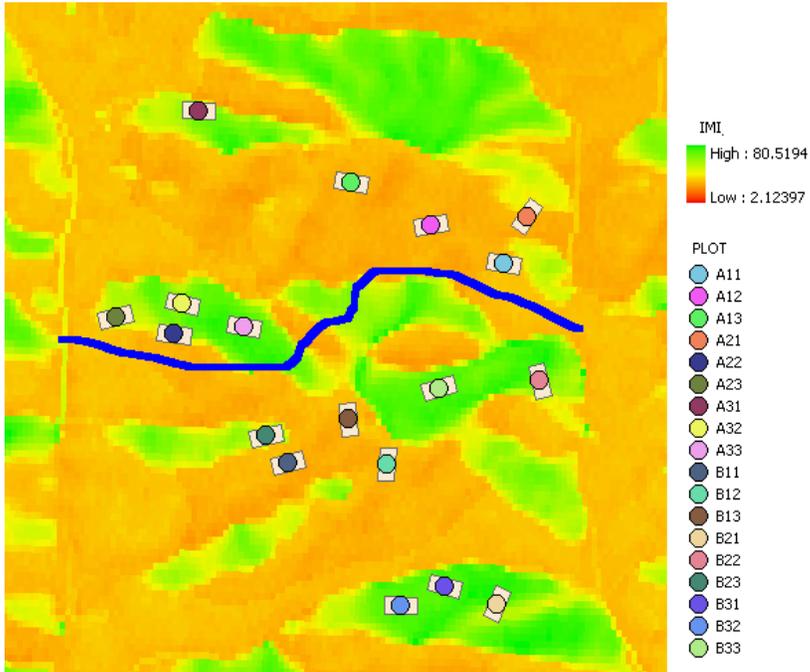
<u>Genus</u>	<u>Species</u>	<u>Common</u>	<u>Abbrev.</u>	<u>Genus</u>	<u>Species</u>	<u>Common</u>	<u>Abbrev.</u>
Acer	rubrum	Red Maple	ACRU	Nyssa	sylvatica	Black Gum	NYSY
Acer	saccharum	Sugar Maple	ACSA	Ostrya	virginiana	Hop-Hornbeam	OSVI
Amelanchier	arborea	Serviceberry	AMAR	Pinus	sp.	Pine	PINUS
Asimina	triloba	Paw Paw	ASTR	Platanus	occidentalis	Sycamore	PLOC
Carpinus	caroliniana	Musclewood	CACA	Populus	grandidentata	Bigtooth Aspen	POGR
Carya	sp.	Hickory	CARYA	Prunus	serotina	Black Cherry	PRSE
Cercis	canadensis	Redbud	CECA	Quercus	alba	White Oak	QUAL
Cornus	florida	Dogwood	COFL	Quercus	coccinea	Scarlet Oak	QUCO
Fagus	grandifolia	American Beech	FAGR	Quercus	prinus	Chestnut Oak	QUPR
Fraxinus	americana	Ash	FRAM	Quercus	rubra	Red Oak	QURU
Hamamelis	virginiana	Witch Hazel	HAVI	Quercus	velutina	Black Oak	QUVE
Juniperus	virginiana	Red Cedar	JUVI	Rhododendron	calendulaceum	Flame Azalea	RHCA
Lindera	benzoin	Spicebush	LIBE	Robinia	pseudoacacia	Black Locust	ROPS
Liriodendron	tulipifera	Tulip Poplar	LITU	Sassafras	albidum	Sassafras	SAAL



**Figure 3. Mortality/recruitment ratios by treatment class.** Mortality/recruitment ratio calculated as number of dead stems/number of new stems. 2001 interval is 1997-2001, 2008 interval is 2001-2008.



**Figure 4. Map of study area with topographic overlay.**  
Plots below red line were burned.



**Figure 5. Map of study area with IMI overlay.**  
Plots below blue line were burned.

### **Community differences among treatments**

Multi-response permutation procedures (MRPP) were run in order to detect multivariate community level differences among treatments (Table 2). For each year individually, as well as all years grouped together in both overstory and sapling level analyses, IMI class groupings were statistically significant. For this test, P can be interpreted as the likelihood that the ranked groupings are as distinct as or greater than due to chance. Effect sizes (A-value) ranged from 0.306 to 0.208. The test statistic values (T) is the separation between groups. The more negative the T value the stronger the separation. Highly negative T values indicate communities with little between group similarities. High values of A indicate that plots are similar within groups. Low A and T values with no statistical significance were found between burned and unburned plots.

**Table 2. MRPP multivariate analysis of treatment classes.**

Grouping	Year	Overstory A	Overstory T	Overstory P-value	Saplings A	Saplings T	Saplings P-value
Burn	Total	0.0008	-0.566	0.3313	0.0134	-1.022	0.1335
Burn	1997	-0.0362	0.819	0.8482	-0.0238	0.617	0.6837
Burn	2001	-0.0331	0.748	0.7862	-0.0315	0.817	0.8083
Burn	2008	-0.0410	0.923	0.9649	-0.0256	0.656	0.7070
<b>IMI Class</b>	<b>Total *</b>	<b>0.3059</b>	<b>-14.746</b>	<b>&gt;0.0001</b>	<b>0.2714</b>	<b>-14.455</b>	<b>&gt;0.0001</b>
<b>IMI Class</b>	<b>1997*</b>	<b>0.2360</b>	<b>-3.653</b>	<b>0.0058</b>	<b>0.2077</b>	<b>-3.687</b>	<b>0.0044</b>
<b>IMI Class</b>	<b>2001*</b>	<b>0.2502</b>	<b>-3.877</b>	<b>0.0044</b>	<b>0.2222</b>	<b>-3.892</b>	<b>0.0032</b>
<b>IMI Class</b>	<b>2008*</b>	<b>0.2673</b>	<b>-4.120</b>	<b>0.0032</b>	<b>0.2104</b>	<b>-3.695</b>	<b>0.0044</b>
A = Chance corrected within group agreement (effect size)							
T = Between group difference							
Statistically significant values marked with * and in Bold							
Note: MRPP sample independence assumption is violated for multiple year designs in Total. In case of "Total" samples are pseudoreplicates.							

### Structural and species differences among treatments

ANOVA analysis did not detect statistically significant differences between burn classes, IMI classes, or their interaction in total number of overstory stems, overstory basal area, or total number of sapling stems.

Interpretation of ANOVA results showed species specific tendencies. In the overstory *Liriodendron tulipifera* has far higher importance values in the mesic sites (Fig 7, Table 3) and *Quercus prinus* has far higher importance values in the xeric sites (Fig 6, Table 3). Saplings of one species, *Carpinus caroliniana*, showed statistical significance across all years and all classes

(Table 3). *Carpinus caroliniana* saplings appear to be disfavored by burning in mesic plots, but favored at intermediate sites, and largely absent from xeric sites (Fig 10). *Acer rubrum* and *Sassafras albidum* exhibit statistical significance across IMI class in all years. *Acer rubrum* saplings were more prevalent in xeric-intermediate plots (Fig 9). *Carya* stems exhibit significance across IMI class and interaction of classes in 1997 (Table 2). *Carya* appears to be favored by burning in intermediate plots (Fig 11). *Sassafras albidum* saplings are significantly different across IMI class in all years (Table 3), showing an overall preference for xeric plots (Fig 12) and a strong positive affinity for burned mesic plots in the overstory in 1997 (Fig 8).

Most species within the study area do not appear to be strongly affected by the single burning. For overstory *Sassafras albidum* and sapling *Carya* the effects of burning are initially strong but fade with time. Effects of burning on *Carpinus caroliniana* lasted through all sample years.

Prevalence of *Quercus prinus*, *Liriodendron tulipifera*, *Acer rubrum*, *Sassafras albidum*, and *Carpinus caroliniana* appear to be influenced by IMI classes. This conclusion excludes the relative number in the overstory of *Quercus*

*coccinea* and *Fagus grandifolia* the year after burning. High single plot abundances and lack of coincident importance value significance make results for these two species probable sampling artifacts due to low overall numbers and high numbers clustered in a single plot.

**Table 3. Total Species Relative Abundance and ANOVA**

Species names are first two letters of genus and species excepting CARYA and PINUS which are genus names.

Total Species Relative Abundance and ANOVA of Classes for Each Species						
Species	Sapling			Overstory		
	1997 Relative Number	2001 Relative Number	2008 Relative Number	1997 Importance Value	2001 Importance Value	2008 Importance Value
QUPR	3.9	3.8	4.8	<b>35.8 T</b>	<b>35.5 T</b>	<b>35.2 T</b>
LITU	3.3	2.7	2.9	<b>13.6 T</b>	<b>14.9 T</b>	<b>15.5 T</b>
ACRU	<b>15.3 T</b>	<b>14.8 T</b>	<b>13.6 T</b>	9.2	9.5	11.3
ACSA	7.3	7.4	6.5	7.4	7.7	8.1
SAAL	<b>12.2 t</b>	<b>12.8 t</b>	<b>12.4 t</b>	<b>7.3 i</b>	6.9	6.3
CARYA	<b>0.4 TI</b>	0.5	0.8	5.0	4.5	4.0
QUAL	0.2	0.2	0.2	3.4	3.5	3.5
NYSY	4.2	4.3	4.0	2.9	3.1	3.0
QUVE	0.6	0.6	0.6	2.8	2.8	2.7
QUCO	0.2	0.4	0.5	2.7	2.3	2.1
FAGR	2.2	2.1	2.1	1.7	1.7	1.8
FRAM	1.6	1.4	1.1	0.9	0.9	1.3
PINUS	0.0	0.1	0.2	1.6	1.6	1.3
JUVI	1.5	1.2	1.0	0.6	0.8	0.7
COFL	5.7	2.3	6.8	1.8	1.1	0.5
ROPS	0.6	0.6	0.6	0.6	0.4	0.5
OSVI	11.4	12.9	11.9	0.1	0.1	0.2
CECA	3.3	3.4	3.5	0.1	0.1	0.0
ASTR	5.3	5.9	5.5	0.0	0.0	0.0
LIBE	6.3	6.9	6.3	0.0	0.0	0.0
CACA	<b>12.0 BTI</b>	<b>13.5 BTI</b>	<b>12.5 BTI</b>	0.1	0.1	0.0

All statistically significant values in bold type  
ANOVA significant difference 0.01 < P <= 0.05 with b = burn classes, t = IMI classes, i = interaction  
ANOVA significant difference P < 0.01 with B = burn classes, T = IMI classes, I = interaction

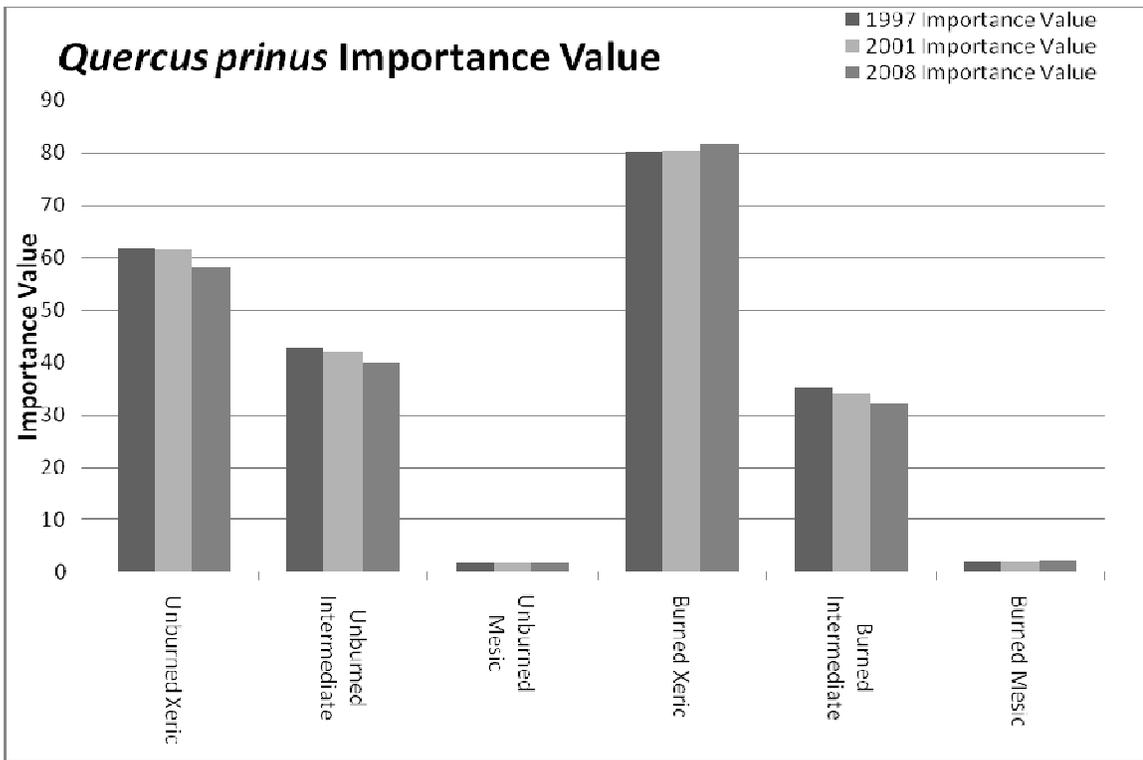


Figure 6. Importance value by treatment across all years for *Quercus prinus*.

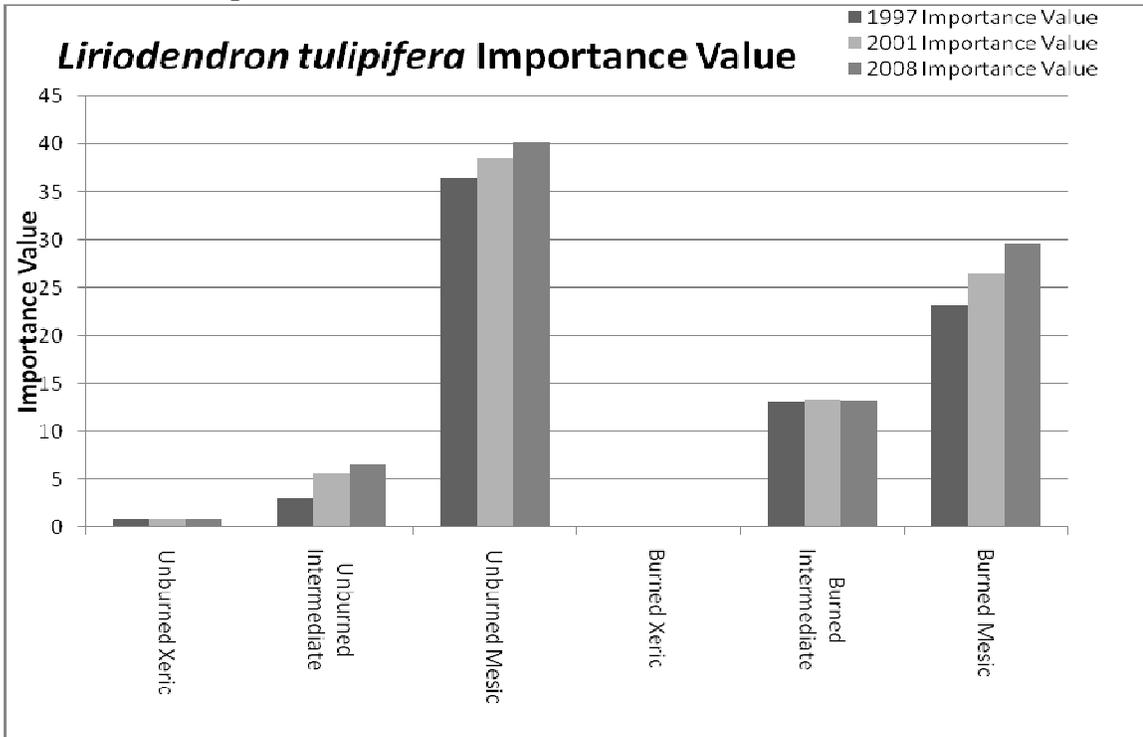


Figure 7. Importance value by treatment across all years for *Liriodendron tulipifera*.

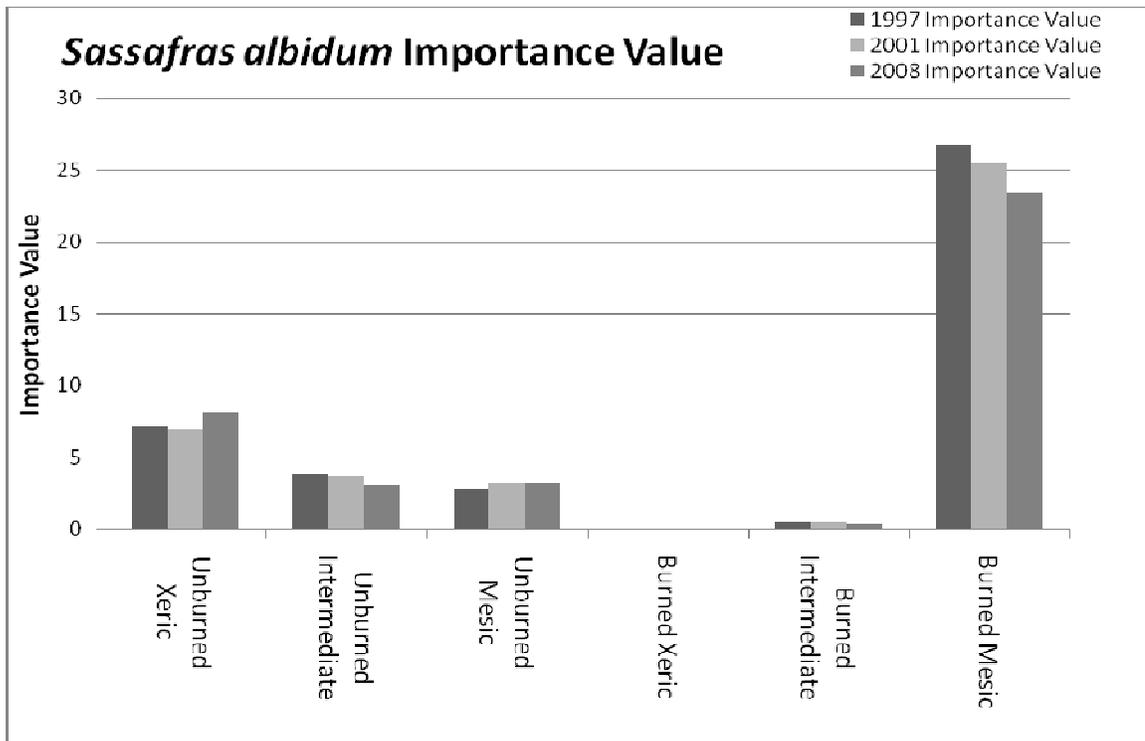


Figure 8. Importance value by treatment across all years for *Sassafras albidum*.

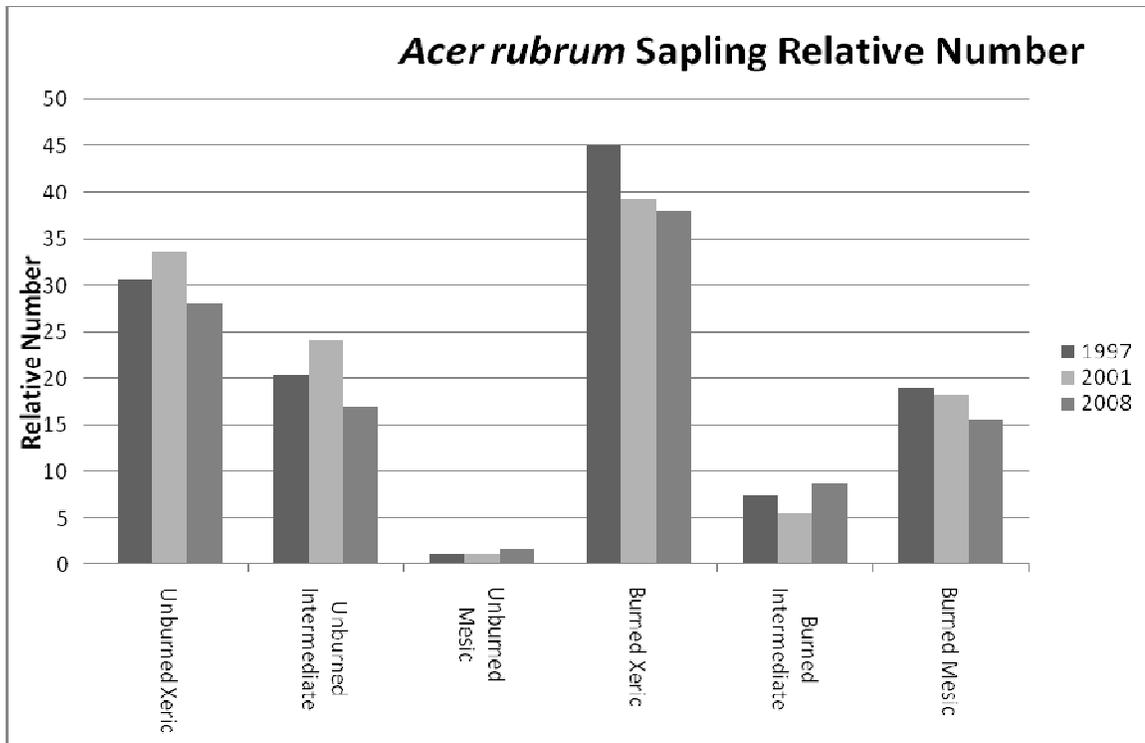


Figure 9. Relative number of saplings across all treatments in all years for *Acer rubrum*.

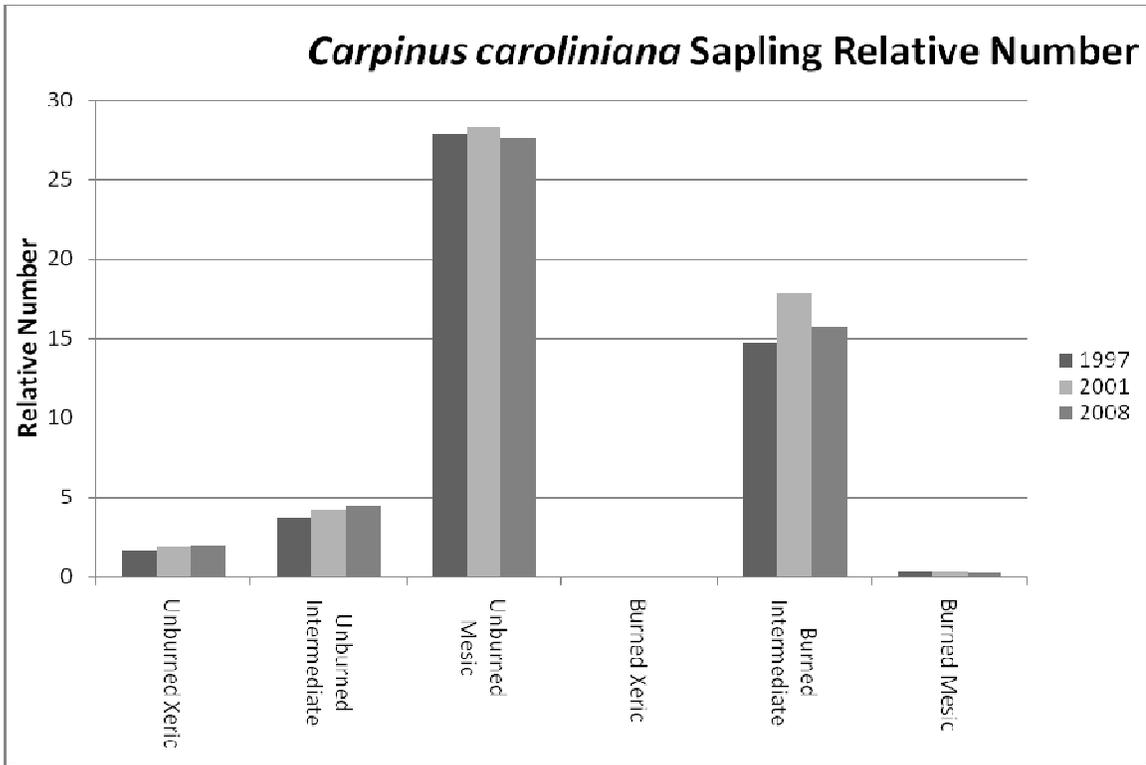


Figure 10. Relative number of saplings across all treatments in all years for *Carpinus caroliniana*.

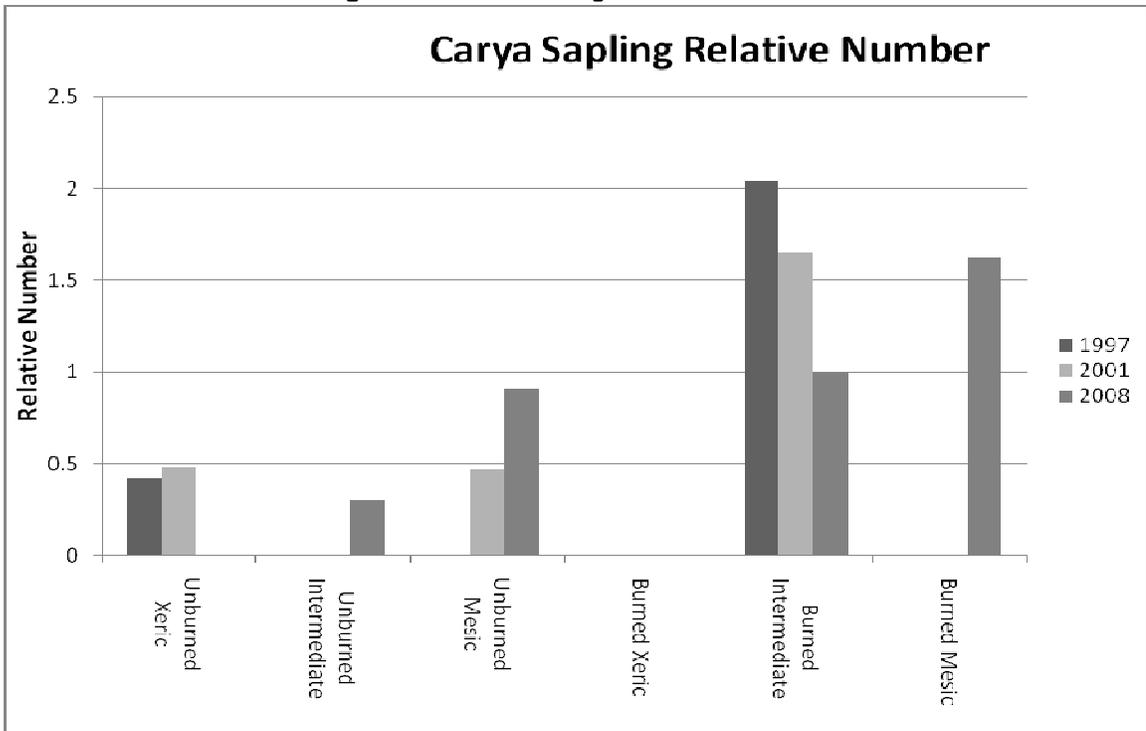
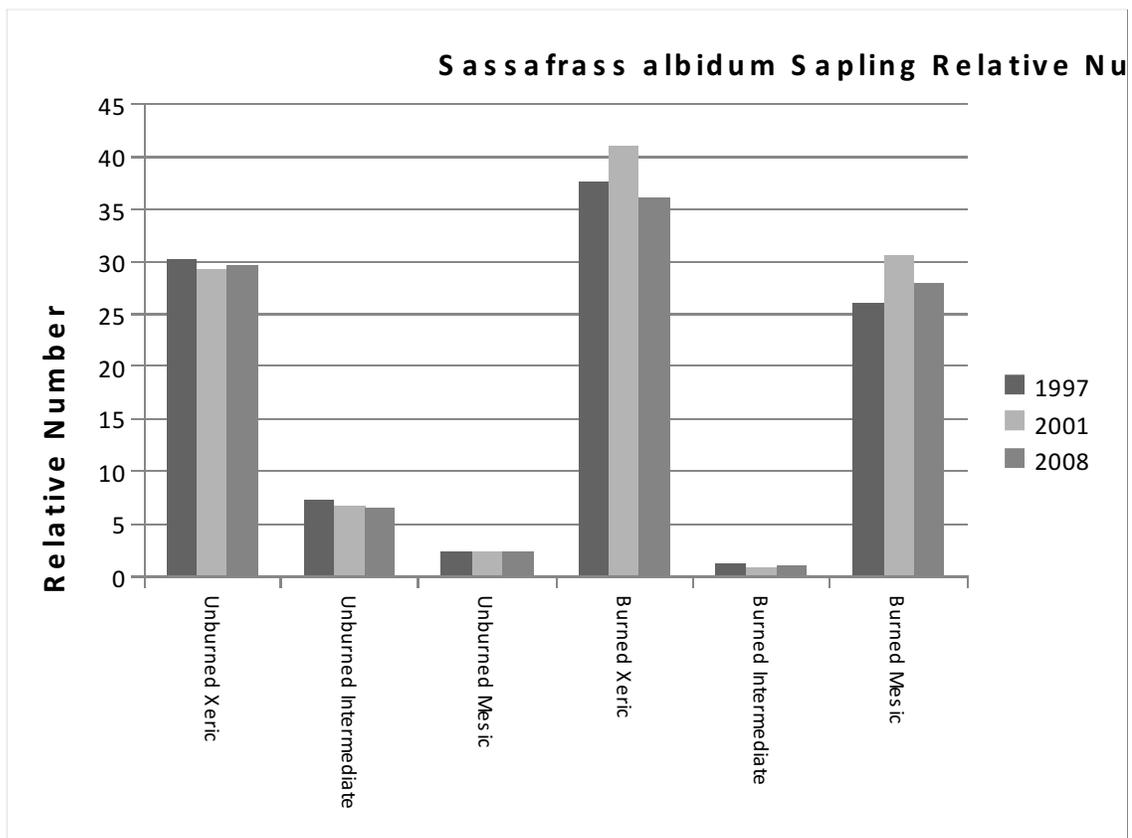


Figure 11. Relative number of saplings across all treatments in all years for *Carya*.

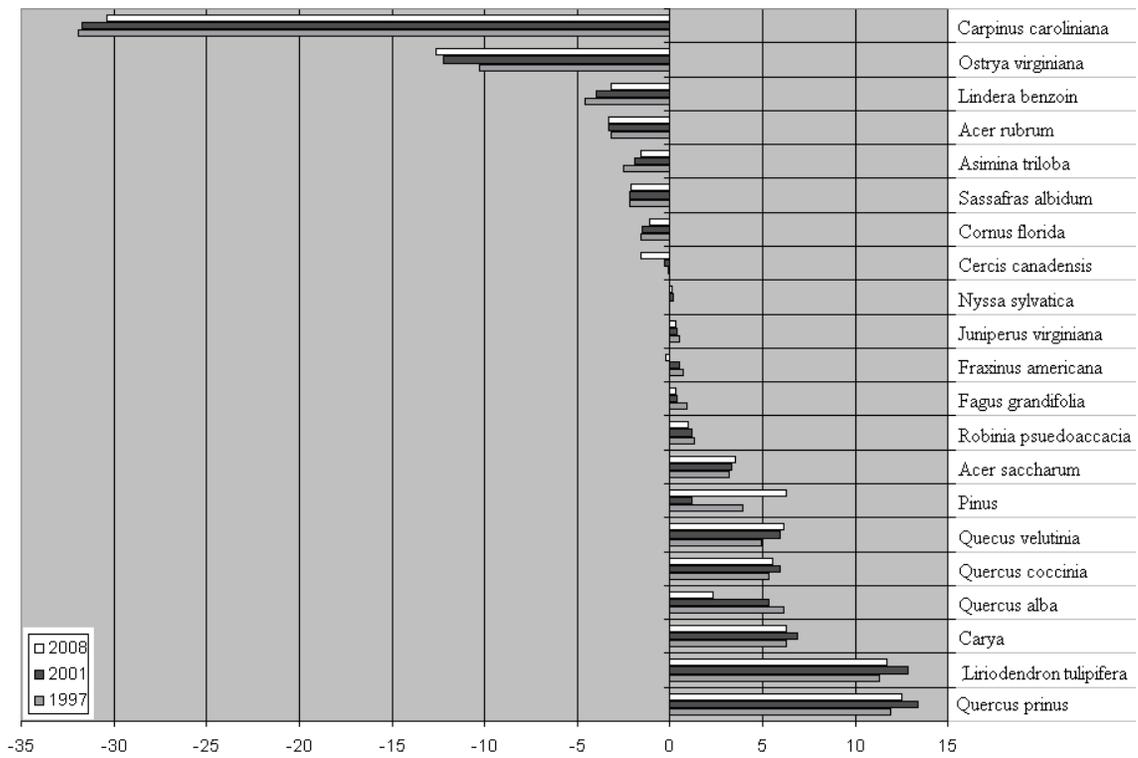


**Figure 12. Relative number of saplings across all treatments in all years for *Sassafras albidum*.**

**Community structural changes over time**

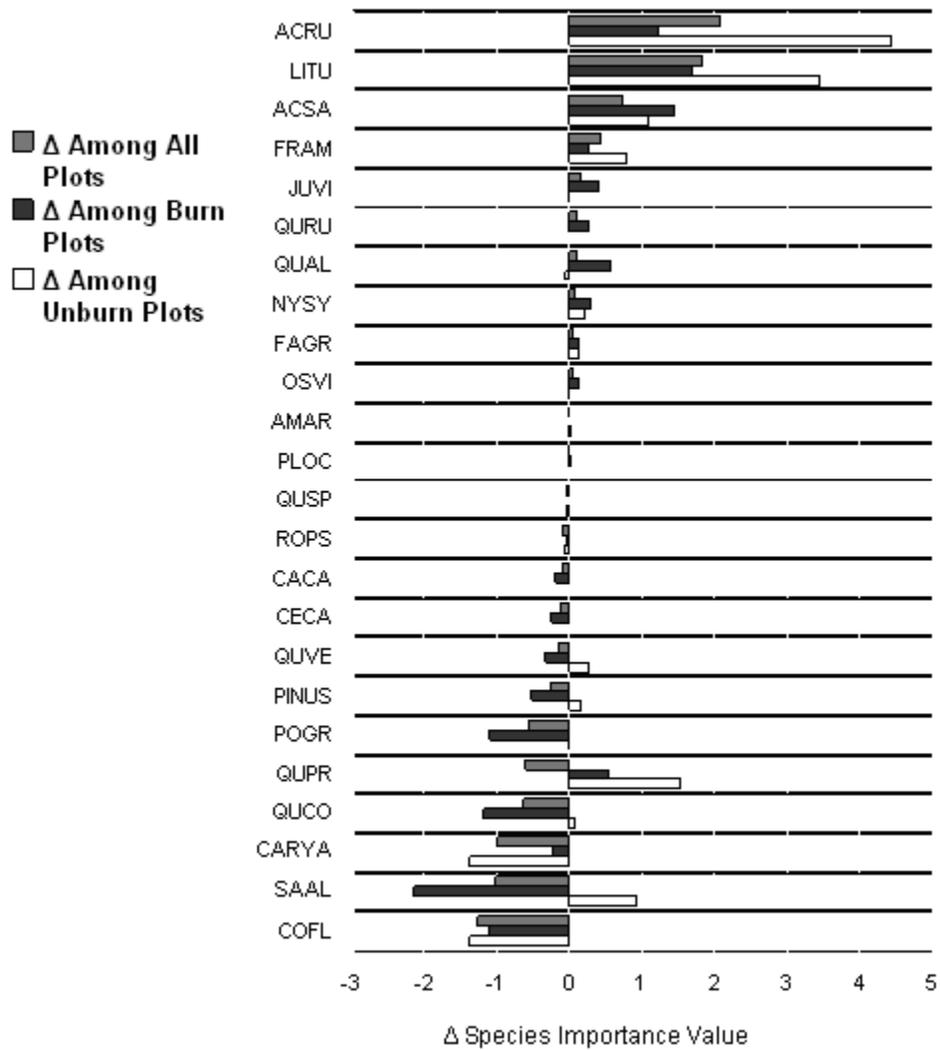
*Quercus prinus*, *Liriodendron tulipifera*, *Carya*, and *Quercus alba* exhibit a high overstory importance value and a low sapling relative number likely representing a lack of replacement (Fig 13). *Carpinus caroliniana*, *Ostrya virginiana*, and *Lindera benzoin* all exhibit higher sapling abundances than overstory, but that is to be expected as these are largely understory species and do not reach

dominance in the overstory (Fig 13). *Acer rubrum* also exhibits much higher sapling numbers, likely indicating that the species is replacing well and will increase in overstory dominance with time (Fig 13). Within the overstory *Acer rubrum*, *Liriodendron tulipifera*, and *Acer saccharum* exhibit the most increase in species importance. *Carya*, *Sassafras albidum*, and *Cornus florida* exhibit the largest decreases in species importance over the study interval (Figure 14). Xeric sites exhibit lower richness, evenness, and both Shannon's and Simpson's diversity index values than mesic or intermediate sites in all years (Table 4). Detailed plot by plot analysis is included in the appendix.



**Figure 13. Differences in abundance between sapling and overstory layers.** Values represent species overstory importance value over whole study area minus species relative number over whole study area.

Change in Species Importance 1997– 2008  
Edge of Appalachia Burn Analysis



**Figure 14. Change in species overstory importance value between 1997 and 2008.** First two letters denote genus, second two denote species, excepting Carya and Pinus.

**Table 4. Overstory and Sapling Diversity values**

Classes/Year	Overstory				Saplings			
	S	E	H	D'	S	E	H	D'
Xeric Unburned 1997	5.33	0.43	0.81	0.36	6.67	0.82	1.47	0.73
Xeric Unburned 2001	5.33	0.44	0.82	0.36	6.33	0.81	1.44	0.72
Xeric Unburned 2008	5.67	0.52	0.94	0.43	6.33	0.84	1.47	0.73
Intermediate Unburned 1997	10.33	0.66	1.55	0.63	11.33	0.83	2.00	0.83
Intermediate Unburned 2001	10.33	0.65	1.52	0.63	10.67	0.83	1.91	0.81
Intermediate Unburned 2008	9.67	0.64	1.48	0.61	11.67	0.82	1.99	0.82
Mesic Unburned 1997	9.33	0.78	1.74	0.76	11.67	0.68	1.66	0.73
Mesic Unburned 2001	9.33	0.76	1.70	0.75	12.00	0.66	1.64	0.72
Mesic Unburned 2008	9.67	0.74	1.69	0.74	13.00	0.67	1.71	0.74
Xeric Burned 1997	4.00	0.49	0.64	0.31	6.00	0.62	1.10	0.53
Xeric Burned 2001	4.00	0.49	0.64	0.31	6.00	0.68	1.19	0.58
Xeric Burned 2008	4.00	0.45	0.58	0.28	6.67	0.70	1.31	0.63
Intermediate Burned 1997	9.33	0.72	1.59	0.67	10.33	0.74	1.71	0.73
Intermediate Burned 2001	10.00	0.70	1.62	0.68	10.33	0.74	1.70	0.73
Intermediate Burned 2008	10.67	0.70	1.66	0.69	10.00	0.74	1.66	0.73
Mesic Burned 1997	9.67	0.80	1.78	0.78	10.33	0.79	1.85	0.78
Mesic Burned 2001	9.33	0.78	1.70	0.77	10.67	0.79	1.86	0.78
Mesic Burned 2008	8.67	0.75	1.60	0.74	12.33	0.78	1.96	0.80

S = Richness = number of non-zero elements in row

E = Evenness =  $H / \ln(\text{Richness})$

H = Diversity =  $-\sum (P_i \cdot \ln(P_i))$  = Shannon's diversity index

D = Simpson's diversity index for infinite population =  $1 / \sum (P_i^2)$   
 where  $P_i$  = importance probability in element  $i$  (element  $i$  relativized by row total)

### **Plot Community Ordination**

Nonmetric multidimensional scaling (NMS) was used to examine the underlying structure of species relationships between plots across the sampling interval. NMS was run on the sapling and overstory stems separately. Real data stress values for saplings leveled between 0.0003–0.0007. Real data stress values for overstory leveled between

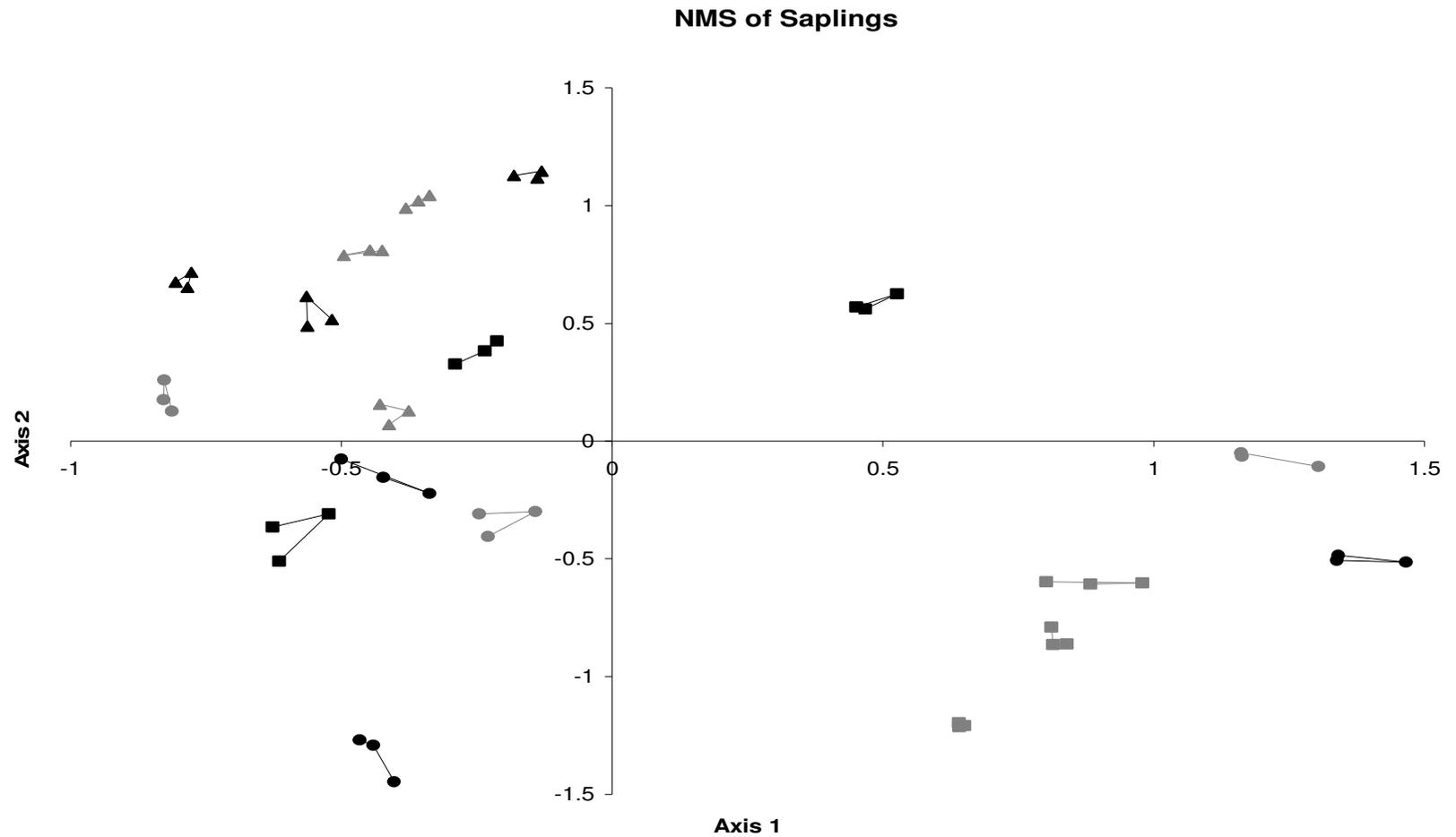
0.001–0.003. Percent variances in sapling and overstory distance matrixes are presented in Table 5.

The sapling ordination (Fig 15) did not appear to exhibit any clustering arrangement; however, overstory ordination plots of axis 1 vs. axis 2 (Fig 16) did exhibit clustering. The cluster was defined as plots A12, A13, A22, B11, B12, B13, and B23 and was mostly influenced by *Quercus prinus*, *Liriodendron tulipifera*, and *Sassafras albidum*, species that show strong IMI trends (Figures 17–19). The statistical significance of this clustering was evaluated using MRPP, first with all years taken together (the most information but technically pseudoreplication) and then for each sampling year separately. All MRPP runs were statistically significant (Table 6).

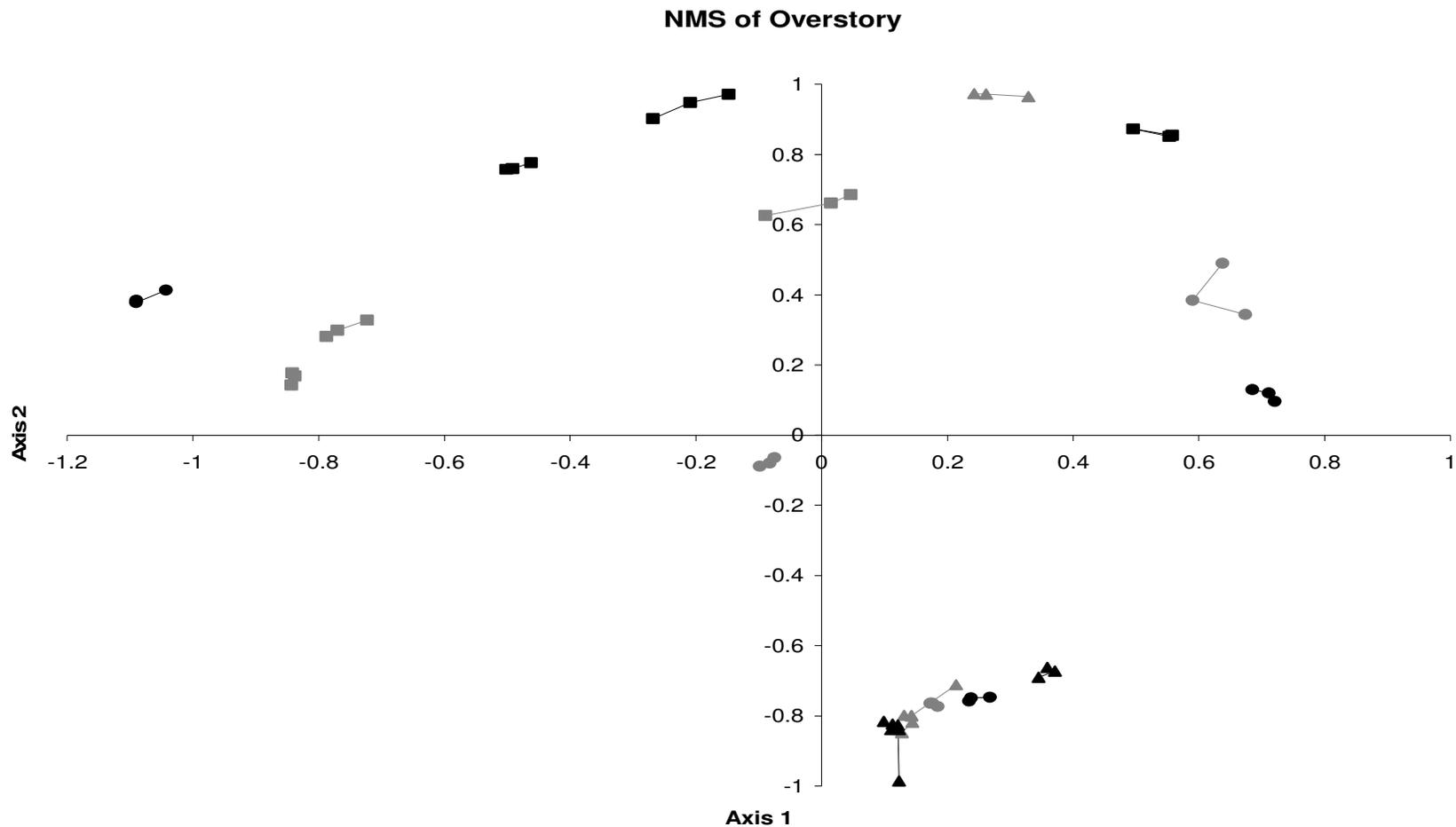
**Table 5. Variance in Distance Matrix**

<b>Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space:</b>				
Axis	R Squared			
	Overstory Increment	Overstory Cumulative	Sapling Increment	Sapling Cumulative
1	0.218	0.218	0.435	0.435
2	0.613	0.831	0.434	0.869
3	0.123	0.954		
	r	Orth	r	Orth
1 vs. 2	0.213	95.5	-0.408	83.3
1 vs. 3	0.221	95.1		
2 vs. 3	0.321	89.7		

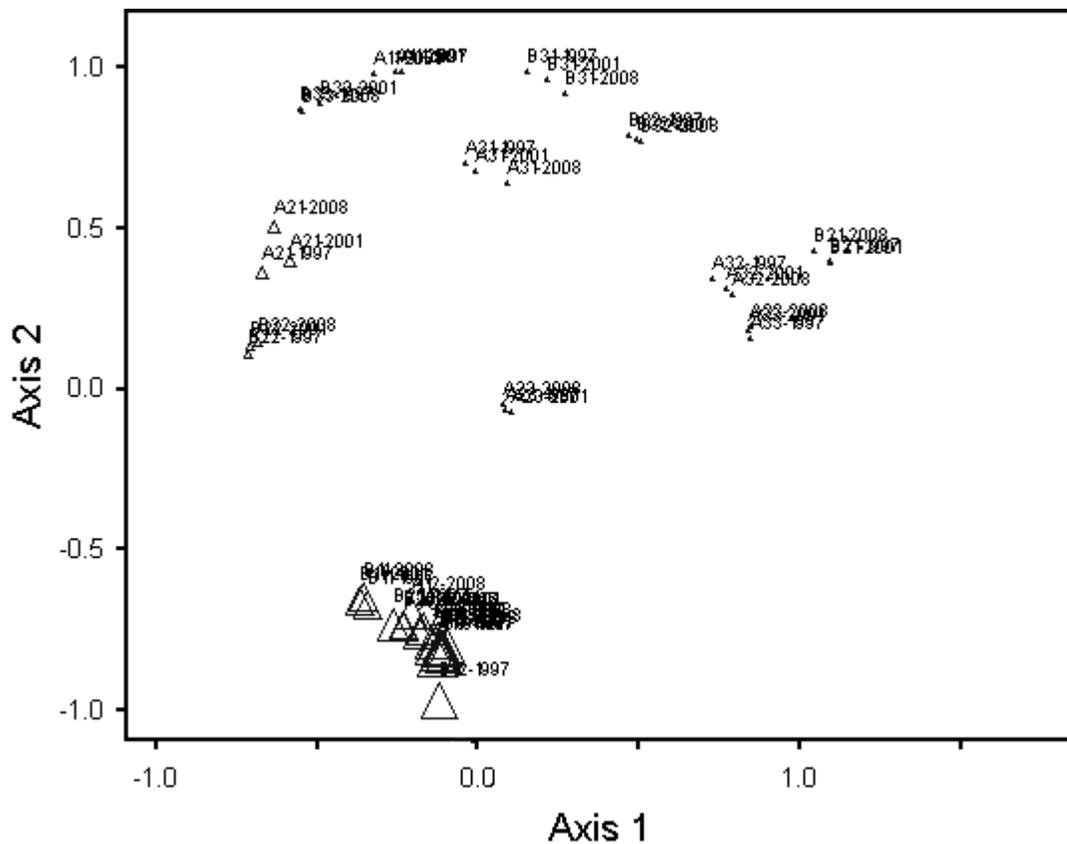
Orth= Orthogonality,% =  $100(1-r^2)$   
 Number of entities=54  
 Number of entity pairs used in correlation = 1431  
 Distance measure for ORIGINAL distance: Sorensen (Bray-Curtis)



**Figure 15. Sapling NMS Ordination Axis 2 vs. Axis 1.** Lines connect three consecutive samples in a plot. Sample descriptions - Shapes: Triangles = Xeric, Circles = Intermediate, Squares = Mesic. Colors: Black = Burn, Grey = Unburned Control



**Figure 16.Overstory NMS Ordination Axis 2 vs. Axis 1.** Lines connect consecutive samples in a plot. Sample descriptions - Shapes: Triangles = Xeric, Circles = Intermediate, Squares = Mesic. Colors: Black = Burn, Grey = Unburned Control.



**Figure 17. Overstory NMS axis 2 vs. 1,**  
*Quercus prinus* importance value determines size of symbol.

Axis 1  $r = -.359$   $\tau = -.144$   
 Axis 2  $r = -.926$   $\tau = -.756$



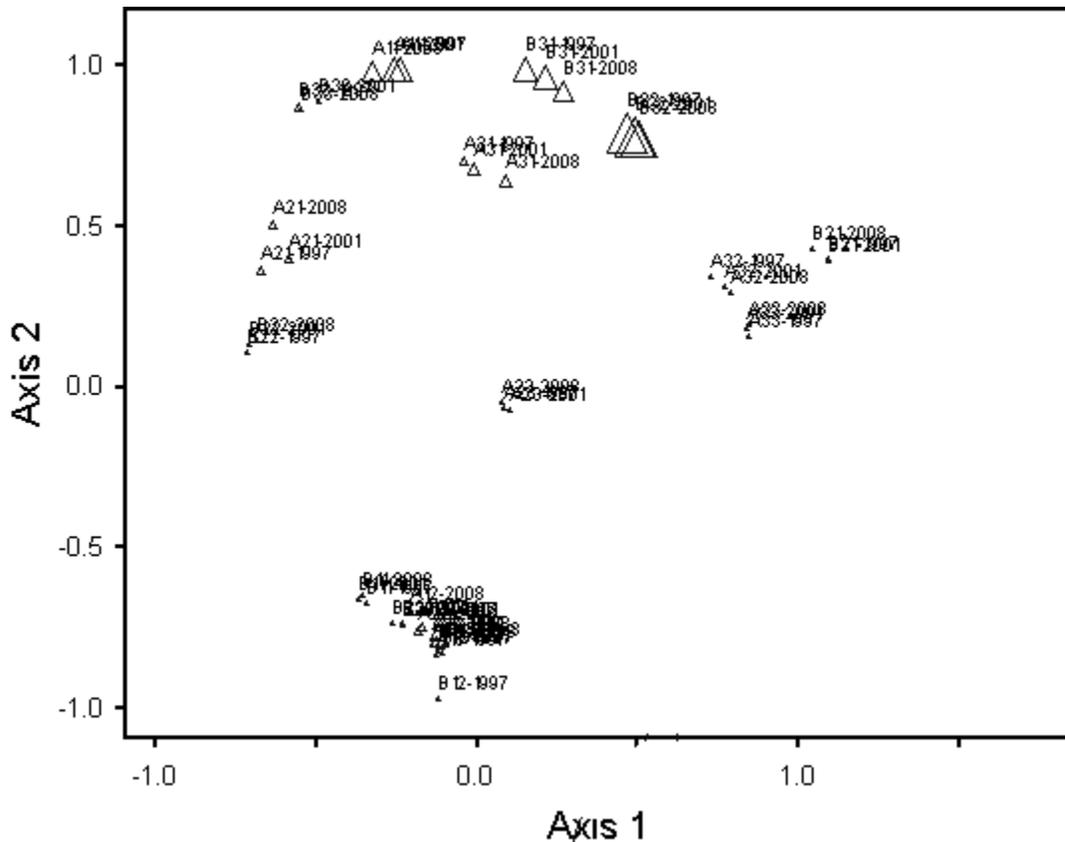


Figure 19. Overstory NMS axis 2 vs. 1, *Sassafras albidum* importance value determines size of symbol.

Axis 1  $r = .179$   $\tau = .165$

Axis 2  $r = .598$   $\tau = .657$

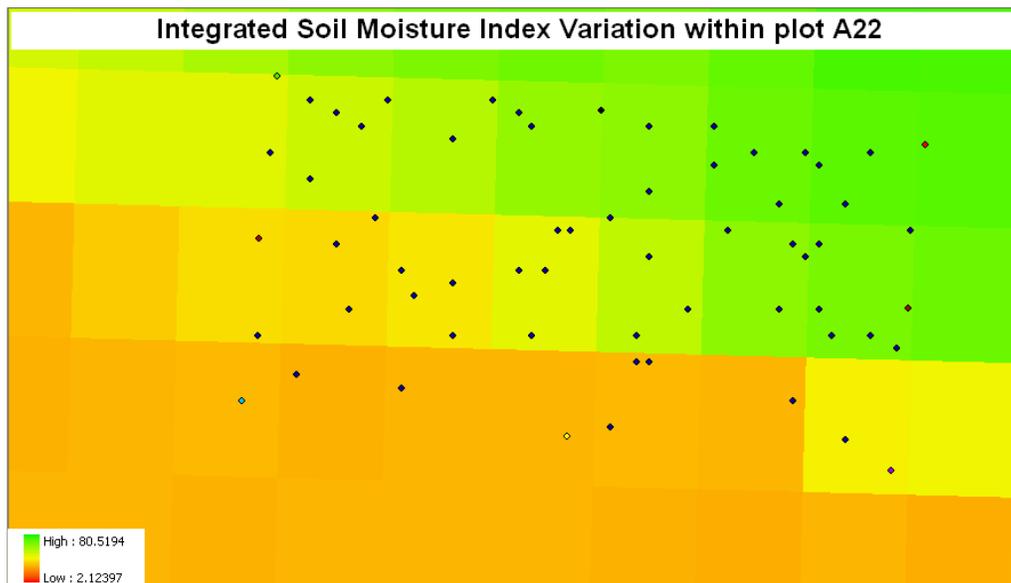
Table 6. MRPP of NMS groupings.

Grouping	Year	Overstory A	Overstory T	Overstory P-value
NMS Grouped	Total *	0.46203984	-31.739709	>0.000001
NMS Grouped	1997	0.4417154	-9.9181072	0.00002062
NMS Grouped	2001	0.44635044	-10.033712	0.00001919
NMS Grouped	2008	0.4531514	-10.131364	0.00001756
A = Chance corrected within group agreement (effect size) T = Between group difference <b>All values are statistically significant</b>				
* Note: MRPP sample independence assumption is violated for multiple year designs. In case of "Total" samples are pseudoreplicates.				

## GIS

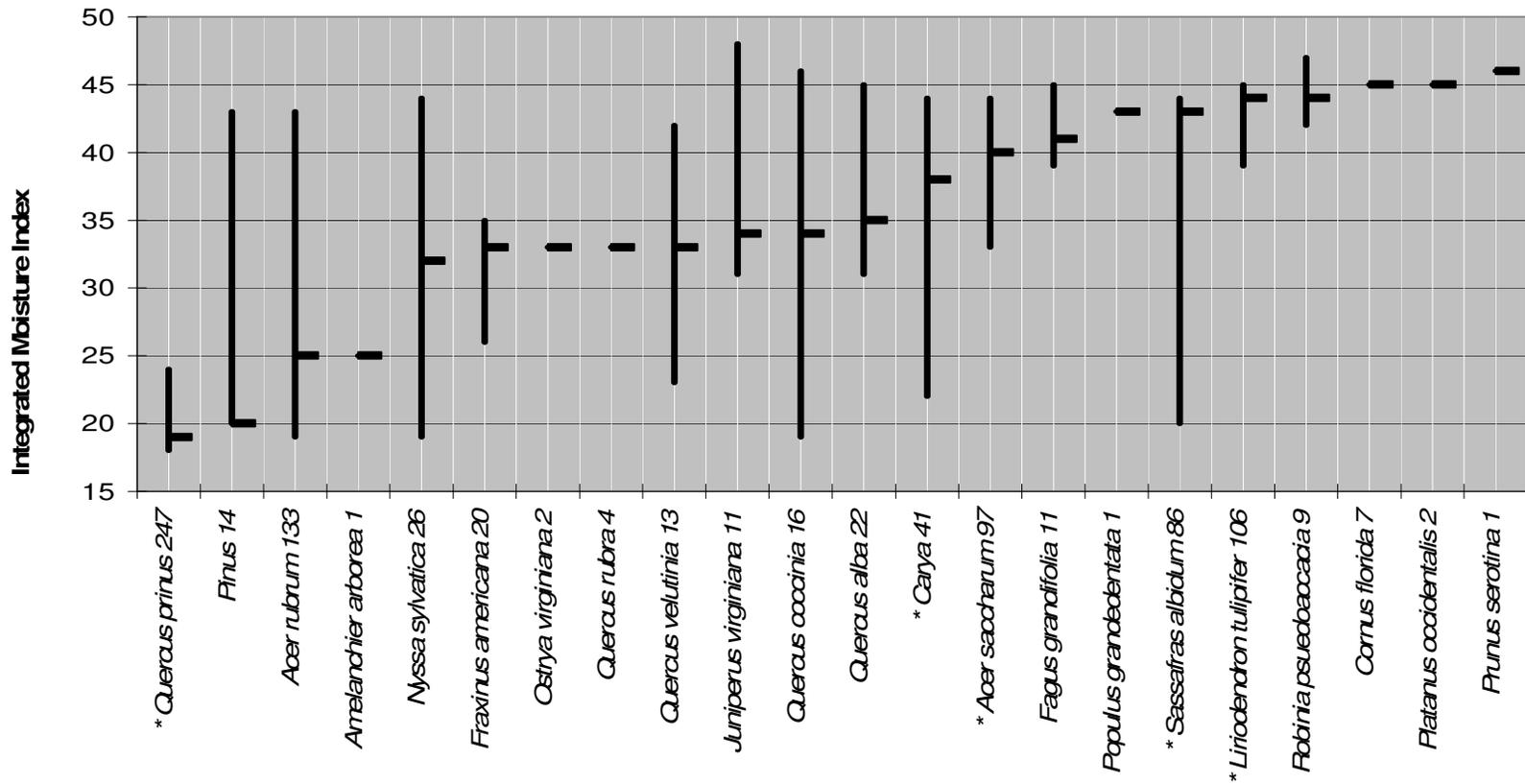
### IMI

Integrated moisture index values (IMI) showed a high degree of variation within plots. Figure 20 is an IMI map overlay of plot A22, a particularly heterogeneous plot presented as an example of this variation. Figure 21 shows 1<sup>st</sup> quartile, median, and 3<sup>rd</sup> quartile IMI values for each overstory stem for species with at least 7 stems. *Quercus prinus*, *Carya*, *Acer saccharum*, *Sassafras albidum*, and *Liriodendron tulipifera* (listed xeric to mesic) all exhibited statistically significant restricted distributions after a Bonferroni correction than stems as a whole (Kolmogorov-Smirnov tests; Table 7).



**Figure 20. IMI map overlay of plot A22.**

Located overstory stems depicted as dark blue dots, all other dots depict corner and midpoint locations.



**Figure 21. IMI species ranges stem by stem GIS analysis.** Black bar represents species IMI range between 1<sup>st</sup> and 3<sup>rd</sup> quartile for species that make up more than 1% of samples. Median represented by black hash mark. Species are presented as abbreviations. First two letters denote genus, second two denote species. Bonferroni corrected Kolmogorov-Smirnov identified restricted species indicated by stars next to species. Numbers listed next to species indicate number of sample stems.

**Table 7. Species IMI, and Kolmogorov-Smirnov Table**

Species acronyms are first two letters genus, then first two letters species. Statistically significant values after Bonferroni correction shaded grey. Species that make up less than 1% presented as median only.

Species	Min	1st Quartile	Median	3rd Quartile	Max	Number of Stems	Kolmogorov-Smirnov P value
<b>QUPR</b>	<b>16</b>	<b>18</b>	<b>19</b>	<b>24</b>	<b>45</b>	<b>247</b>	<b>&gt;0.001</b>
PINUS	18	20	20	43	45	14	0.2024
ACRU	17	19	25	43	46	133	0.2076
AMAR	-	-	25	-	-	1	0.8725
NYSY	18	19	32	44	48	26	0.6158
FRAM	20	26	33	35	48	20	0.0204
OSVI	-	-	33	-	-	2	0.8389
QURU	-	-	33	-	-	4	0.3927
QUVE	18	23	33	42	44	13	0.9152
JUVI	18	31	34	48	48	11	0.105
QUCO	17	19	34	46	47	16	0.2229
QUAL	18	31	35	45	48	22	0.1665
<b>CARYA</b>	<b>20</b>	<b>22</b>	<b>38</b>	<b>44</b>	<b>47</b>	<b>41</b>	<b>0.001</b>
<b>ACSA</b>	<b>18</b>	<b>33</b>	<b>40</b>	<b>44</b>	<b>48</b>	<b>97</b>	<b>&gt;0.001</b>
FAGR	31	39	41	45	47	11	0.0129
POGR	-	-	43	-	-	1	0.6679
<b>SAAL</b>	<b>17</b>	<b>20</b>	<b>43</b>	<b>44</b>	<b>46</b>	<b>86</b>	<b>&gt;0.001</b>
<b>LITU</b>	<b>17</b>	<b>39</b>	<b>44</b>	<b>45</b>	<b>49</b>	<b>106</b>	<b>&gt;0.001</b>
ROPS	18	42	44	47	48	9	0.0411
COFL	-	-	45	-	-	7	0.0084
PLOC	-	-	45	-	-	2	0.2782
PRSE	-	-	46	-	-	1	0.3763

## **Discussion**

### **NMS validity**

NMS performed well in my analysis, implying that the ordinations represent likely community structure. Examination of real data vs. Monte Carlo runs with randomized data suggest that the appropriate number of axes was chosen as further addition of dimensions had low reductions in stress in real data relative to randomized data. As iteration increased, stress values settled on an even stress, implying no competitors for the global minimum, and lack of dependency of results on the number of iterations chosen. Final stress values were low for saplings and overstory analysis by both Kruskal's and Clarke's rules of stress interpretation, (Kruskal 1964, Clarke 1993).

## Examination, Comparison, and Applications

### **Mortality**

Overstory mortality (2.83% annually across the 1997–2001 interval, 2001–2008 mortality was 2.78% annually) was higher than other Ohio forests and than many other old-growth forests (Table 8). One possible explanation of the high mortality is that my study uses a 10 cm minimum dbh. In two of the other studies in Ohio a higher dbh cutoff was used. My data thus include many smaller stems that are characterized by greater mortality rates (Forrester and Runkle 2000). In the Ohio studies with 10 cm and 11 cm dbh minimum, mortality is closer to the values found in my study.

**Table 8. Percentage Mortality Comparison**

Location	Years Sampled	Annual Mortality %	Minimum dbh (cm)	Number of Stems
Edge of Appalachia, Ohio (Current Study)	1997-2001	2.83	10	982
	2001-2008	2.78	10	1000
Ohio, USA	1982-1993	1.21	25	74
	1977-1991	1.23	25	408
	1981-1988	2.13	11	290
	1991-1997	2.51	10	460
Tropical rain forest	1950-1990	1 – 2	varies	varies
Japan	1987-1991	1.21	32.3	5075
Great Britain	1945-1983	3.44	29.7	352
Tennessee and North Carolina, USA	1976-1990	0.78	64.6	1349
Illinois, USA	1977-1995	3.1	4.3	1292
Indiana, USA	1926-1976	1.14	31.5	2722
Pennsylvania, USA	1977-1990	0.66	31	384

(Abrell and Jackson 1977, Peterken and Jones 1987, Campbell 1995, Bell 1997, Forrester 1998, Nakashizuka et al 1992, Runkle 1990, Sheil and May 1996, Runkle 2000)

## **Burn response**

The study area differences in sapling and overstory abundances of *Quercus* and *Acer rubrum* species show a clear disconnect in community structure between overstory and sapling layers consistent with mesophication (Figure 13). In studies of land use history such as Abrams and Norwacki (1992) fire was shown to have significant effects on species composition. Abrams and Norwacki (1992) examined compositional structure and growth patterns in undisturbed and disturbed forests and compared them to pre-settlement forest composition. Under recurring logging and recurrent fire regimes associated with charcoal furnaces between 1790 and 1900, the area changed to a greater dominance of *Quercus* species and a decrease in dominance of *Pinus*. From 1908 to 1989, fire frequency decreased by 99% and logging decreased, favoring *Acer* and *Prunus* understories below the *Quercus* overstory. The logging of the *Quercus* overstory then accelerated canopy dominance of *Acer rubrum*, *Acer saccharum*, and *Prunus serotina*.

### Community response and burn frequency

Our study appears to contradict this scenario in that the community as a whole did not appear shifted by a single burning. MRPP did not detect a significant difference for burn classes, but did for IMI. However more frequent burns

might show an effect. Hutchinson, Sutherland, and Yaussy (2005) have shown that intensity of effects of prescribed burns similar to the one in my study increases with the number of burns. In their study two burns reduced stand density and caused initial shifts at the seedling level but did not cause lasting shifts in the seedling community. They also found that effects of fire on vegetation appear similar across IMI classes. This finding is consistent with my study which did not detect significant differences in overall stand characteristics in burn\*IMI interactions. Iverson et al. (2008) also found increases in stand heterogeneity and mortality with successive fires (2008).

#### Species response and IMI burning interaction

Examination of the significant interaction effects on certain species shows interesting trends. *Carya* and *Sassafras albidum* overstory stems showed effects initially in 1997 that faded below detectable levels by the next sample. These effects varied by IMI class. *Carya* was favored by burning in intermediate and mesic sites, and *Sassafras albidum* was favored by burning in mesic sites. Lasting effects were observed on *Carpinus caroliniana* which was overall disfavored by burning, exceptionally so in mesic sites, but favored in intermediate sites. The important observation is that these effects were

differential across IMI classes. There is evidence in the literature that the effects of fire vary in intensity across topographic and moisture gradients.

Iverson and Hutchinson (2002) measured soil temperatures associated with prescribed burns. Based on sensors imbedded in the ground both at prescribed burn sites and at control sites their results suggest that burning does have a lasting impact on soil temperatures. At the time of burn temperatures spiked 9.3 C° above normal lasting six minutes. The soils returned to normal temperature over a period of hours. But of more importance was the observation that in the following months the burned sites stayed warmer on average. Of special importance to my study is that the burned xeric sites reacted differently than the burned mesic sites. The drier (xeric) sites averaged 5.7 C° warmer than controls for the first 30 days. Elevated temperatures lasted 155 days on burned xeric sites. The burned wetter (mesic) sites averaged 0.5–0.6 C° warmer than controls for the first 30 days. Elevated temperatures lasted 75 days on burned mesic sites.

One confounding issue may be the influence of soil pH on burning effects. Some of the study sites are situated nearer to limestone barren sites than others. Soil

characteristics are influenced by burning. Blankenship and Arthur (1999) studied the effects of single burns in Daniel Boone National Forest in Kentucky in relation to their effect on soils and the microbial community. A single burn caused a loss of 32 percent of the litter layer, but did not cause significant loss of the O horizons. Ashes from the fire shifted soil pH by 0.2–0.3 units. However the effect of fire on soil characteristics is differential based on the starting characteristics of the soil. A study of periodic and annual fires in Lawrence County Ohio found similar pH effects of fire and also extractable Ca<sup>2+</sup> increased and extractable Al<sup>3+</sup> reduced. These changes were significant for nutrient poor soils but were transitory on soils influenced by limestone (Boerner *et al.* 2004).

#### **Soil moisture community level structure**

The observed relationship of community structure to IMI likely results from a high degree of topographic variation in the gently rolling hillsides of un-glaciated Ohio. IMI class results are consistent with studies in other Appalachian forests, where tree species compositional changes also follow a moisture gradient (Boerner 2006). The tree community within the study area does appear to be strongly affected by an IMI gradient. MRPP analysis of the IMI class distinctions showed that the species compositions

of each IMI class differed significantly. The effect size (A value) of this relationship was high suggesting that grouping species by IMI classes creates distinct within class homogeneous groups. Effect sizes for the present study ranged 0.21 to 0.31. McCune et al. (2001) state that for community data an effect size of 0.1 is considered large. The exceptionally large effect sizes for community data suggest a strong relationship to soil moisture. Larger effect sizes overall were found in the overstory suggesting community partitioning in overstory is more distinct than in the sapling layer across IMI classes, agreeing with Racine (1971). In NMS, drier plots clustered closely together while mesic and intermediate plots clustered apart from them in the overstory. Mesic and intermediate plots were also more widely scattered in orientation than drier sites suggesting less community variation within xeric plots.

MRPP analysis of the NMS identified grouping yielded statistically significant results that had an effect size between 0.44 and 0.46. This high effect size value indicates that these clusters are highly distinct. Species that were shown by ANOVA to be highly restricted to either moist or dry plots (Figures 6-8) are shown to follow the detected grouping tightly (Figures 17-19). This result

suggests that Axis 2 of the overstory NMS may be a strong indicator of *Quercus prinus* importance, a statistically significantly xeric species. NMS, MRPP of IMI class, and MRPP of NMS groupings build a strong case that community structure changes along an IMI gradient.

#### IMI specialists

Several species within the study area were strongly affected by the influence of an IMI gradient. Some species occupy narrow IMI ranges and may be replaced by others outside their range (Fig. 21). *Quercus prinus*, *Carya*, *Acer saccharum*, *Sassafras albidum*, and *Liriodendron tulipifera* all were competitively restricted to narrow IMI ranges that were statistically significant (Fig. 21, 22).

*Quercus prinus* dominated the xeric IMI regions. This distribution agrees with other literature. Iverson et al. (2008) found *Quercus* sp. (grouped with *Carya*) mostly on dry and intermediate IMI sites. Runkle and Whitney (1987) found *Quercus prinus* on edges and upper slopes. In upper slopes McCarthy et al. (1984) found *Quercus* sp. more abundant on drier southern aspects. The dominance of xeric IMIs by *Quercus prinus* may be because it is the only important tree species in the area with strong adaptations to areas of moisture limitation. A study of foliar tolerance to dehydration in 12 tree species found *Quercus prinus* to be

highly tolerant to foliar dehydration (Auge et al 1998). Pallardy and Rhoads (1993) found that root development of oaks gave significant drought stress advantage.

*Carya* was most prevalent at intermediate IMI. This is consistent with some studies but not others. *Carya* (grouped with *Quercus* sp.) occupied primarily dry and intermediate IMI sites in the Iverson et al. study (2008). McCarthy et al. (1984) found variation among the genus. *Carya glabra* was most prevalent on upper slopes. *Carya ovata* tended more towards the more mesic north facing slopes and *Carya tomentosa* showed no preference. Runkle and Whitney however found *Carya cordifomis* tended more towards lower slopes.

*Acer saccharum* occupied primarily intermediate to mesic IMIs. These results are consistent with others, Runkle and Whitney (1987) found *Acer saccharum* most present on lower slopes. Iverson et al. (2008) considered *Acer saccharum* (when classed with *Carpinus caroliniana*, and *Cornus florida*) to be part of a larger "mesic shade tolerants" class which when classed together were found prolifically in mesic IMI sites (2008). Auge et al. found *Acer saccharum* to have a greater tolerance to foliar dehydration than *Quercus prinus* (1998), suggesting foliar dehydration tolerance is not a primary factor explaining the IMI occupancy. Competition with species with other

drought favorable adaptations may play a role. Hinckley et al. (1981) found rooting depths in *Acer saccharum* were less than one meter whereas the oak species in their study, *Quercus alba*, exhibited a depth of 4.5 meters.

*Sassafras albidum* overstory stems occupied primarily mesic IMI in both class level analysis and stem by stem analysis; however *Sassafras albidum* saplings were more prevalent in xeric sites. Iverson et al. (2008) found *Sassafras albidum* to occupy primarily dry and intermediate IMI sites. *Sassafras albidum* is not primarily a large overstory tree and tends to present more numbers in the sapling layer where my research and the literature are consistent. One possible explanation of the inconsistency between my overstory analysis and literature is that only under more mesic conditions can *Sassafras albidum* grow large enough to become a detectable portion of the overstory.

*Liriodendron tulipifera* occupied primarily mesic IMI. This agrees with Iverson et al. (2008) who found *Liriodendron tulipifera* most prevalent in mesic sites as well. Runkle and Whitney (1987) found greatest prevalence of *Liriodendron tulipifera* on small floodplains. The competitive restriction to mesic sites may be related to drought tolerance, Auge et al. (1998) found *Liriodendron*

*tulipifera* to be intolerant to dehydration relative to 12 other tree species.

#### IMI generalists

Within the study site other species do not exhibit these differences. Either a trend for them is not detectable due to low sample size or their niche breadth encompasses a broad IMI range that occupies the bulk of the sample area. The latter may likely be the case for species such as *Acer rubrum* which had a high sample size and was prolific in most plots and whose IMI occurrence roughly follows the occupancy of all stems. However sapling class-level results suggest the coming generation of *Acer rubrum* may change this characteristic. Saplings of *Acer rubrum* were more prevalent in xeric sites and less prevalent in mesic sites suggesting that as the saplings age into the overstory size class *Acer rubrum* may become more prevalent in xeric sites and less so in mesic sites within the overstory. This would be consistent with Iverson et al. (2008), who found *Acer rubrum* more prevalent in xeric IMI sites.

## **Hypotheses revisited**

Some of the null hypotheses in the study were rejected, whereas others were not. Below is a summary:

Indistinguishability of community in burn classes was not rejected.

Indistinguishability of community in IMI classes was rejected.

Mortality indistinguishability between burn classes, IMI classes, or the interaction of the two was not rejected for all species taken together.

Individual tree species indistinguishability in relative importance value in the overstory, or relative number in the sapling layer between burn classes, IMI classes, or the interaction of the two was rejected for specific species.

When location was resolved for individual stems:

Species IMI distribution indistinguishability from all species taken together was rejected for specific species.

The implications of this are that the IMI niche of these species is likely not the same as all studied trees.

## **Management Recommendations and Future Study**

Management implications of my conclusions are that a single prescribed burn may not be expected to influence tree community structure in any significant way over short time frames. This result is consistent with other studies (Hutchinson Sutherland and Yaussy 2005). A higher frequency of burning may be required for detectable effects to occur.

My results suggest that it may also be wise for land managers to recognize that the tree community in this region is likely to be as heterogeneous as the IMI landscape. The data suggest a partitioning of continuous forest region into multiple IMI-determined tree communities. The more xeric regions are more often occupied by *Quercus prinus*. *Carya* has tendencies for intermediate sites. Species such as *Liriodendron tulipifera* and *Sassafras albidum* occupy the mesic regions. This heterogeneity within a continuous forest also has interesting research implications. It is likely this heterogeneity of tree community structure within a continuous forest results in a lower degree of gene mobility than would otherwise be expected. Further study of this aspect may be warranted and may be a direction of possible future research, as it may better inform

management practices and would further the understanding of the principles of landscape genetics among trees.

Another aspect of this study that may be of importance to future research is the method by which individual stems were incorporated into a GIS map with an exceptional degree of resolution. A literature search yielded no other studies which resolved similar numbers of individual stems into GIS points. One such possibility would be to layout a survey grid or transect in which various specific points could be ascertained to a high degree of accuracy, either through use of survey methods or high resolution GPS. The range finder and calculation methods used in this study could be employed. These methods could be useful for considering environmental or species gradients as ArcMap can be a powerful tool for examination of spatial relationships.

## **Appendix**

### **IMI derivation**

#### 1/3 arc second topographic map derived maps

After the 1/3 arc second topographic map was loaded into ArcMap, the Spatial Analyst package was used to perform the following operations, each one building a separate map. The Hillshade algorithm was ran on the topographic map to account for slope-determined differences in solar radiation. Solar azimuth was set at 22° and a solar altitude at 45° to approximate solar altitude at growing season as in Iverson et al. (1997). Shadows were not built into this map due to the high degree of relief. When the algorithm was asked to build shadows the high degree of relief caused nearly all hills to have approximately one half covered in maximum values.

The Curvature algorithm measures the degree of convex/concavity of the shape of the landscape. This algorithm was run using the 1/3 arc second topographic map. Higher values are indicative of concavity and thus more indicative of higher land-shape derived moisture potential. A "z factor" of 1 was used.

Next, the flow direction algorithm was used to build a map based upon the 1/3 arc second topographic map. Edges were not forced to flow outward. This map is an intermediate step in building the flow accumulation map. It gives the direction of flow of a hypothetical liquid falling on each raster cell into its nearest adjacent down-slope neighbor. The flow accumulation algorithm was used to build a map based upon the flow direction map. The flow accumulation algorithm models the accumulated flow of water down-slope as it moves due to gravity. No cell weighting map was used (giving equal weights to all cells, thus equal affinity to surface flow), and the output was in floating point data type, as opposed to integer.

#### SSURGO soils derived map

The importation and subsequent build of a total available water capacity map was not as straight-forward a process and was shown to yield strikingly different resolution maps based upon the methods used. SSURGO data comes separated into spatial data and tabular data which must be associated with one another. Microsoft Access 2003 was used to build a database of the relationships of the tables. This was done by opening the database file included in the soil data mart download and giving it the path to

the tabular data. After associations are apparently built, the database was saved and closed.

USDA Soil Data Viewer ArcMap plug-in was used to create an Available Water Capacity map. This map is based upon the shape file provided by SSURGO, and once database associations are in place it can access the tabular information needed to build the map. The Available Water Capacity map was built using this configuration. All layers were included, instead of a specified depth, in order to account for total water capacity of the soil. Since the map can return only a single value, a choice for how the multiple layers are incorporated must be made. A weighted average of the values of each layer was used rather than the dominant component, or maximum or minimum, value to more closely model soil water behavior (Iverson et al. 1997). Soil Data Viewer built the map in temporary files so it was resaved using ArcMap into a permanent directory. The Total Available Water Capacity map built by Soil Data Viewer is built as a feature map instead of a raster map. In order to combine this map smoothly with the raster topographic (hillshade, curvature, and flow accumulation) maps it was transformed into raster. The Conversion Tools algorithm Feature to Raster was used for this task.

The possible options at this step result in greatly varying degrees of map resolution, and thus varying accuracies of feature clarity. The ArcMap default procedure is for the algorithm to build a raster map with a cell size based on the smallest width and smallest length of any feature depicted on the map. Running the algorithm this way resulted in a blocky map that did not closely resemble the original feature map at finer scales. The other option was to set an arbitrary user defined cell size. The lowest possible cell size is one. As cell size increases, resultant data size and processing time decrease. However, the larger the cell size chosen the blockier the resolution becomes resulting in less accuracy to the original map. After several tests at varying cell sizes, a cell size of 1 (greatest possible resolution) was chosen.

#### *Computational Cautions*

Processor and ram load of building and rescaling this map is large relative to the other maps. The algorithm takes 6-8 hours to complete using 2.4 GHz, 2 GB of RAM. Also, if sufficient hard drive space is not clear the algorithm will crash. The final map with a cell size of one was approximately eight GB, and free space needed for building temporary files was nearly 50 GB. Due to the time constraints of the build and the size of the resultant

data, the file will almost certainly be highly fragmented (in my case upwards of 79,000 fragments). As a result, hard drive defragmentation was necessary before the file could be rescaled or used further without crash. Despite the cumbersomeness of this method, it yields a raster map bearing the closest possible approximation of the soil features.

#### IMI Map Build Procedure

First, all map values were set to uniform unit ranges in order to combine them. This was done using the Spatial Analyst tool Single Output Map Algebra, according to the expression:

$(\text{Dataset} - \text{old lowest value}) * \text{New upper value} / (\text{old upper value} - \text{old lowest value}) + \text{new lowest value}$

Then, Single Output Map Algebra was used to combine the resultant maps to build the IMI map according to the expression:

$(\text{Hillshade} * 0.4) + (\text{Flow Accumulation} * 0.3) + (\text{Curvature} * 0.1) + (\text{Total Water Capacity} * 0.2)$  as in Iverson *et al.* (1997).

**Soil texture table.**

Values were derived from soil texture analysis of plot soil cores. Values presented as percentages.

<b>Plot</b>	<b>Sand</b>	<b>Clay</b>	<b>Silt</b>
A11	27.5	25	47.5
A12	22.5	35	42.5
A13	37.5	32.5	30
A21	37.5	30	32.5
A22	27.5	17.5	55
A23	35	27.5	37.5
A31	32.5	20	47.5
A32	27.5	25	47.5
A33	22.5	22.5	55
B11	25	37.5	37.5
B12	30	37.5	32.5
B13	37.5	42.5	20
B21	22.5	30	47.5
B22	25	27.5	47.5
B23	10	45	45
B31	7.5	40	52.5
B32	12.5	25	62.5
B33	25	20	55

**Plot specific diversity measures table.**

Plot/Year	Overstory				Saplings			
	S	E	H	D'	S	E	H	D'
A11_1997	8	0.855	1.777	0.8075	11	0.82	1.966	0.8145
A11_2001	8	0.847	1.762	0.8039	10	0.837	1.927	0.806
A11_2008	8	0.822	1.708	0.7934	10	0.844	1.942	0.8205
A12_1997	5	0.319	0.513	0.2118	4	0.856	1.187	0.6748
A12_2001	5	0.319	0.513	0.2117	4	0.843	1.169	0.6712
A12_2008	6	0.44	0.788	0.3461	4	0.867	1.202	0.6803
A13_1997	3	0.119	0.131	0.0476	5	0.789	1.27	0.6932
A13_2001	3	0.161	0.176	0.0693	5	0.754	1.213	0.6788
A13_2008	3	0.291	0.319	0.1424	5	0.795	1.28	0.6912
A21_1997	10	0.787	1.812	0.7777	14	0.761	2.009	0.8151
A21_2001	10	0.767	1.765	0.7696	15	0.732	1.983	0.8002
A21_2008	10	0.742	1.709	0.749	14	0.769	2.029	0.8167
A22_1997	9	0.346	0.76	0.2973	9	0.899	1.975	0.8395
A22_2001	9	0.339	0.744	0.2899	8	0.866	1.801	0.8022
A22_2008	7	0.356	0.692	0.2809	10	0.868	1.999	0.8393
A23_1997	12	0.833	2.07	0.8276	11	0.843	2.021	0.8359

A23_2001	12	0.83	2.063	0.8257	9	0.879	1.931	0.8281
A23_2008	12	0.815	2.024	0.8128	11	0.811	1.945	0.8127
A31_1997	12	0.891	2.213	0.8735	11	0.621	1.49	0.6707
A31_2001	11	0.886	2.124	0.8607	13	0.569	1.459	0.6526
A31_2008	12	0.862	2.141	0.8585	13	0.621	1.593	0.6929
A32_1997	9	0.727	1.598	0.7137	11	0.759	1.82	0.7807
A32_2001	9	0.696	1.53	0.693	11	0.769	1.843	0.7818
A32_2008	9	0.684	1.504	0.6869	13	0.739	1.894	0.7832
A33_1997	7	0.718	1.398	0.6906	13	0.646	1.657	0.7467
A33_2001	8	0.691	1.437	0.6925	12	0.65	1.616	0.74
A33_2008	8	0.686	1.426	0.6841	13	0.643	1.649	0.7443
B11_1997	6	0.625	1.12	0.5215	8	0.618	1.285	0.593
B11_2001	5	0.655	1.055	0.5167	8	0.686	1.426	0.6553
B11_2008	5	0.649	1.045	0.5127	9	0.711	1.561	0.6948
B12_1997	2	0.503	0.349	0.1973	4	0.557	0.772	0.4304
B12_2001	2	0.52	0.361	0.2064	4	0.598	0.829	0.4535
B12_2008	2	0.467	0.324	0.1791	5	0.597	0.96	0.5163
B13_1997	4	0.331	0.458	0.2211	6	0.688	1.232	0.5744
B13_2001	5	0.304	0.49	0.2106	6	0.742	1.329	0.6252
B13_2008	5	0.223	0.359	0.1387	6	0.782	1.401	0.6639
B21_1997	13	0.727	1.866	0.7348	13	0.745	1.911	0.8223
B21_2001	13	0.717	1.839	0.7315	13	0.688	1.764	0.7942
B21_2008	14	0.713	1.881	0.7348	12	0.747	1.857	0.8146
B22_1997	9	0.897	1.972	0.8393	12	0.846	2.102	0.847
B22_2001	10	0.882	2.031	0.8471	12	0.875	2.174	0.8636
B22_2008	11	0.86	2.062	0.8505	13	0.792	2.032	0.8251
B23_1997	6	0.524	0.939	0.4467	6	0.629	1.128	0.5332
B23_2001	7	0.514	1.001	0.4705	6	0.651	1.166	0.5444
B23_2008	7	0.532	1.034	0.4886	5	0.679	1.092	0.5556
B31_1997	11	0.826	1.982	0.8327	12	0.777	1.93	0.7871
B31_2001	11	0.811	1.946	0.8243	13	0.718	1.841	0.7544
B31_2008	9	0.766	1.683	0.7656	14	0.758	2.001	0.793
B32_1997	11	0.718	1.721	0.7491	9	0.766	1.682	0.7344
B32_2001	11	0.695	1.666	0.7399	9	0.781	1.716	0.7495
B32_2008	10	0.701	1.614	0.7346	12	0.767	1.905	0.7896
B33_1997	7	0.847	1.649	0.7655	10	0.839	1.932	0.8279
B33_2001	6	0.826	1.481	0.7345	10	0.873	2.01	0.8447
B33_2008	7	0.769	1.497	0.7205	11	0.818	1.962	0.8223
Averages	8	0.638	1.336	0.5839	9.6	0.751	1.646	0.73

S = Richness = number of non-zero elements in row

E = Evenness =  $H / \ln(\text{Richness})$

H = Diversity =  $-\sum (P_i \cdot \ln(P_i))$  = Shannon's diversity index

D = Simpson's diversity index for infinite population =  $1 - \sum (P_i \cdot P_i)$  where  $P_i$  = importance probability in element i (element i relativized by row total)

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