

Overstory and Understory Species Composition and Diversity in UNDERC Closed-Canopy
Hardwood Forests

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Abstract

Declining biodiversity is a concern in many eastern deciduous forests because understory diversity is decreasing, which will lead to a much less diverse overstory in several decades without additional management. Forest biodiversity decline impacts resiliency, increasing the chances of ecosystem collapse. These processes have been studied over decades in the state of Pennsylvania and in southern Wisconsin, but not in Northern Wisconsin or Upper Michigan, despite this region's vulnerability due to global warming and the spread of invasive tree pathogens. Woody plants, categorized into seedlings, saplings, and overstory trees, were surveyed on nine closed-canopy deciduous edge forest plots distributed throughout University of Notre Dame Environmental Research Center (UNDERC) property. *Acer saccharum* was the most abundant tree species overall and was dominant in six out of the nine overstory layers. The percentage of *A. saccharum* in the seedling layer was correlated with the percentage of *A. saccharum* and with the average diameter at breast height (DBH) in the overstory layer. Seedling Shannon diversity was negatively correlated with overstory DBH but was not correlated with overstory Shannon diversity. The overall Jaccard index between the overstory and seedling layers was low, indicating dissimilarity between the composition of these layers. These results do not indicate a clear limitation of understory diversity but do indicate that overstory characteristics have some impact on understory composition. This study highlights the importance of continued forest monitoring in the northern hardwood forests of northern Michigan and Wisconsin in the face of environmental change.

Introduction

In most ecosystems, declining biodiversity is a concern because the more species that are lost from an ecosystem, the more likely the ecosystem is to lose species that perform key functions, increasing the chances of ecosystem collapse (Walker 1992, Yoon 1997). In essence, this means if there are more species that are present in an ecosystem, it may be more resilient and adaptable to change (Folke et al. 2004). Within forest ecology in the eastern United States, these questions are relevant due to climate change, as well as the increase in non-native pathogens that have contributed to the loss of key tree species. For example, the ranges and abundance of many species have shrunk in recent decades, including *Castanea dentata* (American chestnut, lost due to chestnut blight), *Tsuga spp.* (hemlocks, lost due to hemlock woolly adelgid), and *Fraxinus spp.* (ash, lost due to emerald ash borer) (Moser et al. 2009).

Altered disturbance regimes have contributed to a sharp decline in tree diversity over the past several decades throughout the eastern deciduous biome. Clear-cut logging occurred for many years in this region until it declined around the beginning of the twentieth century, when disturbance regimes began to shift (W. Carson, pers. comm.). Due to fire suppression, deer overbrowsing and decreased logging and management, understory trees that are fire, browse, and shade tolerant have gained a significant advantage over trees that depend on more frequent disturbance and light availability to compete (Schumacher and Carson 2013).

Lower understory diversity is important in eastern deciduous forests because it is a significant predictor of what the overstory will look like in several decades (Schumacher and Carson 2013). This trend has been observed across northern hardwood forests in the eastern deciduous biome, from Pennsylvania (Schumacher and Carson 2013) to southern Wisconsin (Rogers et al. 2008). One species that has benefited greatly from these altered regimes is *Acer saccharum* (sugar maple), due to its general hardiness, resistance to deer browsing and very high shade tolerance (Burns and Honkala 1990, Schumacher and Carson 2013).

However, despite extensive studies in other parts of the eastern deciduous biome, this trend in declining biodiversity has not been observed as directly in northern Wisconsin and Michigan. Forest ecology in relationship to deer browsing has been studied in this region and researchers concluded that management practices have a more significant effect on biodiversity than browsing (Kraft et al. 2004, Van Deelen et al. 2006). However, there is not a clear consensus on which management tactics, if any, will work best to preserve biodiversity in this vulnerable region (Duvneek et al. 2014, Duvneek and Scheller 2016). Many studies on declining forest biodiversity have focused on the loss of oak trees (*Quercus spp.*) and their replacement by *Acer spp.* (Rogers et al. 2008, Schumacher and Carson 2013). This focus makes

these studies less relevant to forests in northern Wisconsin and Michigan, which have much lower levels of *Quercus spp.* than more southern forests (Burns and Honkala 1990, W. Carson, pers. comm.). Due to higher latitude, which contributes to a shorter growing season and lower light and temperature, the overall hardwood tree diversity in the northern Great Lakes region is more limited than in more southern parts of the eastern deciduous biome (Liu and Fyles 2006, W. Carson, pers. comm.). Climate change will have particularly significant, largely unknown impacts on the northern hardwood forests of Michigan and Wisconsin, which will experience accelerated warming (Duveneck et al. 2014, Arndt 2015, Duveneck and Scheller 2016).

The University of Notre Dame Environmental Research Center (UNDERC) in northern Wisconsin and Michigan is a prime research site for continued study of biodiversity loss trends. Most of the forest ecology research at UNDERC in the past several years has been focused on areas that have undergone disturbances such as wildfires or windstorms that cause canopy gaps (Einecker 2014, Sehl 2016, Doolittle 2018, Laate 2018, Martens 2018). However, historical data from this region show that forest management practices and other ecosystem processes have had a greater effect than natural disturbance on forest biodiversity (Van Deelen et al. 2006). It will be useful to shift away from disturbance-based research to study overstory and understory layers of closed-canopy forests in this region. This work will allow for comparisons to previous closed-canopy studies in other regions, and to discover what characteristics of overstory trees in this region can predict factors about understory layers.

No large-scale forest management takes place at UNDERC, so current understory composition will likely have a large effect on what overstory composition will look like in several decades. In northern Wisconsin and Michigan, logging for timber declined from the 1930s to the 1970s. Since the 1970s, UNDERC has been unmanaged and preserved due to its

designation as a research facility (NEON 2019). For a more comprehensive overview of forest management history in northern Wisconsin and Michigan, see Van Deelen et al. 2006. UNDERC is also an attractive research site because of the availability of LIDAR point cloud and elevation data (NEON 2016). While airborne LIDAR data are not generally usable for species determination or diversity measurement due to low resolution (Davies and Asner 2014), these data are useful for remotely determining baseline forest structure and characteristics.

UNDERC is also a compelling research site because some non-native tree pathogens have not wiped out tree species to the same extent they have further east and south. For example, *Fraxinus spp.*, particularly *Fraxinus nigra*, remain at UNDERC, even though their populations have been greatly reduced in most of the eastern United States due to the emerald ash borer (Moser et al. 2009). However, as previously mentioned, lower baseline diversity and susceptibility to accelerated warming make northern hardwood forests such as those at UNDERC very susceptible to biodiversity loss and subsequent ecosystem collapse (Duveneck et al. 2014, Arndt 2015, Duveneck and Scheller 2016). In all, the lack of previous closed-canopy research, sensitive nature of this forest region, lack of management, and availability of co-located NEON data make UNDERC an ideal site for forest biodiversity studies.

I hypothesized that certain overstory characteristics in closed-canopy northern hardwood forests at UNDERC would affect the diversity of the seedling layer. Specifically, I predicted 1) that in the overstory, less diversity, larger average diameter at breast height (DBH), and a higher percentage of *A. saccharum* would be correlated with decreased seedling diversity, and 2) that for multiple species, there will be a correlation between abundance in the overstory and the understory.

Methods

Research Plots

I used previously collected field observations and a tree species map (Blakely 2018) to choose general forest areas that were close to roads to facilitate access and that were deciduous-dominated. LIDAR-based elevation data was used to verify that study areas had significant canopy cover. Digital terrain model (DTM) and digital surface model (DSM) rasters were downloaded from the NEON data portal (NEON 2016). I merged many rasters over the extent of UNDERC property to form a master DTM and master DSM. Examining and comparing DSM and DTM values at several points within each study area confirmed significant canopy cover, because higher differences between DSM and DTM values indicate the presence of overstory trees (Hart and Wasser 2019).

Nine large selection boundary areas (40,000 m² each) were chosen, and three random points were generated inside each area using the ArcMap tool “Create Random Points” (Environmental Systems Research Institute 2018). The first randomly generated point within each area was used as the center of the nested research plot (Figure 2). A research plot was considered unsuitable and discarded if upon a brief visual scan after arrival at the site, its overstory appeared to be dominated by coniferous instead of deciduous trees, or if there were any large canopy gaps. Some light penetration into the understory was acceptable if it was just due to small gaps between tree crowns. However, if the research plot contained a canopy gap formed by one or more large downed trees, it was discarded, and one of the two other points generated within the selection boundary area was used as the center of the research plot instead. See Figure 1 for a map the locations of all the large boundary areas, as well as the research plots that were used. These controls were put in place to maintain some level of homogeneity in forest structure

while allowing for randomization and variation in species composition. Location precision in the field averaged around 10 meters for all research plots.

Data Collection

I classified woody plants (trees and shrubs) into three vegetation layers: seedlings (0.2 m < height < 1.4 m), saplings (height > 1.4 m and diameter at breast height (DBH) < 11.7 cm), and overstory (height > 1.4 m and DBH > 11.7 cm) (Thomas-Van Gundy et al. 2014). Overstory trees and saplings were sampled for the entire circular plot of radius 10 m. Seedlings were sampled within a central nested subplot of radius 5 m (Figure 2). I defined an individual tree as a plant that had a distinct, separate trunk aboveground. This definition may not have been completely accurate to all species due to asexually reproducing species; however, for the purpose of studying forest structure and diversity across many species, it was an appropriate standard. All individuals were identified as closely to species as possible, and the DBH of all overstory trees was measured.

Statistical Analysis

Summary statistics for each plot and layer (overstory, sapling, and seedling), such as density, species richness, Shannon diversity (alpha diversity), and percentage of individuals in the three most abundant species were calculated. The average DBH for overstory trees and the Jaccard similarity index (beta diversity) for the overstory vs. the seedling layers were also calculated. Pearson's product-moment correlation tests were performed for the following comparisons: percent trees in the overstory vs. seedling layer for *Acer saccharum*, *Fraxinus nigra*, and *Acer rubrum*; overstory DBH vs. percent seedling trees for the same three species; overstory DBH vs. percent overstory trees for *A. saccharum*; overstory DBH vs. seedling

Shannon diversity; and all three correlation comparisons between overstory, seedling, and sapling Shannon diversity.

Due to the non-normally distributed nature of most variables, Friedman tests were used to model whether there were differences in density and species richness between the three layer categories. A Welch two-sample t-test was conducted to compare seedling Shannon diversity in plots with and without an *A. saccharum* dominated overstory. Finally, the Jaccard similarity index was calculated, which represented beta diversity: differences in species richness and composition of seedlings vs. overstory trees at each plot. R was used to perform all statistical tests (R Core Team 2018).

Results

Overview

Research plot characteristics and locations are summarized in Table 1, and calculated variables are summarized in Table 2. Raw counts, calculation data, and more are available in the attached PDF. Twenty-seven total species were found in the seedling layers across all plots. The sapling layer had seventeen species, and the overstory layer had twelve species. *Acer saccharum* was the most abundant species across all three layers (seedling, sapling, and overstory) (Table 3). The next two most abundant species overall were *Fraxinus nigra* and *Acer rubrum*. At five of the plots, over 70 percent of the overstory layer were *A. saccharum* trees, and at the other four plots, the *A. saccharum* overstory percentage was less than 45 percent (Figure 3). At 13 out of the 27 plot & layer combinations (48%), including 6 out of the 9 overstory layers, *A. saccharum* was the most abundant species. The most abundant species in seven out of the nine seedling layers was a highly shade-tolerant species. Of the two remaining plots, one was dominated by black

ash, which has low shade tolerance, and the other had no seedlings at all. Five out of the 27 plot layers (18.5%) were an *A. saccharum* monoculture.

A. saccharum Dominance

There was a significant correlation ($r = 0.7053$, $p = 0.03381$, $t = 2.632$, $df = 7$) between the percentage of *A. saccharum* trees in the overstory and the seedling layer. This correlation was not evident for the next two most abundant species, *F. nigra* ($r = -0.1189$, $t = -0.31691$, $df = 7$, $p = 0.7606$) and *A. rubrum* ($r = 0.08838$, $t = 0.23476$, $df = 7$, $p = 0.8211$). Additionally, according to a Friedman test, the seedling layer was much denser on average than the sapling and overstory layers ($\max T = 2.5927$, $p = 0.02575$, Figure 4).

There was also a significant correlation between the diameter at breast height (DBH) of all overstory trees and the percentage of seedlings in the same plot that were *A. saccharum* ($r = 0.7392$, $t = 2.9042$, $df = 7$, $p = 0.02285$). This correlation was not significant for *A. rubrum* ($r = -0.5789$, $t = -1.8783$, $df = 7$, $p = 0.1024$) or for *F. nigra* ($r = -0.2211$, $t = -0.59989$, $df = 7$, $p = 0.5675$). There was some correlation between DBH and percentage of *A. saccharum* in the overstory ($r = 0.5193$), but it was not significant ($t = 1.6079$, $df = 7$, $p = 0.1519$).

A Welch two-sample t-test showed that there was no significant difference in mean seedling diversity between plots with and without an *A. saccharum* dominated overstory ($t = -1.4805$, $df = 3.8027$, $p = 0.2164$, Figure 5).

Alpha and Beta Diversity

Species richness and the Shannon diversity index were calculated for each forest layer at each plot (Table 2). A Friedman test showed that there was no significant difference in species richness between the three layer categories ($\max T = 1.6641$, $p = 0.219$, Figure 6). When analyzing the relationship between DBH of overstory trees and Shannon diversity index of

seedlings, a negative correlation was observed that is significant at the 10% level ($r = -0.5882$, $t = -1.9244$, $df = 7$, $p = 0.09571$). There was a correlation between seedling and sapling diversity ($r = 0.6941$, $t = 2.5516$, $df = 7$, $p = 0.03801$), but neither of these were significantly correlated with overstory diversity. The average Jaccard similarity index across all plots was 0.2903, and the total Jaccard similarity index for seedlings vs. overstory trees at all plots was 0.3846.

Discussion

The high abundance of *A. saccharum* across many plots indicates that parts of UNDERC property may be experiencing the same trend toward a shade-tolerant monoculture forest that has been reported in other eastern deciduous forests (Rogers et al. 2008, Schumacher and Carson 2013). Many of the baseline results of this study confirm obvious forest ecosystem features. I correctly hypothesized that *A. saccharum* abundance in the overstory and seedling layers would be correlated. However, this prediction was only true for the most abundant species, potentially due to sample size limitations for other species. Seedling density were significantly higher than sapling and overstory density, which is another baseline, intuitively obvious result that validates my methodology and confirms some of my assumptions about UNDERC forest ecosystems.

In contrast to these baseline observations, many results were unexpected. There was no significant difference in seedling diversity between forests with and without an *A. saccharum* dominated overstory. I incorrectly hypothesized that plots with an *A. saccharum* dominated overstory would have lower seedling diversity. Overall, the seedling layer was surprisingly diverse. While there was no difference in average species richness by plot between the three forest layers, the seedling layer contained the greatest number of different species compared to the seedling and sapling layers. Both the average (0.2903) and overall (0.3846) Jaccard indices

were low, indicating generally low similarity between the overstory and the seedling layer. Furthermore, only one of the plots had a homogenized seedling layer (all *A. saccharum*), and one other had no seedlings. These results may indicate that in UNDERC hardwood forests, the diversity and shading of the overstory may have less of an influence on understory diversity than in other eastern deciduous forests studied by Schumacher and Carson (2013) and Rogers et al. (2008).

Schumacher and Carson (2013) extensively discuss the influence of an *A. saccharum*-dominated overstory on the creation of a homogenized understory, and Rogers et al. (2008) saw similar effects. Both of these studies focus on the loss of *Quercus spp.* when discussing declining biodiversity, as oaks are prominent canopy trees in their study areas but are not regenerating in the understory due to fire suppression and over-browsing. *Quercus spp.* are barely present at UNDERC, and are certainly not a dominant overstory tree (NEON 2019, W. Carson, pers comm.). Given typical habitat ranges, the only oak one might expect to find at UNDERC is *Quercus rubra* (Burns and Honkala 1990). Since significant portions of UNDERC overstory trees are *A. saccharum* and not *Quercus rubra*, it is possible that *Acer spp.* at UNDERC have already decreased diversity by taking over traditional *Quercus spp.* habitat, and that this process has moved faster at UNDERC than in Pennsylvania or southern Wisconsin (Rogers et al. 2008, Schumacher and Carson 2013). However, this is unlikely, because both of these studies predicted that once the overstory was mostly made up of *A. saccharum*, the understory would be as well, which was not the case at most of my sites. Therefore, there must be other factors that contribute to the unique, limited effects of overstory trees on understory diversity at UNDERC when compared to other studies.

A strict diversity index value may not be the best measure of differences in composition between UNDERC forest layers. Many plots and layers had large percentages of one or a few species, followed by only a few individuals of other species. Therefore, abundance likely had more of an effect on forest structure and dynamics than a simple count of species, which is reflected in the Shannon and Jaccard index results. These results connect back to several studies which indicated that in some forests, changes in abundance are much more significant to forest structures and processes than species richness (Naeem et al. 1994, 1995).

My small sample size ($N = 9$) and focus on a wide, randomly selected range of closed-canopy deciduous forest plots may have affected my understory vs. overstory diversity results as well. Due to lower density with increasing size, even with my plot/subplot design, throughout the study, far more seedlings (3,522 individuals) than saplings (324 individuals) or overstory trees (167 individuals) were sampled. My low sample size for overstory trees in particular may have limited my overstory diversity results. Furthermore, the Rogers et al. (2008) study examined trends in diversity and species dominance across several decades, and the Schumacher and Carson (2013) study conducted long-term experimental disturbances to observe their effects on diversity. Time constraints and a lack of easily accessible historical data for the area limited the analyses that could be conducted in this study.

While overstory composition did not seem to directly affect understory diversity in my study, some overstory features had influence on understory characteristics. The diameter at breast height (DBH) of overstory trees and *A. saccharum* abundance percentage in the seedling layer were positively correlated. DBH in the overstory was also negatively correlated with Shannon diversity of seedlings. This is likely due to the fact that *A. saccharum* is highly shade tolerant (Burns and Honkala 1990). Trees with a larger DBH typically have a larger area of

canopy cover. Therefore, a forest with higher average DBH will have denser canopy cover, limiting growth of less shade-tolerant species, so *A. saccharum* abundance increases and diversity decreases in the seedling layer. An alternative explanation for these results is that *A. saccharum* trees in general have a higher DBH, so the correlation between *A. saccharum* seedlings and DBH is a result of the already-established correlation between *A. saccharum* seedlings and overstory trees. However, the correlation between DBH and percentage of *A. saccharum* in the overstory was not significant. Thus, there is some relationship between DBH of overstory trees and *A. saccharum* abundance that cannot be explained simply by *A. saccharum* presence in the overstory.

Some of my results raise questions about the artificially created boundaries between seedlings, saplings, and the overstory. The correlation between seedling and sapling diversity most likely relates to the similar sizes of many individual seedlings and saplings. During fieldwork, I frequently had to check whether an individual was above or below the 1.4 m cutoff between seedlings and saplings, so their relatedness in terms of diversity is not surprising. Seedlings and saplings as defined in my study are likely to receive similar amounts of light and be limited in similar ways by shade tolerance under the same overstory layer. Future studies could group seedlings and saplings into one understory layer. Additionally, instead of pulling forest layer categorizations straight from previous literature, future researchers could do initial fieldwork or work with LIDAR data to determine whether there is a more natural boundary between seedlings and saplings in the study area.

Another possible factor contributing to the difference between my results and previous studies in Pennsylvania and Southern Wisconsin is the effect of emerald ash borer (EAB) in these environments. EAB has wiped out *Fraxinus spp.* populations in every Pennsylvania county

(Schumacher and Carson 2013, Pennsylvania Department of Conservation and Natural Resources 2019) and in nearly all of the counties studied in southern Wisconsin (Rogers et al. 2008, Wisconsin Department of Natural Resources 2019). By contrast, EAB has not been detected in Vilas County, Wisconsin or in Gogebic County, Michigan, where UNDERC is located (Ellison 2016, Wisconsin Department of Natural Resources 2019). This absence was reflected in my data: 10.9% of all individuals sampled were *Fraxinus spp.*, including *F. nigra*, which was the second most abundant species overall despite its low shade tolerance (Burns and Honkala 1990).

EAB spread to the westernmost parts of Upper Michigan and to northern Wisconsin is inevitable. Once EAB arrives at UNDERC, it will drastically change forest composition and structure, and may contribute heavily to further homogenization of the forest. This may be especially true since according to my data, after *F. nigra*, *A. rubrum* was the next most abundant species, so if *F. nigra* were eliminated, two shade- and browse-tolerant *Acer* species would likely dominate. However, if EAB worked quickly, the sudden death of many *Fraxinus* trees may alter the disturbance regime, creating canopy gaps that could be filled by less shade-tolerant species. Regardless, with the dual threats of EAB and climate change on the horizon, long-term, regular surveying is of utmost importance to monitor and maintain this vulnerable ecosystem.

UNDERC forests are unmanaged for research purposes, and many of the forested areas surrounding UNDERC undergo little management due to their status as wilderness areas (U.S. Forest Service 2019). If these forests remain unmanaged as they undergo drastic changes due to EAB invasion, a warming climate, and potentially other climate change-related issues or invasive tree pathogens, they may become susceptible to accelerated biodiversity decline and ecosystem collapse. There is not yet sufficient evidence of drastic biodiversity decline from my research

alone, but it is clear that studies from deciduous forests further south do not provide an accurate picture of northern Wisconsin and Michigan hardwood forests. Therefore, more extensive surveying efforts and analysis of historical change are necessary to understand how to preserve forest processes and biodiversity in this unique region.

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Name	Lat	Long	Canopy Status	Herbaceous Layer	Other Characteristics
1: STOR	46.2271	-89.5431	closed, with nearby canopy gaps off plot	dense ferns in part of plot	large height difference between saplings and canopy trees
2: INMO	46.2293	-89.5110	average canopy cover (not completely closed)	fairly open, not very dense, lots of leaf litter	on a hill, near a lake
3: BRCK	46.2106	-89.4911	closed, with nearby canopy gaps off plot	lots of diverse ferns, wildflowers, and grasses	fragmented: close to several roads and a stretch of power lines
4: TPND	46.2398	-89.5594	mostly closed and full canopy	dense and diverse: ferns and wildflowers	trillium: evidence of low levels of deer browsing
5: TNCK	46.2310	-89.5319	average canopy cover (not completely closed)	dense and diverse: grasses, mosses, ferns	low, wet area near a creek
6: PLUM	46.2170	-89.5095	mostly closed and full canopy, but with lots of dead/downed trees	some grasses, lots of leaf litter	fairly dry, near a lake
7: PRES	46.2336	-89.5405	average canopy cover (not completely closed)	diverse grasses, mosses (sphagnum), ferns	forested wetland
8: SMOR	46.2514	-89.5208	mostly closed and full canopy, but younger canopy trees	dense and diverse: ferns and wildflowers	part is wet and dense understory, part is dry and open
9: BPOT	46.2352	-89.5188	average canopy cover (not completely closed)	dense and diverse	low, wet area

Table 1. Plot characteristics, locations, and field notes. All plots had a mostly closed canopy, were dominated by deciduous canopy trees, and were less than 100 m from a road.

Plot	1 - STOR	2 - INMO	3 - BRCK	4 - TPND	5 - TNCK	6 - PLUM	7 - PRES	8 - SMOR	9 - BPOT
Overstory Density (individuals/sq m)	0.01592	0.05411	0.03820	0.01273	0.02626	0.01082	0.01273	0.07321	0.01728
Sapling Density (individuals/sq m)	0.00955	0.01592	0.08594	0.01910	0.02308	0.02467	0.03820	0.01783	0.03592
Seedling Density (individuals/sq m)	0.70792	1.20726	2.91572	1.79686	0.16944	0.00000	0.11141	0.47237	0.44745
% of overstory - sugar maple	90	100	100	75	0	41.18	0	100	10.53
% of saplings - sugar maple	66.67	20	100	5.56	14.94	87.1	0	7.84	2.53
% of seedlings - sugar maple	82.01	94.92	100	94.6	12.14	0	0	2.96	3.66
% of overstory - black ash	0	0	0	0	0.7576	0	0	0	0.0263
% of saplings - black ash	0	0	0	0	0.1609	0	0	0	0.0380
% of seedlings - black ash	0	0.0163	0	0	0.0116	0	0	0.830	0
% of overstory - red maple	0	0	0	0	0	0	0.55	0	0
% of saplings - red maple	0	0	0	0	0.09195	0	0	0	0.07595
% of seedlings - red maple	0.0108	0	0	0.00443	0.462	0	0.229	0.0162	0.756
Average DBH of overstory (cm)	30.44	26.63	30.46	42.92	17.86	25.04	23.97	22.51	20.58
Species richness - overstory	2	1	1	2	4	5	5	1	7
Species richness - saplings	2	6	1	2	12	4	3	5	7
Species richness - seedlings	5	11	1	9	13	0	4	10	7
Overall species richness	5	12	1	9	16	5	8	10	12
Is the overstory sugar maple-dominated?	yes	yes	yes	yes	no	no	no	yes	no
Dominant overstory tree species	SM	SM	SM	SM	BA	SM	RM	SM	QA
Shannon diversity index - overstory	0.6	0.2950	0	0.3126	1.7082	0	1.265	0.7639	0.8911
Shannon diversity index - saplings	0.6365	1.4311	0	0.2338	2.0065	0.5187	0.6811	1.037	1.429
Shannon diversity index - seedlings	0.3251	0	0	0.5623	0.7322	1.430	1.205	0	1.484
Jaccard similarity - overstory vs. seedlings	0.4	0.0909	1	0.2222	0.1333	0	0.5	0.1	0.1667

Table 2. Summary data and calculated values by plot and by layer, including density, percentage of dominant species, DBH of overstory, species richness, and diversity calculations.

Species	Seedlings	Saplings	Overstory	Shade Tolerance
<i>Acer saccharum</i>	2556	84	78	high
<i>Fraxinus nigra</i>	327	17	26	low
<i>Acer rubrum</i>	288	14	6	high
<i>Corylus cornuta</i>	60	47	0	mid
<i>Fraxinus pennsylvanica</i>	53	4	1	mid
<i>Cornus alterniflora</i>	46	1	0	high
<i>Abies balsamea</i>	35	62	4	high
<i>Betula papyrifera</i>	31	56	0	low
<i>Prunus virginiana</i>	25	0	0	high
<i>Lonicera canadensis</i>	11	1	0	mid
<i>Amelanchier spp.</i>	9	2	0	mid
<i>Picea mariana</i> or <i>Picea glauca</i>	8	4	9	mid
<i>Alnus incana</i>	7	4	0	mid
<i>Ulmus rubra</i>	7	0	0	high
<i>Acer spicatum</i>	5	7	0	high
<i>Tilia americana</i>	4	0	0	high
<i>Dirca palustris</i>	4	9	0	high
<i>Fraxinus americana</i>	4	3	3	mid
<i>Prunus serotina</i>	3	0	0	low
<i>Cornus racemose</i>	2	0	0	high
<i>Populus tremuloides</i>	2	9	23	low
<i>Thuja occidentalis</i>	2	1	8	high
<i>Ulmus americana</i>	0	10	2	mid
<i>Betula alleghaniensis</i>	0	4	2	mid
<i>Acer pennsylvanicum</i>	0	1	0	high
<i>Tsuga canadensis</i>	0	0	5	high
No successful ID	17	0	0	n/a

Table 3. Summary of tree species abundance by layer category across all plots. 24 out of 27 morphospecies were identified to species, one was identified to genus, one was identified to two related species, and one morphospecies was not able to be identified. Shade tolerance is also listed for each species (Burns and Honkala 1990).

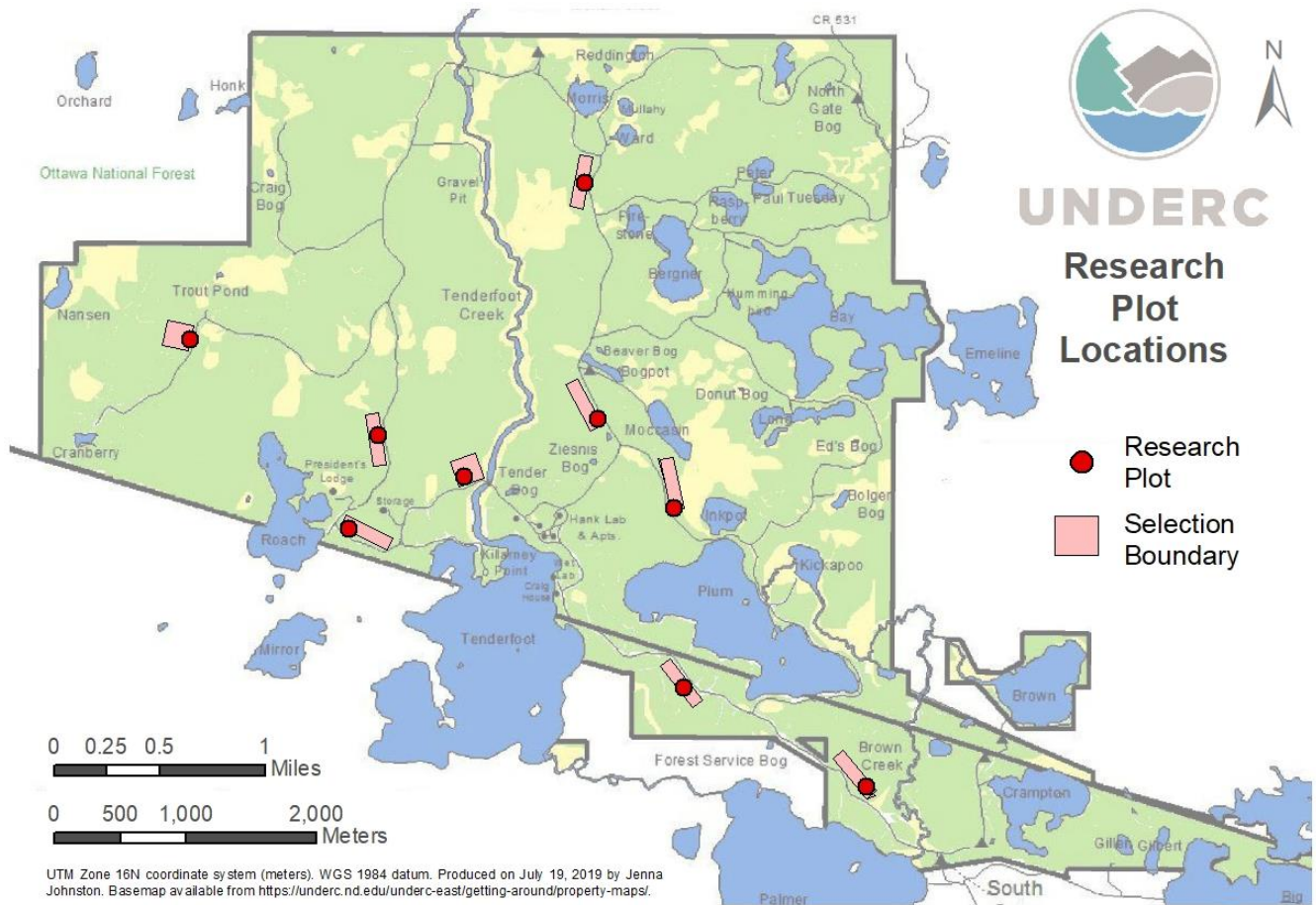


Figure 1. Map of research plot locations with the 40,000 m² selected boundaries in which the plot locations were randomly generated.

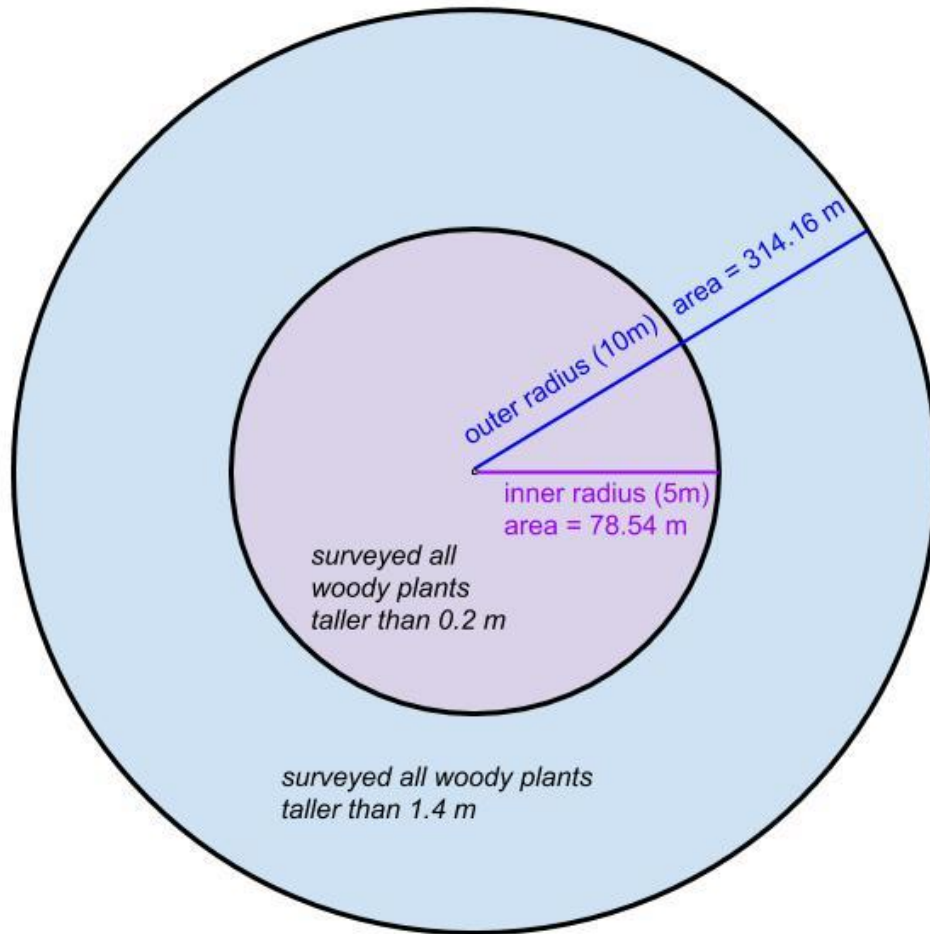


Figure 2. Nested plot setup. Each plot was in a unique selection boundary, and each was between 10 and 100 m from a road.

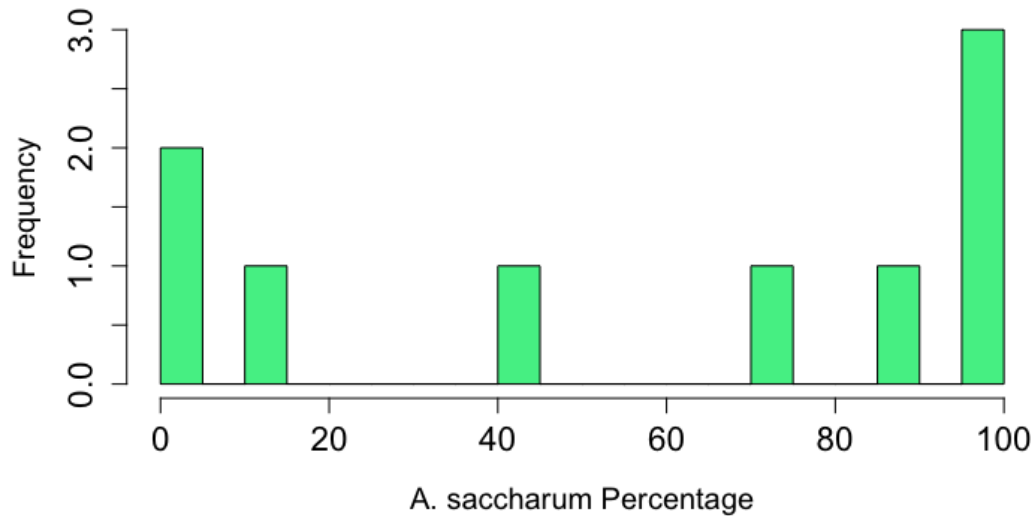


Figure 3. Histogram showing *A. saccharum* overstory percentage, with one data point for each research plot.

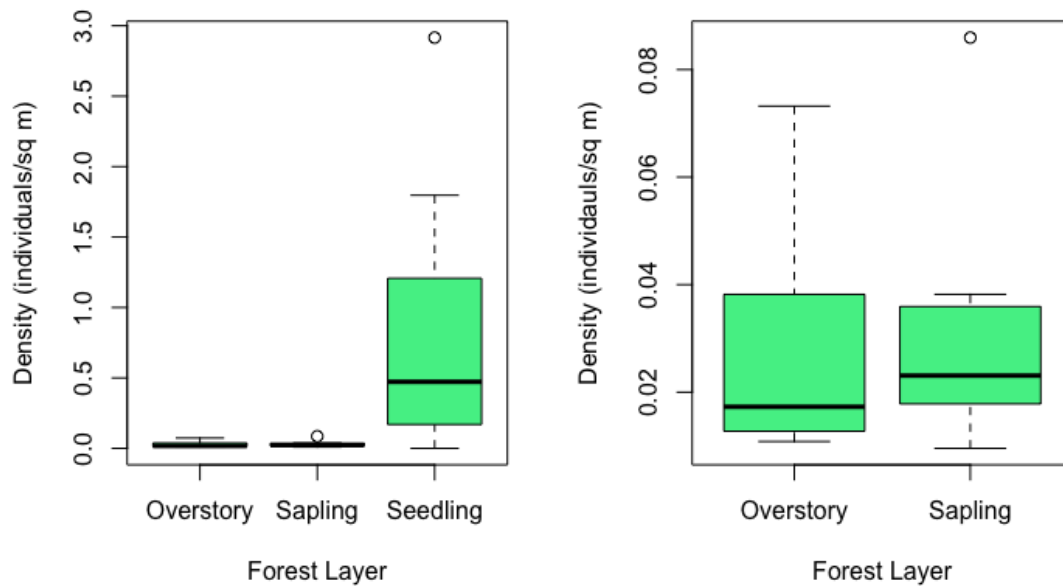


Figure 4. Box plots showing density (individuals / m²) by forest layer type for all three layers (left), and to show more detail, showing density for just the overstory and sapling forest layer types (right). According to the Friedman test results (overall $p = 0.02581$, $\max T = 2.5927$, $n = 9$), seedling density is significantly different than both overstory diversity ($p = 0.02605$) and sapling diversity ($p = 0.04848$), but sapling and overstory diversity are not significantly different ($p = 0.9698$).

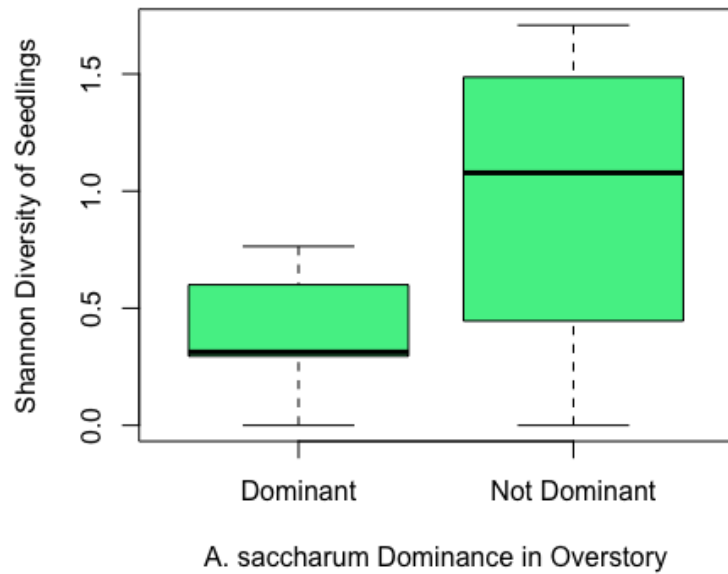


Figure 5. Box plot showing Shannon diversity index for the seedling layer in plots where *A. saccharum* is vs. is not dominant in the overstory. According to a t-test, there was no significant difference between these two categories ($t = -1.4805$, $df = 3.8027$, $p = 0.2164$).

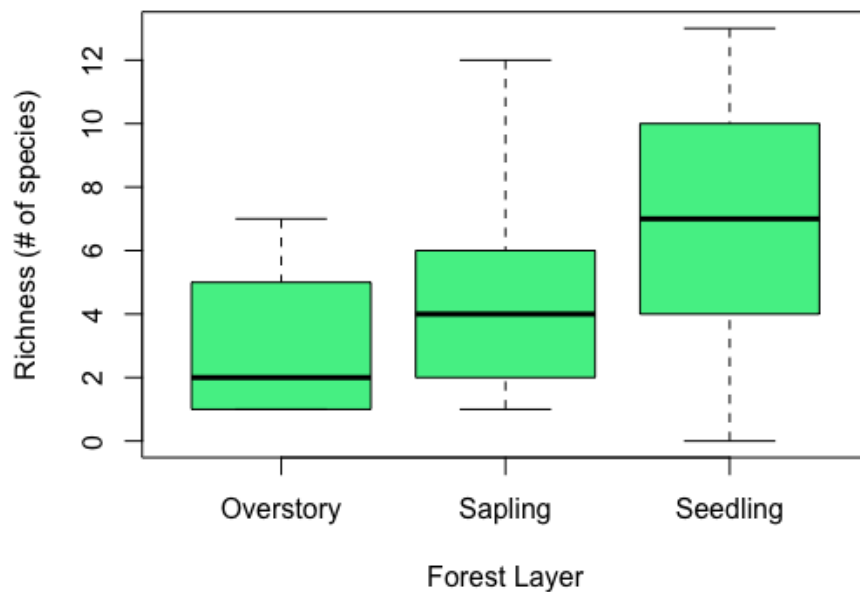


Figure 6. Box plot showing differences in species richness for each forest layer (overstory, seedling, and sapling). Differences were not significant based on a Friedman test ($\max T = 1.6641$, $p = 0.2191$, $n = 9$).

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