HABITAT TYPES – WHAT THEY CAN TELL US NOW AND IN THE FUTURE

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Abstract. Habitat classification systems utilize the relationship between the herbaceous layer and potential climax vegetation to classify forest vegetation. Habitat classification systems have been developed throughout the United States including Michigan. In 2010, ten years after the first sampling, 30 of the original 200 plots throughout the Western Upper Peninsula were resampled twice during the growing season. Exotic earthworm populations were also sampled in early September at all 30 plots. Nonmetric multidimensional scaling (NMS) ordination was used to discern differences in habitat types between years (2000 vs. 2010) and between seasons in 2010 (spring vs. summer). Overstory trees per hectare (TPH) decreased from 2000 to 2010, likely the result of forest management activities. A greater number of herbaceous species were observed in 2010; however, the majority of these new species were weedy or invasive. Exotic European earthworms were observed in all habitat types; earthworm densities generally increased with increasing soil richness and site quality, with herbaceous plant cover negatively associated with earthworm biomass. Continual monitoring of these plots will allow scientists and managers to assess how herbaceous community change through time and observe the effects of invasive species and changing climatic patterns on forest ecosystems of the Great Lakes region.
Keywords: *exotic earthworms, herbaceous species, forest dynamics, Great Lakes Region, forest management*

Introduction

Every forest ecosystem is distinct and requires individual consideration when developing management options. Scientists and managers often classify forests with similar attributes to help guide management decisions and to allow for comparisons when different variables are manipulated. Forest classification systems range from the use of one variable (e.g., dominant overstory vegetation to characterize forest cover type) to the use of many complex variables including climate, soils, geology, and vegetation cover (as used in the Terrestrial Ecological Unit Inventory (TEUI); Winthers et al., 2005). Habitat typing was first developed in the Western United States and relies on the presence/absence of particular herbaceous species (see Daubenmire and Daubenmire, 1968). This system of classification was later developed for the Great Lakes region by sampling plots across the Upper Peninsula of Michigan and Northern Wisconsin (Coffman et al., 1983). Further sampling of the Upper and Lower Peninsulas

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of Michigan allowed for the development of *The Guide to Forest Communities and Habitat Types of Michigan* (Burger and Kotar, 2003).

Early habitat classification systems utilized key concepts from both Clements' (1916, 1936) and Gleason's (1926) theories of vegetation development (Daubenmire, 1976). Habitat typing relies on the early stabilization of the understory, especially the herbaceous layer, compared to the overstory (Daubenmire and Daubenmire, 1968; Pfister and Arno, 1980; Kotar, 1986; Pfister, 1989). This stabilized understory is used to predict the potential climax overstory (resulting in the habitat type name), which is thought to reflect the growth potential of the site (Daubenmire and Daubenmire, 1968; Pfister, 1989). Habitat typing does not view succession as a unidirectional process (Clements, 1916; Clements, 1936) but rather, one that is affected by environmental variables and disturbance history (Daubenmire, 1976).

The concept of habitat typing contains many assumptions about sampling, species interactions, and how species respond to disturbance (see Daubenmire and Daubenmire, 1968; Daubenmire, 1976; Pfister and Arno, 1980; Cook, 1995 for a critical review). Studies within the Great Lakes Region have observed varying responses of the herbaceous layer to disturbance (Metzger and Schultz, 1984; Fredericksen et al., 1999; Jenkins and Parker, 1999; Scheller and Mladenoff, 2002; Zenner et al., 2006; Kern et al., 2006), suggesting potential implications to how this vegetation layer is used to classify site potential. Metzger and Schultz (1981) observed in a northern hardwood forest in the Upper Peninsula of Michigan no large differences in the herbaceous layer between different harvest intensities after 50 years. They did note that spring ephemerals may be more sensitive to repeated disturbances such as single-tree selection. However, Roberts and Gilliam (1995) observed in Northern Lower Michigan a greater change in overall diversity and species composition in disturbed mesic sites than dry/mesic sites when comparing them to undisturbed mesic and dry/mesic sites. The disturbed mesic sites had greater increases in weedy and early successional species. This trend of increasing weedy and early successional species was also observed in mesic northern hardwood forests receiving uneven- aged management compared with even-aged management and old-growth stands in Northern Wisconsin and the Upper Peninsula of Michigan (Scheller and Mladenoff, 2002).

Disturbance is only one factor that can affect herbaceous species composition. Native and exotic species interactions have also been shown to be important (Bohlen et al., 2004; Fisichelli et al., 2012). The introduction of European earthworms in the Great Lakes region, a region that developed without native earthworms following the last glaciation (James, 1995), has not only affected soil nutrient cycling (Scheu and Parkinson, 1994; Tomlin et al., 1995; Bohlen et al., 2004; Suárez et al., 2004; Hale et al., 2005b) but has also affected herbaceous species diversity (Gundale, 2002; Hale, 2006; Holdsworth, 2007).

Habitat typing is just one classification system that both scientists and managers can use to assess and classify forests. *The Guide to Forest Communities and Habitat Types of Michigan* by Burger and Kotar (2003) was developed along a moisture and soil nutrient gradient. The objectives of the resampling in this study were to monitor changes in summer herbaceous vegetation after 10 years, to gain a better understanding of possible shifts in herbaceous species communities, and to observe the potential impacts exotic earthworms may have on the herbaceous community. We hypothesized that the spring and summer herbaceous community would adhere to similar nutrient and moisture gradients that were observed ten years previously. We

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also hypothesized that herbaceous species composition would differ between years (2000 vs. 2010) and between seasons (spring and summer). We could not identify exact mechanisms that could lead to compositional shifts between years and seasons as these were not measured during the first sampling, but we did hypothesize that: 1) herbaceous species composition may be changing due to high earthworm densities which would lead to simplified plant communities between sample periods; 2) increased percent cover of a few invasive or weedy species may outcompete native species, reducing species richness and diversity; and 3) spring ephermals would decrease and summer herbaceous species would increase in percent cover and frequency as the canopy closed.

Methods

Study area

Within the Western Upper Peninsula of Michigan there is approximately two million ha of forested land. Of this, thirty-three percent (650,000 ha) is located within Houghton, Keweenaw, and Ontonagon counties. The vast majority (93%) of this 650,000 million ha is in young forests, under 100 years (Forest Inventory Data Online, 2010). The three most common cover types are the maple/beech/birch (57%), aspen/birch (19%), and spruce/fir (10%) (Forest Inventory Data Online, 2010). Previous glacial activity greatly influenced the surface geology occurring in these counties; common geological features include ground moraines, end moraines, outwash deposits, and glacial lake shoreline (Soil Conservation Service, 1991, 2006, 2010).

All three counties generally have a continental climate, with average daily maximum temperatures of -6.7°C and 23.8°C and average daily minimum temperatures of -13.9°C and 12.4°C for January and July respectively (recorded in Houghton County; Soil Conservation Service, 1991). Temperatures are generally warmer in the summer and cooler in the winter with increasing distance from Lake Superior. Average precipitation is 0.87 m with an additional 5.3 m of average snowfall (Soil Conservation Service, 1991, 2006, 2010). Normal season conditions occurred during the summer sampling of 2000 (personal communication, John Kotar). Abnormal seasonal temperatures and precipitation occurred during the summer of 2010, the year of our resampling. There were only trace snowfall events during the months of March and April; compared to March and April 2000, there was 7.70 cm and 2.21 cm, respectively, less precipitation in 2010 (PRISM Climate Group, 2004). Maximum temperatures during the months of April and May, 2010 were also 5.21°C and 0.79°C above maximum temperatures recorded for April and May, 2000.

Six different habitat types were selected for resampling during the spring and summer of 2010 in Houghton, Keweenaw, and Ontonagon counties. The six habitat types span a range of moisture and nutrient richness. General characteristics of each habitat type, along with the full and abbreviated name, can be found in *Table* 1.

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Table 1. *Summary information of habitat types that were resampled in 2010. Habitat types are arranged from least productive to most productive. Additional information on each habitat type can be found in The Guide to Forest Communities and Habitat Types of Michigan by Burger and Kotar, 2003.*

Habitat Type	Acronym	Common Overstory Species	Soils	Moisture/ Nutrient
Pinus strobus - Acer rubrum/ Vaccinium angustifolium - Cornus canadensis variant	PArV-Co	*Pinus resinosa, Pinus strobus, Pinus banksiana, Acer rubrum, Betula papyrifera*	Deep lacustrine deposits of sand & gravel	Dry/poor nutrient
Acer saccharum – Acer rubrum/ Aster macrophyllus	AArAst	*Acer saccharum, Acer rubrum, Quercus rubra, Abies balsamea, Betula papyrifera*	Sand and loamy sand soils over bedrock	Dry-mesic / poor to medium nutrients
Acer saccharum – Acer rubrum/ Lycopodium annotinum	AArLy	*Acer saccharum, Acer rubrum, Betula alleghaniensis*	Loamy sand to loam soils over	Dry-mesic / poor to medium nutrients
Acer saccharum- Tsuga canadensis/ Maianthenum canadense - Osmorhiza claytoni variant	ATM-O	*Acer saccharum, Acer rubrum, Tilia americana*	Sandy loam soils with clay subsurface layers	Mesic/medium nutrient
Acer saccharum- Tsuga canadensis/ Maianthenum canadense - Smilacina racemosa variant	ATM-Sm	*Acer saccharum, Acer rubrum, Tilia americana, Betula alleghaniensis, Tsuga canadensis*	Loamy sand to sandy loam soil with cobbly subsurfaces	Mesic/medium nutrient
Acer saccharum- Tsuga canadensis/ Dryopteris spinulosa - Caulophyllum thalictroides variant	ATD-Ca	*Acer saccharum, Tilia americana, Fraxinus americana, Betula alleghaniensis, Tsuga canadensis*	Clay deposits with loamy textured surface layer	Mesic/medium to rich nutrient

Vegetation sampling

Thirty of the 200 plots used to create *The Guide to Forest Communities and Habitat Types of Michigan for the Western Upper Peninsula* (Burger and Kotar, 2003) were relocated and resampled during the spring and summer of 2010. Original plot locations were not permanently marked during the summer of 2000 but clear directions were recorded for each plot. Plots were relocated in spring 2010 and a GPS location was taken at each plot to document plot location and to relocate plots during the summer sampling period. Three of the thirty plots (10%) had to be offset slightly due to extreme changes at the original plot location such as a new trail or building. Even with these offsets and lack of permanent plots, we are confident that the sample locations are representative of the forest communities sampled during the summer of 2000.

Sampling in 2010 was modified slightly from the original sampling during the summer of 2000 (Burger and Kotar, 2003). Sampling in 2010 occurred during the spring (May 4th – May 24th) before full leaf on and in summer (June 24th – July 13th). Summer sampling coincided with phenological changes in plants, such as the ripening of *Vaccinium* spp. and *Rubus* spp. berries.

At each plot location, a 21 m x 14 m macroplot was established (Burger and Kotar, 2003). Modification of the original sampling included the use of 1-m^2 plots to measure herbaceous species (*Fig. 1*). Environmental data such as topography, configuration, slope, and time since last harvest activity were recorded. Topography was described as a ridge, upper slope, mid slope, lower slope, or bench. Configuration was described as

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convex, straight, concave, or undulating. Slope was categorized into four classes: 1) 0-10%, 2) 11-25%, 3) 26-50%, and 4) 51% and greater. Harvest activity was identified by the presence of stumps and small diameter harvest slash and was estimated as having occurred within the last five years, six to ten years ago, eleven to fifteen years ago, sixteen to twenty years ago, and greater than twenty one years.

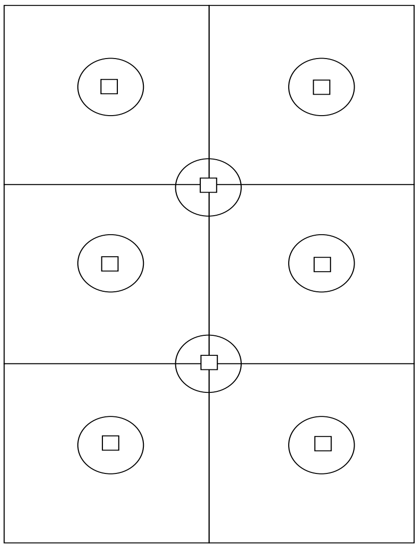

Figure 1. *Sampling design used during the spring and summer of 2010 was slightly modified from Burger and Kotar (2003). Within the 21 m by 14 m macroplot, eight 1-m^2 square quadrats were established to measure herbaceous species. Eight circular 0.0004-ha plots were used to measure seedlings and saplings.*

Inside each macroplot, all overstory species greater than 10 cm dbh were identified to species, and diameter was measured at breast height (1.37m). Overstory trees were divided into five canopy classes: open grown, dominant, co-dominant, intermediate, or suppressed (Oliver and Larson, 1996). Diameter at breast height was also measured on all snags. Overstory measurements were conducted last to decrease trampling of the herbaceous layer.

Within the macroplot, eight 1-m^2 quadrats were used to sample herbaceous species (*Fig. 1*). All herbaceous species within the quadrat were identified to species with the exception of grasses, sedges, mosses, and certain families where identification could only be made to genus. After identification, species were placed into a coverage class. The same coverage classes were used as the original sampling in 2000: 1) 0-1%, 2) 1-5%, 3) 5-10%, 4) 10-25%, 5) 25-50%, 6) 50-75%, and 7) greater than 75%. All estimates of percent cover in 2010 were done by one researcher to minimize bias. Using the quadrat locations, two opposite corners were selected to estimate canopy cover using a spherical concave densitometer for a total of 16 measurements per macroplot. The macroplot was then searched for any new herbaceous species that were not present in any quadrat; these species were recorded as present.

At the center of each of the eight quadrats, a 0.0004-ha circular plot was established to measure the seedling and sapling layers. Seedlings were defined as any woody tree species less than 30.5 cm in height. Saplings were subdivided into small saplings (30.6 cm to 1.4 m in height) and large saplings (1.5 m in height to 9.9 cm in diameter).

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Density and percent cover were measured for seedlings, small saplings, and large saplings by species. Percent cover was estimated using the same coverage classes used for the herbaceous species.

Earthworm sampling

Three 0.5-m^2 metal quadrats were placed randomly within the macroplot to sample earthworm populations by liquid extraction during the first two weeks of September (Sept 2-12, 2010) to ensure that leaf litter sampled was from the previous fall. The quadrats were placed into the soil to ensure that the extraction solution would not leak outside the sample area; leaf litter depth was measured to one-tenth of a centimeter and classified based on the major overstory species present. The leaf litter was then collected.

The liquid extraction solution consisted of 40 g ground yellow mustard mixed in 3.8 L of water. This solution has been shown to be a skin irritant and causes earthworms to surface (Hale, 2007). After the solution was poured, we collected earthworms for 3 minutes (no additional earthworms were found after 3 minutes). Earthworms were collected and later identified in the lab.

In the lab, the wet weight of the leaf litter samples were measured after each sampling day and then placed in a drying oven at 30°C for a minimum of seven days. Oven dried samples were then weighed to the nearest tenth of a gram.

Collected earthworms were identified within 48 hours. Due to the high amount of juveniles present, earthworms were only identified to genus with three genera collected throughout the sample location: *Aporrectodea* spp., *Dendrodilus* spp., and *Lumbricus* spp. All earthworms were measured to the nearest millimeter for their total length. For each macroplot, total earthworm biomass (ash-free dry mass) was determined for all earthworm species combined and each genus (Hale et al., 2004).

Data analysis

Herbaceous species were divided into different growth forms based on the USDA PLANTS Database (2011): 1) equisetum, 2) fern, 3) forb/herb, 4) graminoids, 5) lichen, 6) moss, 7) shrub, 8) sub-shrub, and 9) vine. Species were also classified as native or invasive using information about invasive species from the USDA PLANTS Database (2011). The definition used for invasive species was from Executive Order 13112, Appendix 1 (1999) where an invasive species is defined as “non-native (or alien) to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm to human health.” Weedy plants were classified as invasive due to the potential decrease diversity. Species shade tolerance was also classified using the USDA PLANTS Database. When tolerance was not listed, the description of the habitat that the species was normally found in was used (Voss, 1985; Newcomb, 1989; Voss, 1996). Herbaceous species with habitat descriptions of woodlands or woods were classified as tolerant; open woods and thickets were classified as midtolerants; and waste places, roadsides, and meadows were classified as intolerant.

Data was summarized two ways due to slight differences in sampling methods between 2000 and 2010. Herbaceous species richness was summarized at the macroplot level between years and between seasons. Diversity and evenness could not be compared between years in the understory layer due to differences in area sampled. Overstory species were summarized by trees per hectare and basal area per hectare.

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Comparison of overstory basal area between summer 2000 and 2010 required overstory trees to be placed into 5.1 cm diameter classes with all trees greater than 55.6 cm in diameter (dbh) excluded to be consistent with the original data collection. Therefore, all overstory basal area measurements are underestimates as there is no way to calculate basal area of trees with unknown diameters above 55.6 cm. Diameter to the nearest tenth of a centimeter was used to calculate overstory basal area when comparing spring and summer data collected in 2010.

Trees per hectare within the macroplot was used to calculate overstory species richness. Trees per hectare was also used to calculate Shannon's Index of Diversity (Maguurran, 1988),

$$H = -\Sigma\ p_i/p_t * \ln(p_i/p_t) \qquad \text{(Eq.1)}$$

where H is Shannon's Index of Diversity, p_i is the cover of species i, and p_t is the total species richness for all species in the plot.

Evenness was also calculated using trees per hectare (Margurran, 1988)

$$EH = H/Hmax \quad Hmax = H/lnS \qquad \text{(Eq.2)}$$

where E_H is evenness, H_{max} is the maximum potential evenness, and lnS is the natural log of species richness.

Shannon's index of diversity and evenness for herbaceous species sampled in spring and summer of 2010 were summarized by averaging the percent cover of the eight 1-m^2 quadrats in each plot.

Repeated measures ANOVA in statistical interface R (R Development Core Team, 2011) was used to test for significant differences between habitat types and between either years or seasons. Tukey's Honest Significant Difference (Tukey, 953) was used when there were significant differences between years (2000 vs. 2010), seasons (spring vs. summer), and habitat types (see *Table 1*). Linear regression was used to explore relationships between exotic earthworms and percent cover of vegetation and environmental variables.

Nonmetric multidimensional scaling (NMS) ordination using PC-ORD Version 5 (McCune and Mefford, 2011) was used to compare the shift in the herbaceous layer between sampling periods and between habitat types. NMS has relaxed normality assumptions and does not assume a linear response to different gradients which is common in ecological data (McCune and Grace, 2002). Herbaceous species presence/absence data at the macroplot level was used to run the ordination. NMS was run on herbaceous species presence/absence data for summer 2000 versus summer 2010 and spring 2010 versus summer 2010. Autopilot mode (slow and thorough) was selected using Sørensen (Bray-Curtis) distance measurement and a random starting point for both datasets. Two hundred and fifty runs were completed for both the real data and randomized data to determine dimensionality for both data sets. Correlation analysis in statistical interface R (R Development Core Team, 2011) was used to test environmental variables used in the ordinations for significance.

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Results

Herbaceous species composition

During the summer of 2000, 80 herbaceous species were identified across all habitat types with only four species (5% of all species) considered invasive. A total of 130 herbaceous species were sampled during both spring and summer of 2010 across all habitat types with 25 species (19% of all species) considered invasive. There were 69 new species observed in 2010 with 22 or 33% of these new species considered invasive. Seventeen species were only observed in 2000; none were considered invasive. A complete list of herbaceous species can be found in Appendix A (*Table A.1*).

A greater number of species, 114, were sampled during the summer 2010 period compared with 90 species sampled during spring 2010 across all habitat types. Sixteen herbaceous species were captured in the spring sampling period which would have been missed with only summer sampling. Habitat types are delineated on the basis of floristic differences. However, few species were unique to only one habitat type; herbaceous species overlap between habitat types ranged from 11-57%. Habitat types occur across range of nutrient and moisture conditions (*Table 1*). PArV-Co and ATD-Ca represent the least and most productive habitat types, respectively. These two habitat types, PArV-Co and ATD-Ca contained the fewest species in common (11%) in summer 2010. However, habitat types with more similar moisture and nutrient conditions shared more species in common with AArAst and AArLy sharing over half (57%) of the same species. Species such as *Dryopteris spinulosa, Maianthemum canadense, Maianthemum racemosoum* ssp. *racemosum, Polygonatum pubescens,* and *Trientalis borealis* exhibited a high frequency of occurrence within habitat types and between habitat types in both the summer 2000 and spring and summer 2010 sampling periods.

Comparison between summer 2000 and 2010

Overstory trees per hectare significantly decreased from 2000 to 2010 ($p < 0.001$); there was an average 31% decrease between all habitat types, with no significant difference between habitat types (*Table 2*). A similar trend was observed with overstory basal area per hectare ($p<0.001$) (*Table 2*) with a significant difference between habitat types; PArV-Co had greater basal area per hectare than AArAst ($p=0.03$) and AArLy ($p=0.03$). All habitat types had at least one plot that was surmised through the identification of recent stumps to have had management activities within the past 10 years. Habitat types ATM-Sm and AArLy had the greatest number of plots (three and two respectively) with management activity occurring in the last five years, while also experiencing the greatest decrease in overstory basal area (47% and 48% respectively).

Total herbaceous species richness significantly increased between years ($p<0.001$) with significant differences between habitat types ($p<0.001$; *Table 2*). Native herbaceous species richness did not vary between years but was significantly different between habitat types ($p<0.001$; *Fig. 2*). The most productive habitat type, ATD-Ca, had greater total herbaceous species richness and native herbaceous species richness than all other habitat types except ATM-O (*Table 2*). Invasive herbaceous species richness increased between years ($p<0.001$) but there was no significant difference between habitat types (*Fig. 2*).

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***Table 2.** Response of overstory structure and herbaceous species richness to year of sampling, habitat type, and their interaction. All variables are summarized at the macroplot level The associated standard errors are in parentheses.*

	Habitat Types	Summer 2000	Summer 2010	Year		Habitat Type		Interaction	
				$F_{1,48}$	p-value	$F_{5,48}$	p-value	$F_{5,48}$	p-value
Trees Per Hectare	PArV-Co	945 (39)	898 (176)	4.67	<0.001	0.83	0.53	1.22	0.31
	AArAst	1007 (66)	660 (128)						
	AArLy	1034 (140)	537 (46)						
	ATM-Sm	959 (113)	510 (108)						
	ATM-O	980 (129)	694 (110)						
	ATD-Ca	850 (63)	653 (54)						
Basal Area Per Hectare (m^2ha^{-1})	PArV-Co	50 (3)	36 (5)	35.20	<0.001	3.25	0.01	0.52	0.76
	AArAst	42 (5)	24 (7)						
	AArLy	38 (4)	20 (3)						
	ATM-Sm	39 (5)	19 (3)						
	ATM-O	40 (5)	25 (4)						
	ATD-Ca	31 (2)	24 (4)						
Total Herbaceous Species Richness	PArV-Co	17.4 (0.8)	15.4 (2.4)	7.69	0.007	7.01	<0.001	2.24	0.07
	AArAst	15.8 (2.4)	16.0 (2.5)						
	AArLy	14.8 (1.8)	18.0 (2.0)						
	ATM-Sm	11.8 (1.1)	21.0 (1.3)						
	ATM-O	17.2 (0.4)	24.0 (2.2)						
	ATD-Ca	24.4 (2.2)	26.0 (3.0)						

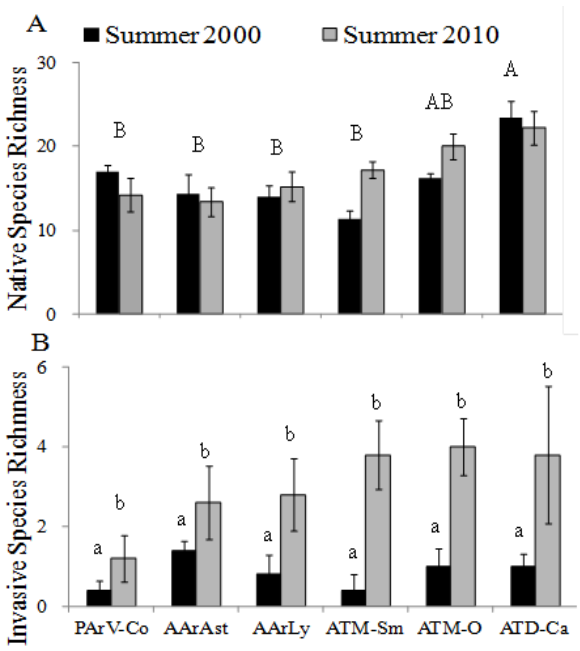

***Figure 2:** Native (A) and Invasive (B) herbaceous species richness observed at the macroplot level in summer 2000 and 2010. Upper case letters that are different represent significant differences between habitat types at α=0.05. There were no significant differences observed between years for native herbaceous species richness. Lower case letters represent a significant difference between years at α=0.05. There were no significant differences between years across habitat types for invasive species richness.*

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Comparison between spring and summer 2010

Canopy cover increased from spring 2010 to summer 2010 (p<0.001) but did not differ significantly between habitat types (*Table 3*). Herbaceous species percent cover, richness, and evenness all increased significantly from spring to summer (p<0.001; p=0.01; p<0.001) (*Table 3*). The two least productive habitat types, PArV-Co and AArAst, had significantly lower herbaceous species richness than the three richest habitat types, ATM-Sm (p=0.006, p=0.02), ATM-O (p<0.001, p=0.03), and ATD-Ca (p=0.005, p=0.02) (*Fig. 3*). There were significantly greater diversity, using Shannon's Index of Diversity, in ATM-Sm than AArAst (p=0.03) and ATM-O and ATD-Ca than AArAst (p=0.07; p=0.04); herbaceous evenness was significantly greater in ATM-Sm than AArAst (p=0.02) (*Fig. 3*).

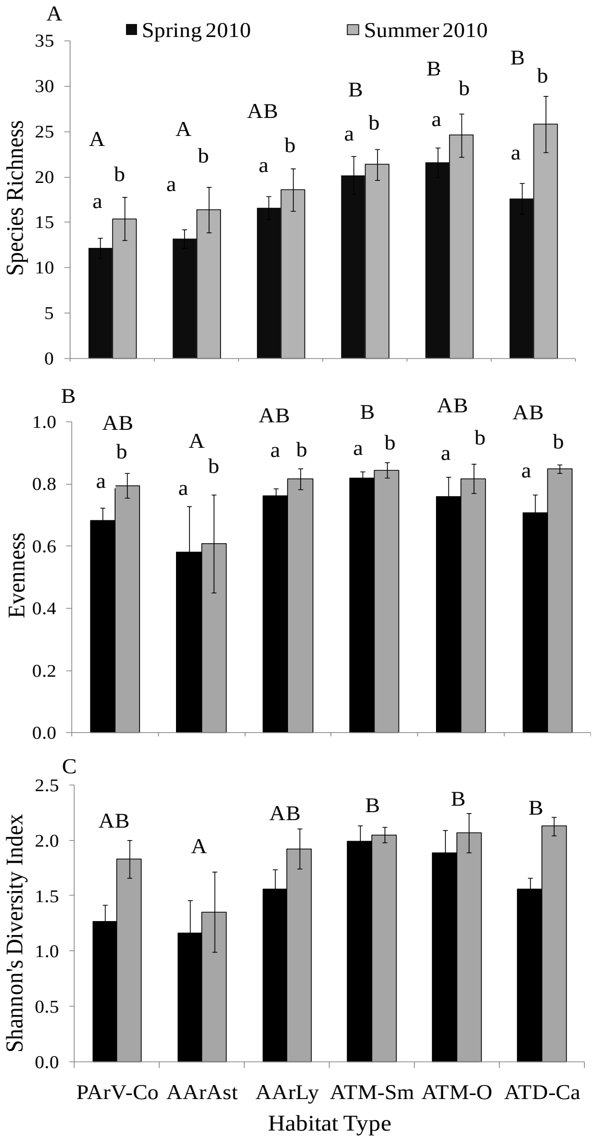

Figure 3: *Herbaceous Species Richness (A), Evenness (B), and Shannon's Diversity (C) for spring and summer 2010. Species richness was observed at the macroplot level. Herbaceous evenness and Shannon's diversity were calculated from 1-m² plots. Upper case letters that are different represent a significant difference between habitat types at α=0.05. Lower case letters that are different represent a significant difference between seasons at α=0.05. There was no significant difference between years for Shannon's Diversity.*

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Table 3. *Response of the canopy and herbaceous species percent cover to season, habitat type and their interaction. Herbaceous species percent cover was summarized at the subplot level (eight 1-m2 quadrats). The associated standard errors are in parentheses.*

	Habitat Types	Spring 2010	Summer 2010	Season		Habitat Type		Interaction	
				$F_{1,48}$	p-value	$F_{5,48}$	p-value	$F_{5,48}$	p-value
Percent Canopy Closure	PArV-Co	86 (0.7)	90 (0.9)	45.77	<0.001	0.71	0.62	1.19	0.33
	AArAst	73 (0.8)	92 (1.2)						
	AArLy	78 (1.0)	93 (0.5)						
	ATM-Sm	81 (0.6)	92 (0.8)						
	ATM-O	79 (1.0)	93 (0.5)						
	ATD-Ca	80 (1.0)	91 (0.7)						
Herbaceous Species Percent Cover	PArV-Co	25 (11)	61 (27)	21.06	<0.001	2.38	0.052	0.40	0.84
	AArAst	16 (7)	40 (18)						
	AArLy	25 (11)	55 (25)						
	ATM-Sm	28 (12)	73 (33)						
	ATM-O	33 (15)	66 (30)						
	ATD-Ca	38 (17)	67 (30)						

Herbaceous composition shifts

A three-dimensional solution was found through NMS with a final stress of 16.9 in the comparison between summer 2000 and 2010. The ordination explained 83% of the variation in the data; axis 1 and axis 2 explained the most variation, 18% and 67% respectively (*Fig. 4*).

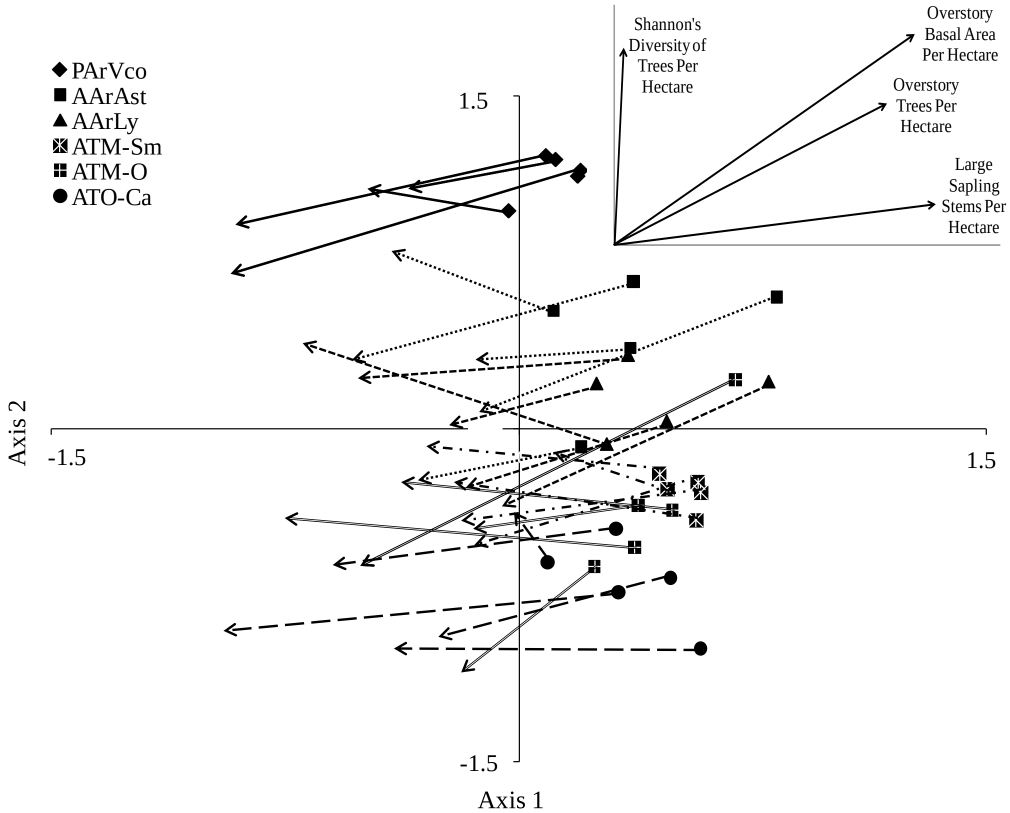

Figure 4. *Non-metric multi-dimensional scaling ordination of herbaceous species communities for six habitat types in the western Upper Peninsula for summer 2000 and summer 2010. Axis 1*

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explains 18% percent of the variation while Axis 2 explains 67% of the variation. Habitat type are displayed in order of productivity; PArV-Co the least productive to ATO-Ca the most productive. Markers represent summer 2000 conditions and arrows represent direction and magnitude of composition change. Where the arrows end represent summer 2010 herbaceous community composition. Longer arrows represent greater difference between years. The insert is the significant environmental variables (p=0.05) and their relation to ordination space.

Overstory TPH and basal area per hectare were both strongly associated with axis 1 and axis 2 (*Fig. 4*). Overstory Shannon's diversity calculated with TPH was strongly associated with axis 2; large sapling density was strongly associated with axis 1 (*Fig. 4*). There was generally strong and consistent movement in all habitat types to areas of decreased overstory TPH and basal area per hectare (*Fig. 4*). However, even with increasing invasive species and changes in overstory density, the productivity gradient between habitat types was still evident.

A three-dimensional solution with a final stress of 17.5 was also found in the comparison between spring and summer 2010. The ordination explained 77% of the variation in the data; axis 1 and axis 3 explained the most variation, 54% and 14% respectively (*Fig. 5*). Percent canopy cover is the main driving variable in this ordination and is strongly associated with axis 3 (*Fig. 5*). Species shifted from a more open canopy in the spring to a closed canopy in the summer. Percent down dead wood and seedling richness were associated with axis 3, while overstory TPH and basal area per hectare were associated with axis 1 (*Fig. 5*).

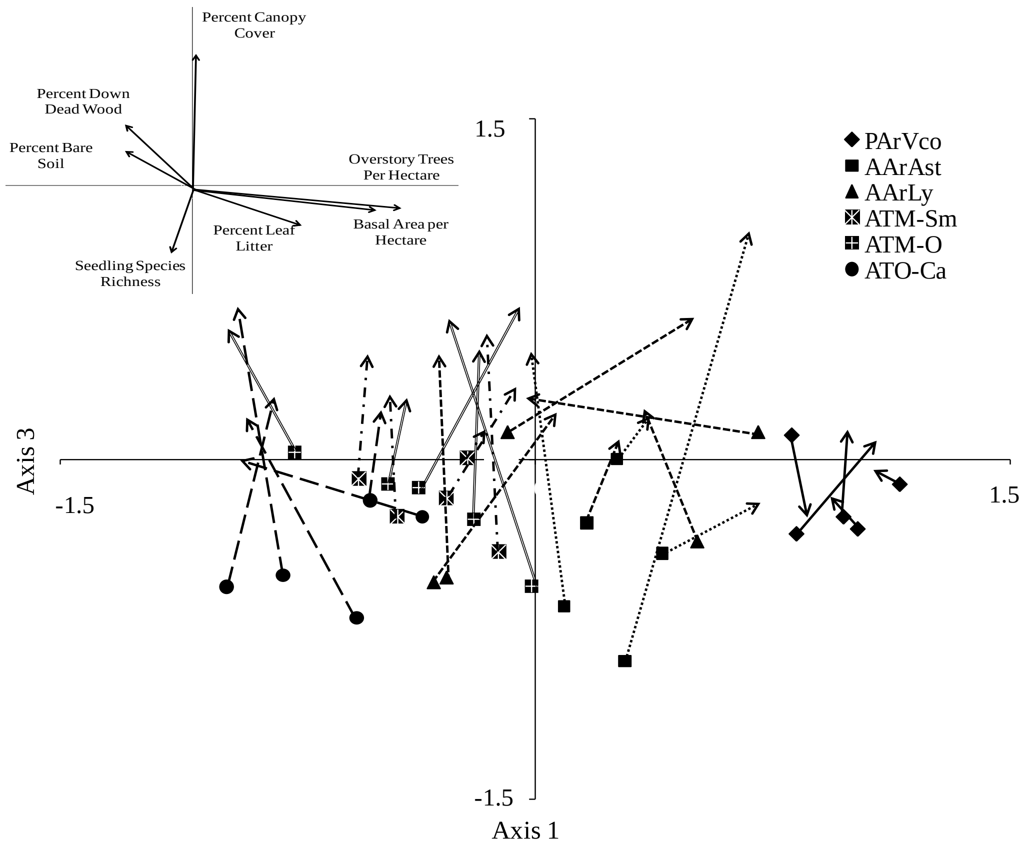

Figure 5. *Non-metric multi-dimensional scaling ordination of herbaceous species communities for six habitat types in the western Upper Peninsula for spring and summer 2010. Axis 1*

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explains 54% percent of the variation while Axis 3 explains 14% of the variation. Habitat type are arranged in order of productivity; PArV-Co the least productive to ATO-Ca the most productive. Markers represent spring 2010 conditions and arrows represent direction and magnitude of composition change. Where the arrows ends represent summer 2010 herbaceous community composition. Longer arrows represent greater difference between spring and summer. The insert is the significant environmental variables (p=0.05) and their relation to ordination space.

Earthworm densities

Overall earthworm ash-free dry mass generally increased from less productive habitat types to more productive habitat types, with *Lumbricus* spp. generally following the same trends (*Fig. 6*). The PArV-Co and AArLy habitat types had significantly lower ash-free dry mass than ATD-Ca (p = 0.01; p = 0.03) (*Fig. 6*). There were significant negative relationships between ash-dry weight of *Lumbricus* spp. and both spring and summer herbaceous species percent cover (p=0.010, r^2=0.21; p=0.019, r^2=0.18). Total ash-dry weight of all earthworms followed this same trend (p=0.049, r^2=0.24; p=0.005, r^2=0.13). There was a significant negative relationship between ash-dry weight of *Dendrobaena* spp. and total herbaceous species richness, native species richness, and invasive species richness (p=0.003, r^2=0.27; p=0.031, r^2=0.15; p=0.006, r^2=0.23), respectively.

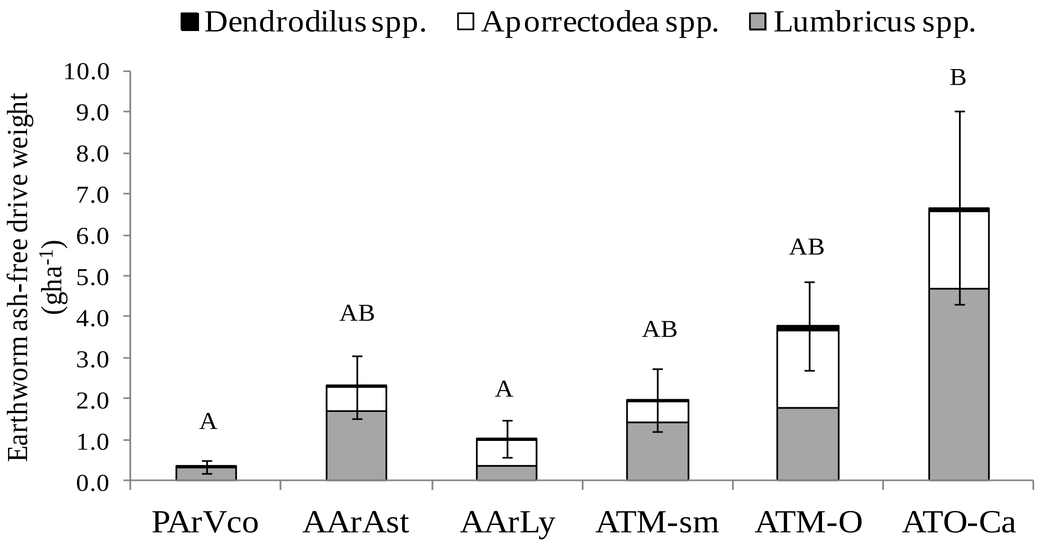

Figure 6. *Earthworm ash-free dry weight (g ha-1) by genus for each habitat type. Letters that are different represent a significant (α=0.05) difference between habitat types comparing total ash-free dry weight of earthworms, not by individual species.*

Discussion

Even with changes in herbaceous species composition, overstory density, and canopy cover between years (2000 vs 2010) and between season (spring vs summer) there was still an identifiable productivity gradient between different habitat types (*Fig. 4 - 5*). Overstory density significantly decreased between 2000 and 2010, which we hypothesize is a result of forest management as all habitat types contained at least one plot where recent stumps and logging slash were observed. It is not known the exact intensity of past harvest activities or the season in which the harvests took place. Forest

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management has been shown to have a variety of effects on the herbaceous layer in a variety of forest types (Metzger and Schultz, 1981; Gilliam et al., 1995; Roberts and Gilliam, 1995; Fredericksen et al., 1999; Jenkins and Parker, 1999; Crow et al., 2002; Scheller and Mladenoff, 2002; Gilliam and Roberts, 2003; Zenner et al., 2006; Kern et al., 2006; Wolf, 2008; and others).

The Argonne Experimental Forest in northern Wisconsin observed no difference in the spring or summer herbaceous communities in even, uneven-aged, or unmanaged stands after 40 years of consistent treatment (Kern et al., 2006). However, at the Ford Forest (Michigan Technological University) differences in summer herbaceous community composition were observed between different harvest intensities after 50 years of management. After a recent harvest, the diameter-limit treatments generally had herbaceous communities with more weedy and invasive herbaceous species (Campione et al., 2012). Scheller and Mladenoff (2002) also observed this increase in early successional and weedy species in uneven-aged northern hardwood stands compared to even-aged or unmanaged stands.

The seasonality of logging can also affect herbaceous species composition. A study in the Chequamegon-Nicolet National Forest observed that herbaceous species that are more vulnerable to disturbance were observed more often in winter-logged sites than summer-logged sites (Wolf et al., 2008). Logging intensity and seasonality may be two unknown variables contributing to increases in invasive species richness between years in this and other studies (Wiegmann and Waller, 2000; Watkins et al., 2003).

Another group of invasive species, European earthworms, may also be having an effect on the herbaceous species composition. Exotic earthworm densities and ash-dry mass were estimated for each habitat type in the present study. There was a general increasing trend between total earthworm ash-free biomass and habitat type productivity. There is no way to estimate exactly how long earthworm populations have been present at each site. All habitat types except for PArV-Co (the habitat type with lowest productivity) had all three genera of earthworms. No earthworms from the *Aporrectodea* genus were collected during sampling at PArV-Co sites. *Aporrectodea* species are classified as endogeic, living in soil down to depths of 50 cm, and feed on mineral soil (Hale, 2007). Hale and others (2006) observed that *Aporrectodea* species were generally behind the leading edge of the earthworm invasion front. The lack of observed *Aporrectodea* species at the PArV-Co sites during sampling may be a result of their population size being too small to pick up in our sampling. Alternatively, the sandy soils and pine leaf litter of this habitat type may inhibit this genus of earthworms from establishing or creating large populations. The other two genera observed, *Dendrobaena* and *Lumbricus*, can be classified as epigeic and anecic or epi-endogeic respectively (Hale, 2007). The genus *Dendrobaena* is commonly the first earthworm genus to colonize new locations (Hale, 2007).

Our results of a negative relationship between total earthworm ash-free biomass and percent cover of herbaceous species are consistent with Hale and colleagues (2005). However, our results are different than Holdsworth (2007) in that plant species richness increased with increasing mass of the earthworm genera *Dendrobaena* and *Aporrectodea*. We observed decreases in total herbaceous species richness, native species richness, and invasive species richness with increasing mass of *Dendrobaena* ($p=0.003$, $r^2=0.27$; $p=0.031$, $r^2=0.15$; $p=0.006$, $r^2=0.23$), respectively. Invasive species richness also decreased with increasing mass of *Aporrectodea*. These differences may be due to the low total earthworm and individual species biomass that was observed.

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The habitat type ATD-Ca had the highest mass of *Aporrectodea* which averaged 1.1 g/m^2 compared to an average of 4.8 g/m^2 observed in northern Wisconsin and 3.9 g/m^2 in northern Minnesota (Holdsworth et al., 2007).

These low earthworm populations may be one of the reasons we did not observe the same changes in species richness as other authors (e.g. Gundale, 2002; Hale, 2006; Holdsworth, 2007; Powers and Nagel, 2008). Both earthworm densities and herbaceous species richness generally but not significantly increased with increasing nutrient richness and moisture. We also did not observe simplified herbaceous communities dominated by *Carex pensylvanica* (Holdsworth et al., 2007; Powers and Nagel, 2008) which does grow in this area but at much lower abundance than in these other studies. Future climate conditions have the possibility to not only affect the current dynamics in forests but also the dynamics of invasive species (e.g. Walther et al., 2002).

These changing climatic conditions have already been observed in the Upper Peninsula of Michigan. Myers and colleagues (2009) observed an increase of approximately 2.1°C in the daily minimum and 0.42°C in the daily maximum temperatures from 1970 to 2007. Spring ephermals may be more sensitive to these changing conditions since flowering times are closely related to mean monthly temperatures (Miller-Rushing and Primack, 2008). These early flowering plants are an important functional component of ecosystems, reducing nutrient losses from soils (Muller and Bormann, 1976). However, spring ephermals may be more sensitive to repeated disturbances such as uneven-aged management (Metzger and Schultz, 1981; Scheller and Mladenoff, 2002) or may show no difference between managed and unmanaged forests (Kern et al., 2006). We observed a distinct shift in vegetation from spring to summer sampling. As canopy closure occurred at the end of spring/beginning of summer, the herbaceous community shifted from one dominated by spring ephemerals like *Claytonia virginica* and *Erythronium americanum* to a herbaceous community dominated by *Dryopteris spinulosa, Maianthemum canadense*, and *Trientalis borealis*. Increasing temperatures, especially daily minimum temperatures, may change the relationship spring ephermals have with overstory tree species. Spring ephermals may be important species to monitor and use as early detectors of changing conditions in forest ecosystems. Continual monitoring within these forest communities will allow scientists and managers to observe how a management activity, changing climate, and invasive plants and earthworms interact and influence forest composition.

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APPENDIX

Appendix A

Appendix A.1 Full list of species observed in 2000 and 2010.

Scientific name	Common Name	Family	Growth Form	Shade Tolerance
Acer pensylvanicum L.	striped maple	Sapindaceae	Shrub	Tolerant
Acer spicatum Lam.	mountain maple	Sapindaceae	Shrub	Tolerant
Achillea millefolium L. *	common yarrow	Asteraceae	Forb/herb	Intermediate
Actaea spp.	Baneberries	Ranunculaceae	Forb/herb	Tolerant
Adiantum pedatum L.	northern maidenhair fern	Pteridaceae	Forb/herb	Tolerant
Allium tricoccum Aiton	ramp	Liliaceae	Forb/herb	Tolerant
Amaranthus retroflexus L.	redroot amaranth	Amaranthaceae	Forb/herb	Intolerant
Amelanchier spp.	Serviceberry	Rosaceae	Shrub	Tolerant
Amphicarpaea bracteata (L.) Fernald	American hogpeanut	Fabaceae	Vine	Intermediate
Anemone quinquefolia L.	wood anemone	Ranunculaceae	Forb/herb	Tolerant
Antennaria neglecta Green	field pussytoes	Asteraceae	Forb/herb	Intolerant
Apocynum androsaemifolium L.	spreading dogbane	Apocynaceae	Forb/herb	Intermediate
Aquilegia canadensis L.	red columbine	Ranunculaceae	Forb/herb	Intermediate
Aralia nudicaulis L.	wild sarsaparilla	Araliaceae	Forb/herb	Tolerant
Aralia racemosa L.	American spikenard	Araliaceae	Subshrub Forb/herb	Tolerant
Arctostaphylos uva-ursi (L.) Spreng.	kinnikinnick	Ericaceae	Shrub	Intermediate
Arisaema triphyllum (L.) Schott	Jack in the pulpit	Araceae	Forb/herb	Tolerant
Asarum canadense L.	Canadian wildginger	Aristolochiaceae	Forb/herb	Tolerant
Athyrium filix-femina (L.) Roth	common ladyfern	Dryopteridaceae	Forb/herb	Tolerant
Barbarea vulgaris W.T. Aiton *	garden yellowrocket	Brassicaceae	Forb/herb	Intolerant
Berberis thunbergii DC. *	Japanese barberry	Berberidaceae	Shrub	Intolerant
Botrychium virginianum (L.) Sw.	rattlesnake fern	Ophioglossaceae	Forb/herb	Tolerant
Cardamine bulbosa (Schreb. Ex Muhl.) Britton, Sterns & Poggenb.	bulbous bittercress	Brassicaceae	Forb/herb	Tolerant
Caulophyllum thalictroides (L.) Michx.	blue cohosh	Berberidaceae	Forb/herb	Tolerant
Chimaphila umbellata (L.) W.P.C. Barton	pipsissewa	Pyrolaceae	Subshrub	Tolerant
Circaea alpina (L.)	small enchanter's nightshade	Onagraceae	Forb/herb	Tolerant
Circaea quadrisulcata (L.) Asch. & Magnus	broadleaf enchanter's nightshade	Onagraceae	Forb/herb	Tolerant
Cirsium arvense (L.) Scop. *	Canada thistle	Asteraceae	Forb/herb	Intolerant
Cladina mitis (Sandst.) Hustich	reindeer lichen	Cladoniaceae	Lichen	Intolerant
Claytonia virginica L.	Virginia springbeauty	Portulaceae	Forb/herb	Intermediate
Clintonia borealis (Aiton) Raf.	bluebead	Liliaceae	Forb/herb	Intolerant
Comptonia peregrina (L.) J.M. Coult.	sweet fern	Myricaceae	Shrub	Intermediate
Coptis groenlandica (L.) Salisb.	threeleaf goldthread	Ranunculaceae	Forb/herb	Tolerant
Cornus alternifolia L. f.	alternateleaf dogwood	Cornaceae	Shrub	Tolerant
Cornus canadensis L.	bunchberry dogwood	Cornaceae	Forb/herb	Tolerant
Cornus racemosa Lam.	gray dogwood	Cornaceae	Shrub	Tolerant
Cornus stolonifera Michx.	redosier dogwood	Cornaceae	Shrub	Intolerant
Corylus cornuta Marshall	beaked hazelnut	Betulaceae	Shrub	Tolerant
Crataegus spp.	Hawthorn	Rosaceae	Shrub	Midtolerant
Cuphea viscosissima Jacq.	blue waxweed	Lythraceae	Forb/herb	Intolerant
Cypripedium acaule Aiton	pink lady's slipper	Orchidaceae	Forb/herb	Intermediate
Desmodium glutinosum (Muhl. ex Willd.) Alph. Wood	pointedleaf ticktrefoil	Fabaceae	Forb/herb	Tolerant
Dicentra cucullaria (L.) Bernh.	dutchman's breeches	Fumariaceae	Forb/herb	Intermediate
Diervilla lonicera Mill.	northern bush honeysuckle	Caprifoliaceae	Shrub	Intermediate
Dirca palustris L.	eastern leatherwood	Thymelaeaceae	Shrub	Tolerant
Dryopteris spinulosa (O.F. Müll.) Watt	spinulose shield fern	Dryopteridaceae	Forb/herb	Tolerant
Epifagus virginiana (L.) W.P.C. Barton	beechdrops	Orobanchaceae	Forb/herb	Tolerant
Epigaea repens L.	trailing arbutus	Ericaceae	Subshrub	Tolerant
Epipactis helleborine (L.) Crantz *	broadleaf helleborine	Orchidaceae	Forb/herb	Midtolerant
Equisetum spp.	Horsetail	Equisetaceae	Equisetum	Midtolerant - Intolerant
Erigeron spp.	Fleabane	Asteraceae	Forb/herb	Intolerant
Erythronium americanum Ker Gawl. subsp. *americanum*	yellow trout lily	Liliaceae	Forb/herb	Tolerant
Eupatorium purpureum L.	green-stemmed Joe-Pye-weed	Asteraceae	Forb/herb	Intermediate
Eurybia macrophylla (L.) Cass.	bigleaf aster	Asteraceae	Forb/herb	Tolerant
Fallopia convolvulus (L.) A.Löve *	black-bindweed	Polygonaceae	Vine	Intolerant
Fragaria spp.	Strawberry	Rosaceae	Shrub	Midtolerant
Frangula alnus Mill. *	glossy buckthorn	Rhamnaceae	Shrub	Intolerant
Galeopsis tetrahit L. *	brittlestem hempnettle	Lamiaceae	Forb/herb	Intolerant
Galium boreale L.	northern bedstraw	Rubiaceae	Forb/herb	Intermediate

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Appendix A.1 *Continued***.**

Scientific name	Common Name	Family	Growth Form	Shade Tolerance
Galium triflorum Michx.	fragrant bedstraw	Rubiaceae	Forb/herb Vine	Tolerant
Gaultheria hispidula (L.) Muhl. ex Bigelow	creeping snowberry	Ericaceae	Subshrub Shrub	Tolerant
Gaultheria procumbens L.	wintergreen	Ericaceae	Subshrub	Tolerant
Gaylussacia baccata (Wangenh.) K. Koch	black huckleberry	Ericaceae	Shrub	Tolerant
Geranium maculatum L.	spotted geranium	Geraniaceae	Forb/herb	Intermediate
Grasses & Sedges	grasses & sedges	-	Graminoid	-
Gymnocarpium dryopteris (L.) Newman	western oak fern	Dryopteridaceae	Forb/herb	Tolerant
Hamamelis virginiana L.	American witchhazel	Hamamelidaceae	Shrub	Intermediate
Helenium nudiflorum Raf.	purplehead sneezeweed	Asteraceae	Forb/herb	Intolerant
Heliopsis helianthoides (L.) Sweet	smooth oxeye	Asteraceae	Forb/herb	Intolerant
Hepatica acutiloba DC.	sharplobe hepatica	Ranunculaceae	Forb/herb	Tolerant
Hepatica americana (DC.) Ker Gawl.	roundlobe hepatica	Ranunculaceae	Forb/herb	Tolerant
Hieracium aurantiacum L. *	orange hawkweed	Asteraceae	Forb/herb	Intolerant
Hieracium paniculatum L.	Allegheny hawkweed	Asteraceae	Forb/herb	Tolerant
Hieracium pilosella L. var. *pilosella* *	mouseear hawkweed	Asteraceae	Forb/herb	Intolerant
Hieracium venosum L.	rattlesnakeweed	Asteraceae	Forb/herb	Intermediate
Huperzia lucidula (Michx.) Trevis.	shining clubmoss	Lycopodiaceae	Subshrub	Intermediate
Hydrophyllum virginianum L.	eastern waterleaf	Hydrophyllaceae	Forb/herb	Intermediate
Hypericum perforatum L. *	common St. Johnswort	Clusiaceae	Forb/herb	Intolerant
Hypochaeris radicata L. *	hairy cat's ear	Asteraceae	Forb/herb	Intolerant
Impatiens capensis Meerb.	jewelweed	Balsaminaceae	Forb/herb	Tolerant
Juniperus communis L.	common juniper	Cupressaceae	Shrub	Intolerant
Laportea canadensis (L.) Weddell	Canadian woodnettle	Urticaceae	Forb/herb	Tolerant
Lapsana communis (L.) *	common nipplewort	Asteraceae	Forb/herb	Intolerant
Leucanthemum vulgare (Lam.) *	oxeye daisy	Asteraceae	Forb/herb	Intermediate
Linnaea borealis L. subsp. *americana* (Forbes) Hultén ex R.T.Clausen	twinflower	Caprifoliaceae	Forb/herb	Tolerant
Lithospermum canescens (Michx.) Lehm.	hoary puccoon	Boraginaceae	Forb/herb	Intermediate
Lonicera canadensis W. Bartram ex Marshall	American fly honeysuckle	Caprifoliaceae	Shrub	Intermediate
Lycopodium annotinum L.	stiff clubmoss	Lycopodiaceae	Subshrub Forb/herb	Tolerant
Lycopodium clavatum L.	Running clubmoss	Lycopodiaceae	Subshrub Forb/herb	Intermediate
Lycopodium complanatum L.	groundcedar	Lycopodiaceae	Subshrub Forb/herb	Tolerant
Lycopodium obscurum L.	rare clubmoss	Lycopodiaceae	Subshrub Forb/herb	Tolerant
Lysimachia quadrifolia L.	whorled yellow loosestrife	Primulaceae	Forb/herb	Intermediate
Maianthemum canadense Desf.	Canada mayflower	Liliaceae	Forb/herb	Tolerant
Maianthemum racemosum (L.) Link *ssp. racemosum*	feathery false lily of the valley	Liliaceae	Forb/herb	Intermediate
Maianthemum stellatum (L.) Link	starry false lily of the valley	Liliaceae	Forb/herb	Intermediate
Matteuccia struthiopteris (L.) Todaro	ostrich fern	Dryopteridaceae	Forb/herb	Tolerant
Medeola virginiana L.	indian cucumber-root	Liliaceae	Forb/herb	Tolerant
Melampyrum lineare Desr.	narrow-leaf cow-wheat	Scrophulariaceae	Forb/herb	Intermediate
Mitchella repens L.	partridgeberry	Rubiaceae	Subshrub Forb/herb	Tolerant
Mitella diphylla L.	twoleaf miterwort	Saxifragaceae	Forb/herb	Intermediate
Mitella nuda L.	naked miterwort	Saxifragaceae	Forb/herb	Tolerant
Monotropa uniflora L.	Indian-pipe	Monotropaceae	Forb/herb	Tolerant
moss				
Myosotis scorpioides L. *	true forget-me-not	Boraginaceae	Forb/herb	Intermediate
Myosotis verna Nutt.	spring forget-me-not	Boraginaceae	Forb/herb	Intermediate
Onoclea sensibilis L.	sensitive fern	Dryopteridaceae	Forb/herb	Tolerant
Osmorhiza claytoni (Michx.) C.B. Clarke	Clayton's sweetroot	Apiaceae	Forb/herb	Tolerant
Osmunda cinnamomea L.	cinnamon fern	Osmundaceae	Forb/herb	Tolerant
Osmunda claytoniana L.	interrupted fern	Osmundaceae	Forb/herb	Tolerant
Oxalis montana Raf.	common woodsorrel	Oxalidaceae	Forb/herb	Tolerant
Panax trifolius L.	dwarf ginseng	Araliaceae	Forb/herb	Tolerant
Parthenium integrifolium Britton	wild quinine	Asteraceae	Forb/herb	Intermediate
Parthenocissus quinquefolia (L.) Planch.	Virginia creeper	Vitaceae	Vine	Intermediate
Pedicularis canadensis L.	Canadian lousewort	Scrophulariaceae	Subshrub Forb/herb	Tolerant
Petasites frigidus (L.) Fr. var. *palmatus* (Aiton) Cronquist	northern sweet-colt's-foot	Asteraceae	Forb/herb	Intermediate
Phegopteris connectilis (Michx.) Watt	long beechfern	Thelypteridaceae	Forb/herb	Tolerant

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Appendix A.1 *Continued.*

Scientific name	Common Name	Family	Growth Form	Shade Tolerance
Phryma leptostachya L.	American lopseed	Verbenaceae	Forb/herb	Tolerant
Plantago lanceolata L. *	narrowleaf plantain	Plantaginaceae	Forb/herb	Intolerant
Podophyllum peltatum L.	mayapple	Berberidaceae	Forb/herb	Intolerant
Polygala paucifolia Willd.	gaywings	Polygonaceae	Forb/herb	Tolerant
Polygonatum pubescens (Willd.) Pursh	hairy Solomon's seal	Liliaceae	Forb/herb	Tolerant
Prenanthes alba L.	white rattlesnakeroot	Asteraceae	Forb/herb	Intermediate
Prunella vulgaris L.	common selfheal	Lamiaceae	Forb/herb	Intermediate
Prunus serotina Ehrh.	black cherry	Rosaceae	Shrub	Intolerant
Prunus virginiana L.	chokecherry	Rosaceae	Shrub	Intolerant
Pteridium aquilinum (L.) Kuhn	western brackenfern	Dennstaedtiaceae	Forb/herb	Tolerant
Pyrola elliptica Nutt	waxflower shinleaf	Pyrolaceae	Subshrub	Tolerant
Pyrola spp.	Shinleafs	Pyrolaceae	Forb/herb	Tolerant
Ranunculus abortivus L.	littleleaf buttercup	Ranunculaceae	Forb/herb	Tolerant
Ranunculus recurvatus Poir. var. *recurvatus*	hooked buttercup	Ranunculaceae	Forb/herb	Tolerant
Ribes cynosbati L.	eastern prickly gooseberry	Grossulariaceae	Shrub	Intolerant
Rosa spp.	Rose	Rosaceae	Shrub	Intolerant
Rubus spp.	Raspberry	Rosaceae	Shrub	Intolerant
Rumex acetosella *	common sheep sorrel	Polygonaceae	Forb/herb	Intolerant
Sambucus canaadensis L. var. *canadensis*	American black elderberry	Caprifoliaceae	Shrub	Intolerant
Sambucus racemosa L. subsp. *pubens* (Michx.) House var. *pubens* (Michx.) Koehne	red elderberry	Caprifoliaceae	Shrub	Intermediate
Sanguinaria canadensis L.	bloodroot	Papaveraceae	Forb/herb	Tolerant
Sanicula marilandica L.	black snake-root	Apiaceae	Forb/herb	Tolerant
Senecio obovatus Muhl. Ex Willd.	roundleaf ragwort	Asteraceae	Forb/herb	Midtolerant
Smilax herbacea L.	smooth carrionflower	Smilacaceae	Vine Forb/herb	Tolerant
Smilax tamnoides L.	bristly greenbrier	Smilacaceae	Shrub Vine	Intermediate
Solanum dulcamara L. *	climbing nightshade	Solanaceae	Vine	Intermediate
Solidago flexicaulis L.	zigzag goldrenrod	Asteraceae	Forb/herb	Intermediate
Streptopus lanceolatus (Aiton) Reveal var. *Longipes* (Fernald) Reveal	rosey twistedstalk	Liliaceae	Forb/herb	Tolerant
Symplocarpus foetidus (L.) Salisb. ex W.P.C. Barton	skunk cabbage	Araceae	Forb/herb	Tolerant
Taraxacum officinale F.H. Wigg. *	common dandelion	Asteraceae	Forb/herb	Intermediate
Taxus canadensis Marshall	Canada yew	Taxaceae	Shrub	Tolerant
Thalictrum dioicum L.	early meadow-rue	Ranunculaceae	Forb/herb	Intermediate
Tiarella cordifolia L.	foamflower	Saxifragaceae	Forb/herb	Intermediate
Toxicodendron radicans (L.) Kuntza subsp. *negundo* (Greene) Gillis	eastern poison ivy	Anacardiaceae	Forb/herb Vine	Intermediate
Trientalis borealis Raf. subsp. *borealis*	starflower	Primulaceae	Forb/herb	Tolerant
Trifolium pratense L. *	red clover	Fabaceae	Forb/herb	Intolerant
Trillium cernuum L.	nodding trillium	Liliaceae	Forb/herb	Tolerant
Trillium grandiflorum (Michx.) Salisb.	white trillium	Liliaceae	Forb/herb	Tolerant
Uvularia grandiflora Sm.	largeflower bellwort	Liliaceae	Forb/herb	Tolerant
Uvularia sessilifolia L.	sessileleaf bellwort	Liliaceae	Forb/herb	Intermediate
Vaccinium angustifolium Aiton	lowbush blueberry	Ericaceae	Shrub	Intolerant
Vaccinium myrtilloides Michx.	velvetleaf huckleberry	Ericaceae	Shrub	Intermediate
Verbascum thapsus L. *	common mullein	Scrophulariaceae	Forb/herb	Intolerant
Veronica arvensis L. *	corn speedwell	Scrophulariaceae	Forb/herb	Intolerant
Veronica chamaedrys L. *	birdeye's speedwell	Scrophulariaceae	Forb/herb	Intolerant
Veronica officinalis L. *	Common Gypsyweed	Scrophulariaceae	Forb/herb	Intolerant
Viburnum acerifolium L.	mapleleaf viburnnum	Caprifoliaceae	Shrub	Tolerant
Viburnum lentago L.	nannyberry	Caprifoliaceae	Shrub	Tolerant
Viburnum rafinesqueanum Schult.	downy arrowwood	Caprifoliaceae	Shrub	Tolerant
Viola canadensis L.	Canadian white violet	Violaceae	Forb/herb	Tolerant
Viola conspersa Schrank	dog violet	Violaceae	Forb/herb	Intermediate
Viola macloskey F.E.Lloyd subsp. *pallens* (Banks ex Ging.) M.S.Baker	wild white violet	Violaceae	Forb/herb	Intermediate
Viola pubescens Aiton	downy yellow violet	Violaceae	Forb/herb	Tolerant
Viola sororia Willd.	common blue violet	Violaceae	Forb/herb	Intermediate
Vitis riparia Michx.	riverbank grape	Vitaceae	Forb/herb	Intermediate
Waldsteinia fragarioides (Michx.) Tratt. subsp. *fragarioides*	Appalachian barren strawberry	Rosaceae	Forb/herb	Tolerant

* Invasive species
woodlands, woods = tolerant
open woods, thickets = midtolerant
waste places, roadsides,meadows = intolerant

ELECTRONIC APPENDIX:
This article has an electronic appendix with basic data.

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