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Comparative Analysis of Urban and Rural Forest Fragment Structure and Diversity in Northeastern Indiana

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COMPARATIVE ANALYSIS OF URBAN AND RURAL FOREST FRAGMENT STRUCTURE AND DIVERSITY IN NORTHEASTERN INDIANA

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ABSTRACT

Although it was once continuously forested, the land cover in northeastern Indiana is now dominated by agriculture, and sparsely occurring forest fragments now constitute only approximately 8% of the land cover. A majority of these forest fragments are privately owned and have a history of some form of active forest management. We conducted a systematic ecological survey of understory, midstory, and overstory plant species in three forests that have differing protection and management histories to compare the effects of these different histories. Historical aerial images of each forest were compared to gauge the canopy structure and to clarify the management history for the forests. The percentage of canopy cover and the floristic quality indices (FQI) each followed expected trends, whereby the highest FQI value and percentage of canopy cover occurred in the forest with the longest history of preservation. Lower values of species richness for the understory, midstory, and overstory strata, respectively, were found in the forest that has a history of overstory management and for which there is no defined protection status. The understory species were each generally limited to one of the forests, whereas the species composition of the midstory and overstory strata were much more similar among the three forests. Measurements of forest basal area and percentage of canopy cover provide some explanation of the distribution of understory and midstory species in nonmetric multidimensional scaling ordination plots. The amount of forest protection, measured by the time since disturbance and the percentage of canopy closure, influenced the richness of the understory and the FQI of a given plot. Furthermore, the location of a forest was an important factor in the relative occurrence of non-native species, the most rural forest having no non-native species.

KEYWORDS: Fogwell Forest Nature Preserve, Mengerson Nature Preserve, fragmentation, floristic quality index, forest management

INTRODUCTION

According to the National Land Cover Database (Fry et al. 2011), the Midwest region of the United States is dominated by agriculture with over 60% of land cover in cultivated crops, pasture land, or other open-field agricultural practices; forests account for only 20% of the land cover. Urban and suburban development has increased fairly continuously in the region for well over 60 years

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(Radeloff et al. 2005). Because there are large areas of contiguous forested land in northern Michigan, Minnesota, and Wisconsin, the percentage of land cover devoted to agricultural uses in the Midwest as a whole understates the situation in the southern part of the region, where cultivated and pastoral agricultural lands account for 80–90% of the land cover (Radeloff et al. 2005) and where forests are fragmented into relatively small woodlots. These woodlots generally have high edge-to-interior ratios, thereby increasing the area of forest subject to influence by the surrounding land matrix, which is typically agricultural, but also includes developed urban and suburban land (Brothers and Spingarn 1992; Gonzalez et al. 2010). Urbanization results in changes to the understory of forest fragments, shifting community composition away from native species toward non-native species, as well as potentially homogenizing previously distinct communities (Kühn and Klotz 2006; Dolan et al. 2011).

Much of the Central Till Plain region of Indiana was forested prior to European settlement and was dominated by flatwoods (Hedge 1997). This physiographic region covers much of the central and northeastern portions of Indiana with the southern boundary delineated by the southern reaches of the Wisconsinan ice sheet (Hedge 1997). As a result of extensive agricultural and urban development, forests now account for only 20.3% of the land cover in the entire state, the majority of which is privately owned (Woodall et al. 2009). Forest conservation efforts in Indiana have increased steadily with the inclusion of private forests in classified forest and cooperative forest management programs (IDNR 2010).

Understory and midstory plant communities are directly influenced by the structure and composition of the overstory community (Jameson 1967; Roberts 1992). Changes in the overstory by anthropogenic manipulation will alter those lower strata, which could be positive or negative depending on the community and the manipulation (Meier et al. 1995; Albrecht and McCarthy 2006). Additionally, isolation of forest fragments from other forests alters understory composition, negatively affecting a large proportion of species (McKinney and Lockwood 1999). Fragmentation impacts are long term and may persist on local or regional scales (Vellend et al. 2006). Land managers are therefore interested in quantifying the floristic integrity of a given plant community in light of forest fragmentation and anthropogenically induced disturbances (Rothrock 2004). Floristic quality assessments, as defined by Swink and Wilhelm (1994), have been applied to several different ecosystem types and, within a single ecosystem type, to those under different management strategies (e.g., Francis et al. 2000; Lopez and Fennessy 2002, Bacone et al. 2007; Rothrock et al. 2011). The need to understand the influence of forest protection and preservation on the floristic structure and composition of forest fragments is the principal reason we have undertaken this study.

The objectives of this study were 1) to quantify the understory, midstory, and overstory plant communities in three forests in northeastern Indiana with respect to species richness, diversity, and evenness, 2) to relate the composition and diversity of plant communities to characteristics of forest structure, and 3) to test the hypothesis that the management history and the characteristics of the surrounding land matrix will influence the species composition of the understory and midstory of these three forest fragments.

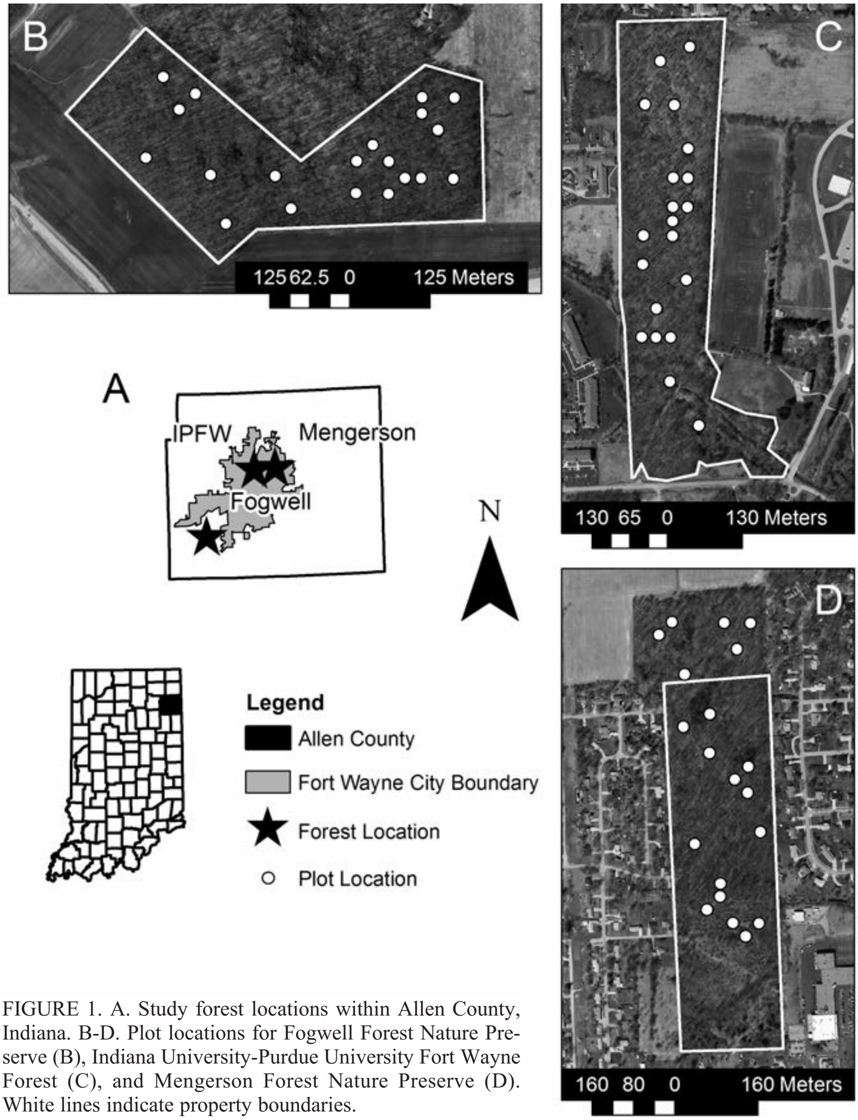

FIGURE 1. A. Study forest locations within Allen County, Indiana. B-D. Plot locations for Fogwell Forest Nature Preserve (B), Indiana University-Purdue University Fort Wayne Forest (C), and Mengerson Forest Nature Preserve (D). White lines indicate property boundaries.

MATERIALS AND METHODS

Study Sites

Three forests in Allen County, Indiana, were selected for comparison (Figure 1A). Two of them, Fogwell Forest Nature Preserve (Fogwell) (40°59′50″ N, 85°14′37″ W; Figure 1B) and Mengerson Nature Preserve (Mengerson) (41°7′35″ N, 85°4′4″ W; Figure 1D), are owned and managed by ACRES Land Trust and are designated nature preserves by the Indiana Department of Natural Resources. The third forest (IPFW) (41°7′22″ N, 85°7′18″ W; Figure 1C) is owned and managed by Indiana University-Purdue University Fort Wayne. IPFW and Mengerson are in the Auburn Morainal

Complex physiographic division, and Fogwell is in the Bluffton Till Plain physiographic division (Franzmeier et al. 2004). All three forests are located adjacent to the boundary between these two physiographic divisions, which are contained in the broader Central Till Plain Natural Region, and all three are dominated by Blount-Morley silt loam soils (NRCS 2013).

Fogwell Forest Nature Preserve is a 24.8 ha property, approximately 12.3 ha of which has a continuous forest canopy (ACRES 2008). A small housing subdivision lies to the north of Fogwell, and the remaining adjacent land consists of cultivated agricultural land and privately-owned hardwood forest. Rothrock (1997) described the forested portion of Fogwell as being donated to ACRES Land Trust in 1976, prior to which the land had been designated a classified forest in the 1930s, which placed limits on the removal of trees from the forest. The Classified Forest program in Indiana is managed by the Department of Natural Resources Division of Forestry and provides protection of privately-owned forests against large anthropogenic disturbances, while providing the land owner with a reduced tax assessment (IDNR 2015). Because of this designation, Fogwell has remained a mature closed canopy forest since the 1930s (Figure 2A).

IPFW, a forested tract of land approximately 13.8 ha in area that is adjacent to the university campus, was acquired by the university in 2004. Little documentation is available regarding its management history, but historical aerial photos indicate that the property has been continuously forested since the late 1930s (Figure 2B). However, the canopy does not appear to have been as dense or as completely closed as the canopy at Fogwell. IPFW is bounded by residential neighborhoods to the north and west, commercial properties to the west and south, and intensely managed athletic fields to the east.

Mengerson Nature Preserve is an approximately 14.4 ha forest that was donated to ACRES Land Trust in 1973 (ACRES 2008). Unlike Fogwell and IPFW, Mengerson was forested only in the northern 1/3 during the 1930s (Figure 2C). Over the subsequent decades, several species of trees have colonized the southern 2/3 of Mengerson, resulting in an early successional forest. Even now, however, the southern 1/3 of Mengerson is only sparsely forested (Figure 1D).

Methods

Within each forest, an initial grid of points with 25.25 m spacing was overlaid on aerial images, and 20 grid points were randomly selected to serve as plot center locations, using ArcMap (version 9.3.1, ESRI, Redlands, California). The spacing of the initial grid points was selected in a manner to ensure that adjacent overstory plots (defined below) did not overlap. At each plot center, understory, midstory, and overstory survey plots were established. Each understory plot consisted of two 1 m^2 quadrats diagonal from each other with sides parallel to the cardinal directions (the southwest corner of one quadrat and the northeast corner of the other were each at the plot center). Within the understory survey plots, all individual plants less than 2 m in height were identified to the finest taxonomic level possible (typically species) and counted. Each midstory survey plot consisted of a 5 * 5 m square plot with the sides parallel to the cardinal directions. All individual stems greater than 2 m in height and less than 8 cm diameter at breast height (dbh) were identified to species and counted. Overstory survey plots consisted of 500 m^2 circular plots (12.62 m radius). All overstory stems (i.e., those greater than 8 cm dbh) were measured for dbh, identified to species, and counted. Voucher specimens for each taxon identified in the understory plots were deposited in the Indiana University-Purdue University Fort Wayne Department of Biology herbarium. All surveys and data collection were conducted during September and October 2013.

At each plot center, basal area per species was assessed with a basal area 10-factor prism. Canopy cover was measured using a concave spherical densiometer following standard protocols (i.e. taking measurements 1 m above ground, averaging measurements taken facing the four cardinal directions). Litter depth was also measured in each plot at the plot center and at a point 6.3 m from the center toward each of the four midstory plot corners. Measurements of canopy cover and litter depth were compared between forests using analysis of variance (ANOVA) with a Tukey-Kramer post-hoc test. Relationships between litter depth, total overstory density (stems / 500 m^2 plot), and total midstory density (stems / 25 m^2 plot) were tested with a Spearman-Rank correlation (due to violations of normality assumptions).

Species richness (S = number of species), Shannon's diversity index ($H' = -\Sigma\, p_i \ln p_i$, where p_i is the proportion of the ith species), and Pielou's evenness index ($J' = H' / \ln S$), were calculated for each strata at the plot level. These three measures were then compared among the forests using ANOVA with a Tukey-Kramer post-hoc test. Using the coefficient of conservatism for the understory species listed by Rothrock (2004), we calculated an unweighted mean coefficient of conser-

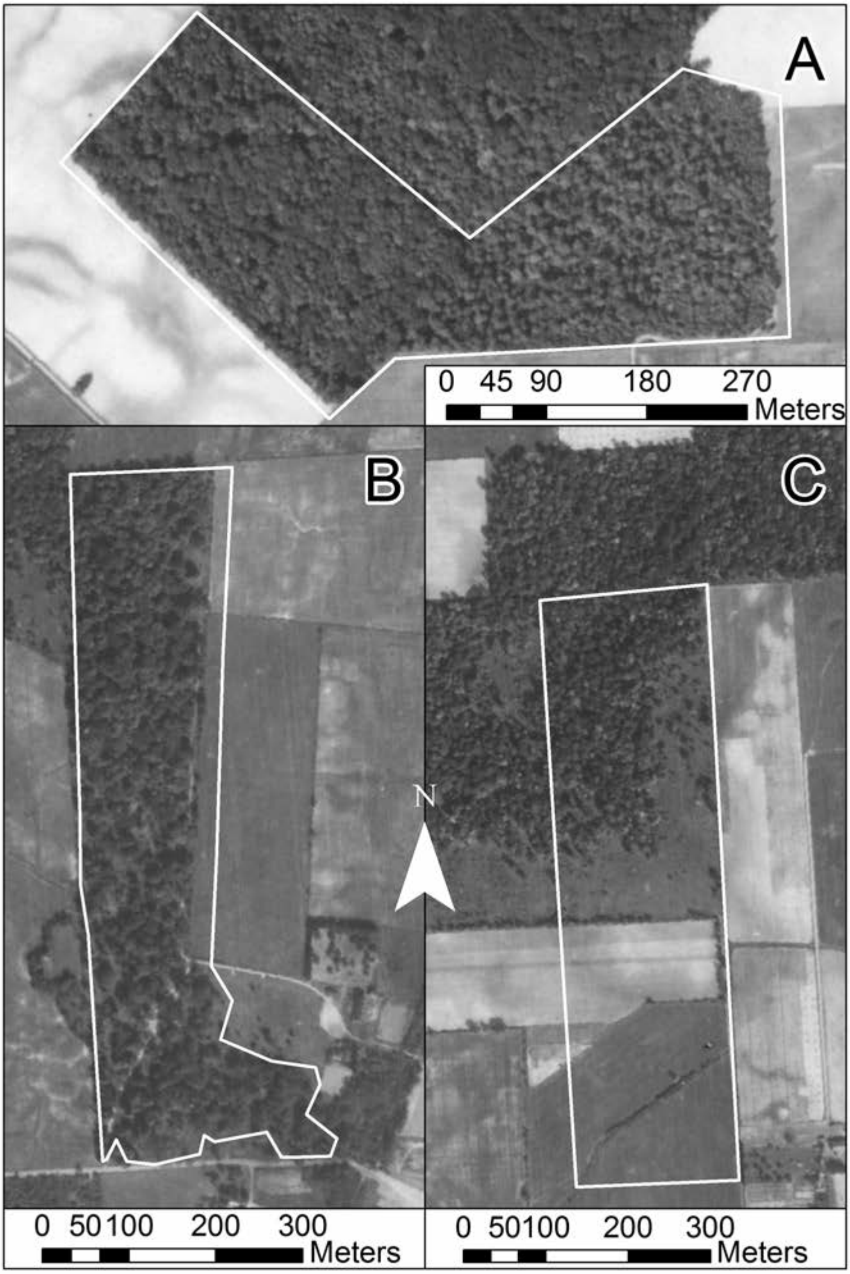

FIGURE 2. Aerial images from 1938 for (A) Fogwell (IHAPI 2013a), (B) IPFW (IHAPI 2013b), and (C) Mengerson (IHAPI 2013c) forests. White forest boundaries are from the 2013 field study. Georectification complications resulted in boundary errors on the eastern edges of Fogwell and IPFW.

vatism (C_{mean}) for each forest and the floristic quality index (FQI = C_{mean} * √number of native plant species) for each forest. Coefficient of conservatism (C-value) is a numerical value used to describe the "nativeness" of a plant species in relation to anthropogenic disturbance (Swink and Wilhelm 1994, Rothrock 2004); the greater the C-value assigned to a species, the more likely it is associated with remnant habitats similar to those existing prior to European settlement (range 1–10, 0 for non-native species). FQI provides a calculated value for the quality and natural importance of a plant community based on the C-values assigned to the species within that community (Rothrock 2004). Similarities among the forests in the understory and midstory survey plots were visualized with non-metric multidimensional scaling (NMDS) ordination using methods described by Kruskal (1964a,b). Dissimilarities were characterized using Bray-Curtis distances, which allow for a visual representation of dissimilarity in species abundances. Within the NMDS figure, species plotted closer together are less dissimilar than those farther apart. For both understory and midstory NMDS ordinations, relationships between species and forest basal area, percent canopy cover, and litter depth were visualized with vector plots associated with the ordination (cutoff α = 0.1, iterations = 1000). We selected our cutoff for the vectors in order to increase the likelihood of displaying basal area, canopy cover, and litter depth on the NMDS ordination plot. Importance values for each overstory species in each forest were calculated as the sum of the relative frequency, the relative dominance, and the relative density of that species; where relative frequency = number of plots in which a species occurred / total number of plots * 100, relative dominance = basal area of a species / total forest basal area * 100, and relative density = number of stems of a species / total number of stems * 100. All statistical analyses were conducted using R (version 3.0.2, The R Foundation for Statistical Computing) base and vegan packages.

RESULTS

In both IPFW and Mengerson, all 20 plot locations were surveyed. However, due to time constraints, only 17 plots at Fogwell were surveyed. In Mengerson, six plots were outside of the north property boundary at the time of study, but were in a section of the forest in the process of being acquired by ACRES Land Trust (Figure 1D). Canopy cover was significantly greater in Fogwell than in the other two forests (F = 5.77, df = 2,54, P = 0.005; Figure 3A). Litter depth at

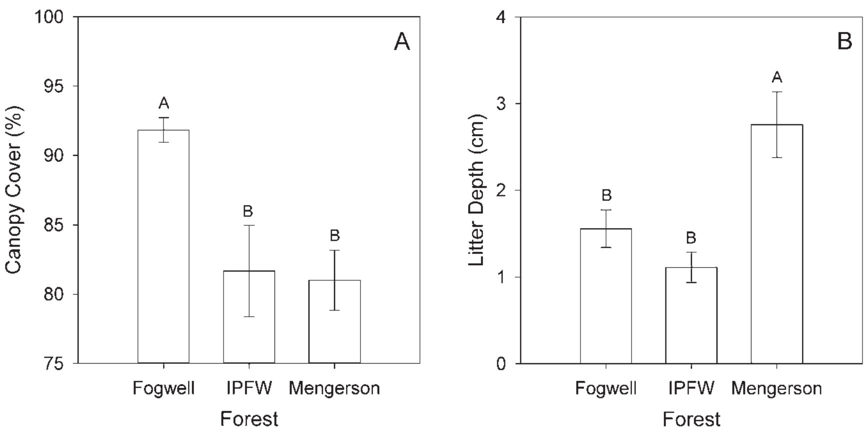

FIGURE 3. Percentage of canopy cover (A) and litter depth (B) in Fogwell, IPFW, and Mengerson forests. Bars that do not share the same letter are significantly different. Error bars represent one standard deviation about the mean.

Mengerson was significantly deeper than at the other two forests (F = 9.76, df = 2,54, $P < 0.001$; Figure 3B).

Understory

A total of 75 species was encountered within the understory strata of the surveyed forests (Appendix I). Fogwell and IPFW were significantly different in species richness (F = 3.82, df = 2,54, $P = 0.028$) (Figure 4A). However, the three forests were not significantly different in understory diversity (F = 2.67, df = 2,53, $P = 0.079$) (Figure 4B), which is likely related to a lack of difference in evenness between forests (F = 1.10, df = 2,46, $P = 0.341$). Similarly, C_{mean} was not significantly different between the forests (F = 0.94, df = 2,84, $P = 0.396$) (Table 1). However, Fogwell had both the greatest percentage of species with a coefficient of conservatism ≥ 5 and the highest FQI value (Table 1). The forest understories had limited overlap in species composition, sharing only 14.6% of species between Fogwell and IPFW, 14.3% between IPFW and Mengerson, and 12.5% between Fogwell and Mengerson. The limited overlap in species was visually evident in the NMDS ordination analysis (Figure 5A). The basal area, the canopy cover, and the litter depth each met the cutoff for inclusion as vectors (Figure 5B).

Midstory

A total of 16 species was encountered within the midstory strata of the surveyed forests (Appendix II). IPFW and Mengerson differed significantly in both species richness (F = 10.23, df = 2,54, $P < 0.001$) (Figure 4C) and in diversity (F = 5.03, df = 2,49, $P = 0.010$) (Figure 4D). Species evenness was not significantly different between the forests (F = 3.07, df = 2,48, $P = 0.056$). Midstory density (stems / 25 m^2 plot) was significantly greater in Mengerson, with 4 and 3 times more stems per plot than in Fogwell and IPFW, respectively (F = 20.24, df = 2,54, $P < 0.001$). Furthermore, midstory density and litter depth were positively correlated (r = 57.00, $P = 0.003$). However, litter depth was not correlated with either midstory species richness (r = 0.07, $P = 0.611$) or diversity (r = 0.06, $P = 0.635$). Unlike the understory strata, the midstory strata in the three forests were fairly similar in species composition, sharing 40.0% of species between Fogwell and IPFW, 31.3% between IPFW and Mengerson, and 35.7% between Fogwell and Mengerson. The similarity was visually evident in the NMDS ordination analysis (Figure 6A). Vector angle indicates relative direction of influence and vector length indicates relative strength of the influence. For example, *Acer saccharum* (ACSA3) and *Ostrya virginiana* (OSVI), both shade-tolerant species, increased in abundance as the percentage of canopy cover increased. Similarly, the shade-intolerant *Crataegus mollis* (CRMO2) decreased in abundance as the percentage of canopy cover increased (Figure 6B).

Overstory

A total of 34 species was encountered within the overstory strata of the surveyed forests (Appendix III). The relationship of the species richness of the

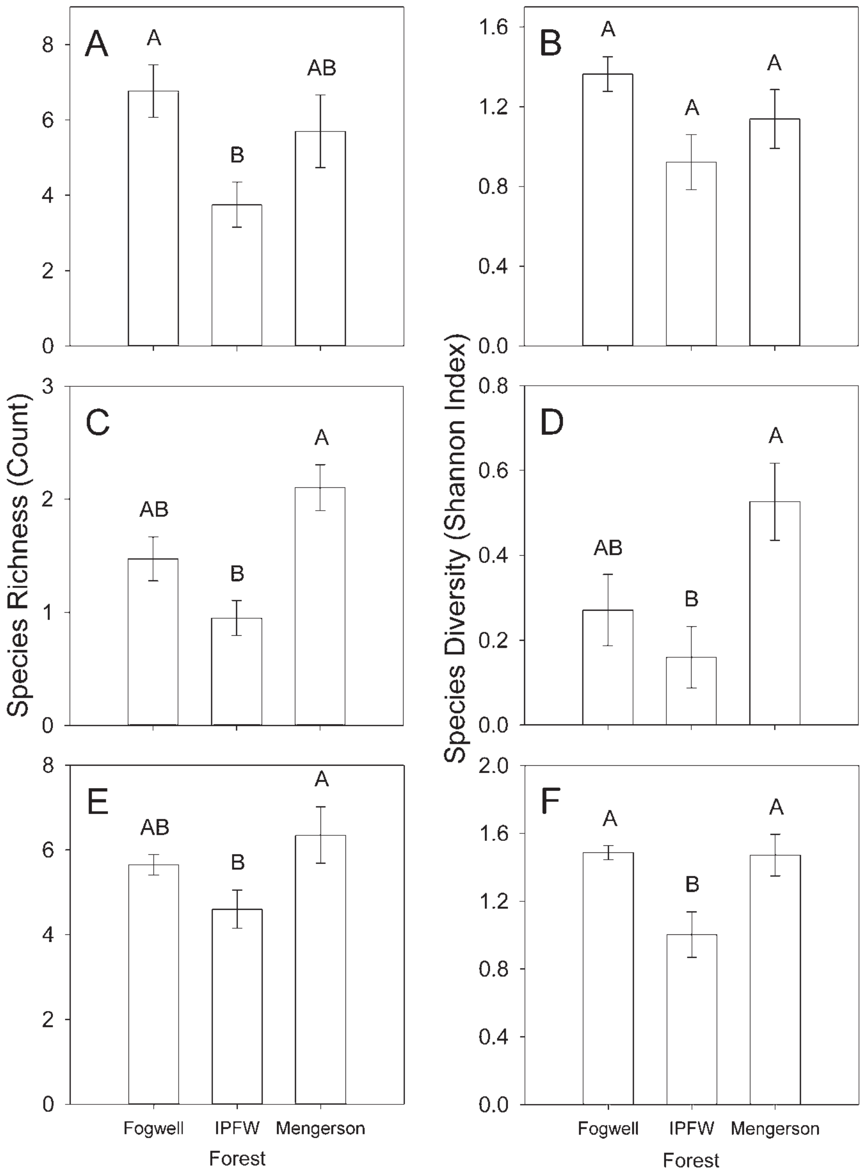

FIGURE 4. Species richness and species diversity for understory (A, B), midstory (C, D), and overstory (E, F) strata plants in Fogwell, IPFW, and Mengerson forests. Bars that do not share the same letter are significantly different. Error bars represent one standard deviation about the mean.

TABLE 1. For the understory stratum in each forest studied, the mean coefficient of conservatism (C_{mean}) (standard error in parentheses), the count of species for which the coefficient of conservatism (C) is ≥ 5 (the percentage of those species relative to all species in the midstory stratum of the forest is given in parentheses), and the floristic quality index (FQI).

Forest	C_{mean} (standard error)	Count for C ≥ 5 (percentage)	FQI
Fogwell	4.1 (0.4)	13 (41.9%)	23.4
IPFW	3.4 (0.5)	8 (28.6%)	18.6
Mengerson	3.6 (0.4)	7 (25.0%)	18.9

overstory strata of the three forests followed a pattern similar to that observed in the midstory strata. IPFW and Mengerson differed significantly from each other (F = 3.20, df = 2,54, *P* = 0.049) (Figure 4E). However, the overstory diversity of IPFW was significantly lower than that of Fogwell and Mengerson (F = 6.09, df = 2,54, *P* = 0.004) (Figure 4F). As a result, IPFW had the lowest evenness value of the three forests (F = 7.18, df = 2,54, *P* = 0.002). At IPFW, *A. saccharum* accounted for 62.1% of the overstory individuals. Overstory densities were not significantly different between the three forests, with an overall mean of 19.6 stems / 500 m^2 (± 8.3 stems) (F = 0.68, df = 2,54, *P* = 0.509). Litter depth was not correlated with overstory density (r = –0.07, *P* = 0.588), species richness (r = 0.07, *P* = 0.644), or diversity (r = 0.04, *P* = 0.784). As with the midstory, the overstory strata of the three forests were more similar in species composition than were the understory strata, sharing 35.7% of species between Fogwell and IPFW, 37.5% between IPFW and Mengerson, and 58.6% between Fogwell and Mengerson. A strong visual overlap can be seen in the NMDS ordination analysis between Mengerson and the other two forests, but less so between Fogwell and IPFW (Figure 7A). Basal area and percentage of canopy cover vectors were not included in the NMDS ordination analysis of pooled species due to collinearity (Figure 7B).

Acer saccharum was the most important overstory species in all three forests (Table 2). It had the greatest values for density of stems, for frequency, and for basal area. There was some overlap in the top five overstory species. *Tilia americana* occurred in all three forests, *Quercus rubra* in Fogwell and Mengerson, and *Ulmus americana* in IPFW and Mengerson (Table 2). Some species occupied high ranking positions in only one of the three forests. For example *A. saccharinum* was among the top five in Mengerson (#3), but did not occur at all in the other two forests; *Carya ovata* (#2) and *Fagus grandifolia* (#3) were both in the top five in Fogwell, but were less important in the other two forests; and *Juglans nigra* (#5) and *Ulmus rubra* (#4) were much more important in IPFW than in the other two forests (Table 2).

DISCUSSION

The three selected forests are located within close proximity of each other (each is approximately 4-16 km from the other two) and, prior to the large-scale

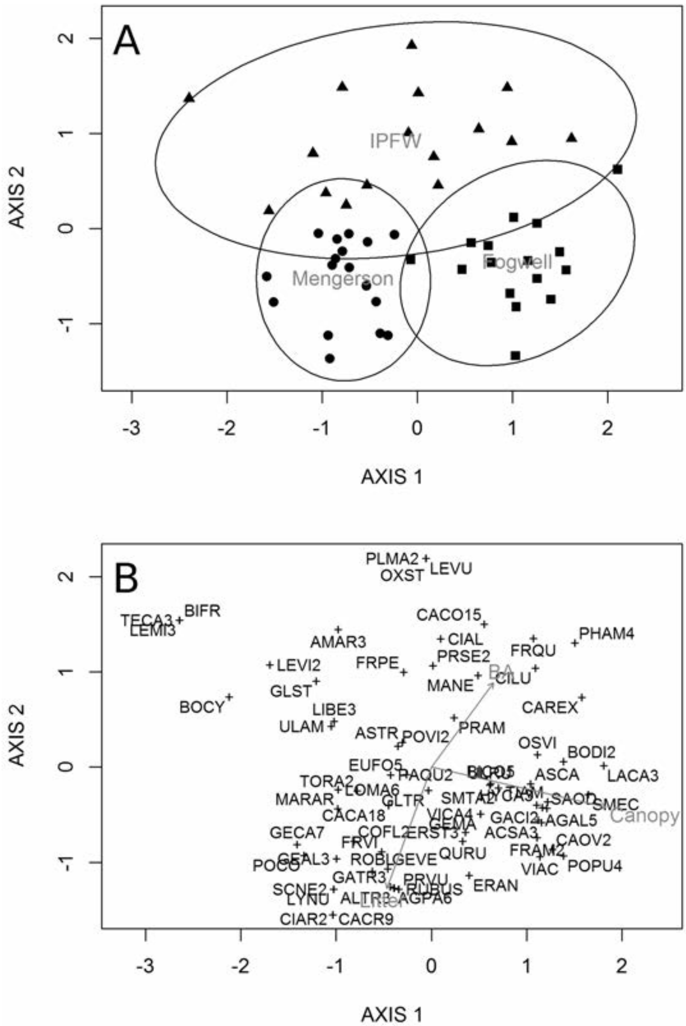

FIGURE 5. Nonmetric multidimensional scaling (NMDS) ordination of understory (final stress = 0.12) for (A) survey plots for Fogwell (squares), IPFW (triangles), and Mengerson (circles) with 95% confidence ellipses for each forest; and (B) pooled species. Direction and length of vectors (gray) for basal area (BA), percentage canopy cover (Canopy), and litter depth (Litter) indicate influence on species occurrence. Species letter codes follow USDA (2014).

conversion of forest to cultivated agricultural land and urban development, were likely connected by contiguous forested land. There have been distinct differences in the protection and management regimes of these forests. Fogwell has received protection for over 80 years, while IPFW and Mengerson have received protection for only 10 years and 40 years, respectively. IPFW has undergone

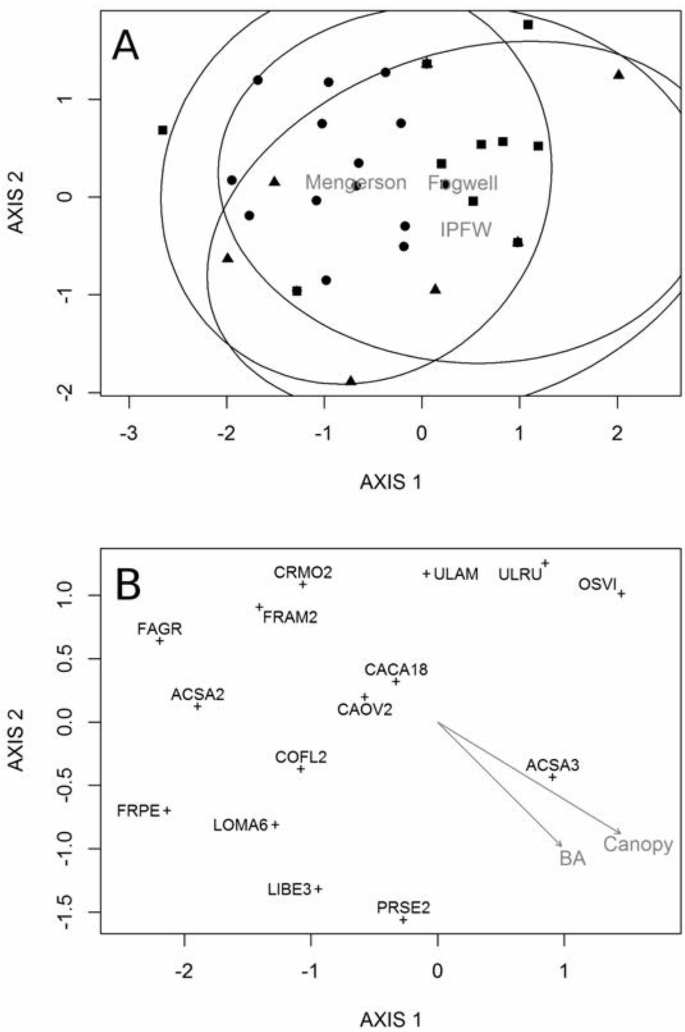

FIGURE 6. Nonmetric multidimensional scaling (NMDS) ordination of midstory (final stress = 0.08) for (A) survey plots for Fogwell (squares), IPFW (triangles), and Mengerson (circles) with 95% confidence ellipses for each forest; and (B) pooled species. Direction and length of vectors (gray) for basal area (BA) and percentage canopy cover (Canopy) indicate influence on species occurrence. Species letter codes follow USDA (2014).

decades of passive protection (i.e. without management), and the closure of its canopy likely occurred decades after that at Fogwell, but before that at Mengerson. Although Mengerson has been actively protected since the 1970s, its canopy has only recently closed, as is apparent from historical aerial imagery.

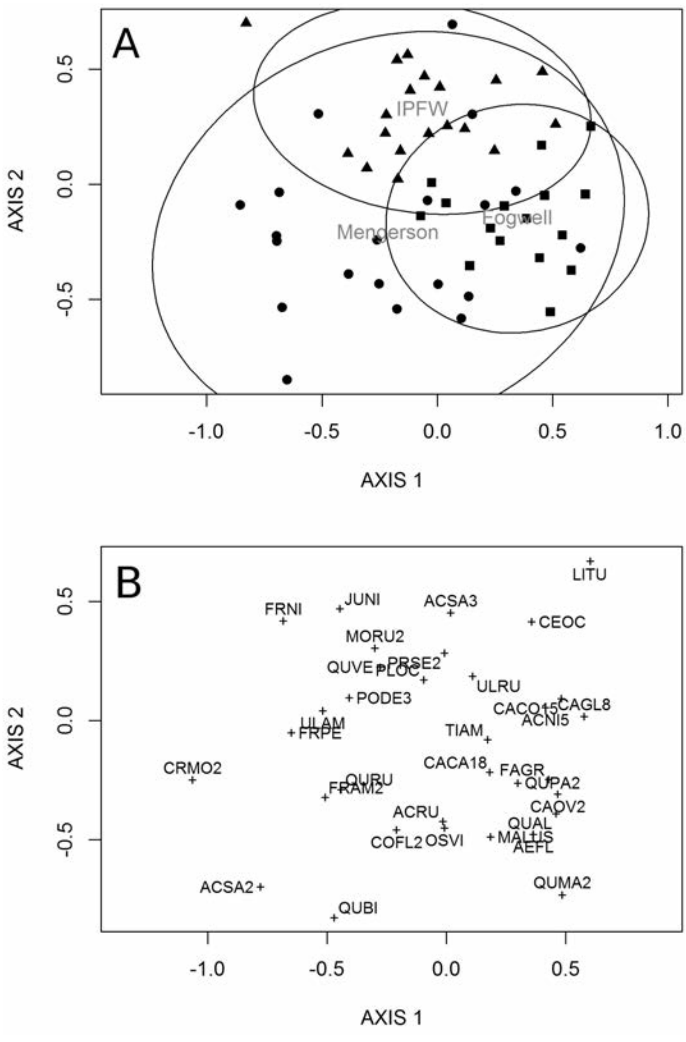

FIGURE 7. Nonmetric multidimensional scaling (NMDS) ordination of overstory (final stress = 0.22) for (A) survey plots for Fogwell (squares), IPFW (triangles), and Mengerson (circles) with 95% confidence ellipses for each forest; and (B) pooled species. Species letter codes follow USDA (2014).

The difference observed in canopy cover was expected, given the differences in the history of management at the three forests. Both IPFW and Mengerson have histories of overstory tree removal, which is evidenced by the patchy canopy visible in aerial images from the late 1930s (Figure 2). A simple visual comparison of aerial images indicates that IPFW and Mengerson are likely now at a canopy closure state similar to that of Fogwell from the 1930s to the 1950s.

TABLE 2. Importance values of the top 10 overstory species in each of the forests studied. The rank of each species within a forest is given in parentheses.

Species	Fogwell	IPFW	Mengerson
Acer saccharinum	—	—	22.7 (3)
Acer saccharum	87.6 (1)	129.0 (1)	40.1 (1)
Carya cordiformis	9.7 (8)	—	—
Carya ovata	39.6 (2)	—	20.4 (6)
Celtis occidentalis	—	9.6 (9)	—
Fagus grandifolia	37.1 (3)	—	—
Juglans nigra	6.4 (10)	21.7 (5)	12.1 (10)
Ostrya virginiana	—	—	15.9 (7)
Platanus occidentalis	—	6.6 (10)	—
Prunus serotina	—	13.2 (6)	—
Quercus alba	18.7 (6)	—	12.6 (9)
Quercus bicolor	—	—	12.7 (8)
Quercus rubra	25.0 (5)	11.0 (7)	35.5 (2)
Quercus velutina	—	10.9 (8)	—
Tilia americana	29.2 (4)	28.3 (2)	21.2 (5)
Ulmus americana	7.6 (9)	24.1 (3)	22.0 (4)
Ulmus rubra	15.7 (7)	23.5 (4)	—

Although litter depth was significantly different statistically between the three forests, of which Mengerson had the deepest litter, the numerical difference (ranging from 1.1 to 2.8 cm) may not have been biologically significant. Litter depth is a complex and dynamic relationship between addition and removal of litter (Facelli and Pickett 1991). Because of the close proximity of the three forests to each other, climate differences are likely to be very minor, resulting in little difference in rainfall or length of the growing season; decomposition rates are typically regulated by moisture and temperature (Facelli and Pickett 1991). The cause of the differences in litter depth would likely be related to differences in midstory densities, Mengerson had both the deepest litter, as well as the richest and densest midstory.

Rothrock (1997) originally calculated a C_{mean} of 5.6 for Fogwell. However, after Rothrock (2004) modified the coefficient of conservation values for Indiana specifically, C_{mean} for Fogwell was recalculated as 4.1 (Rothrock and Homoya 2005). This new value aligns exactly with our calculated C_{mean} for Fogwell (4.1). However, our calculated FQI (23.4) was less than half the value (59.3) calculated for previous surveys (Rothrock and Homoya 2005). This demonstrates the difficulty of comparing floristic survey and ecological survey studies in relation to various metrics of diversity or ecology. Rothrock (1997) conducted a floristic survey of Fogwell with the explicit intent of producing a full inventory of the preserve, which formed the basis of the calculation by Rothrock and Homoya (2005). In contrast, we conducted an ecological survey with the intent of providing a comparison between forests with different management histories and different types of surrounding development. Thus, C_{mean} for each of the three forests is based on species with moderately high to high tolerances for disturbance, using the C-values assigned by Rothrock (2004). All three forests have experienced anthropogenic disturbances related to forest management, although at different times for each forest. While using C-values to compare communities should done cautiously, comparing counts of species above or below a threshold may provide insight into forest disturbance or persistence. A C-value ≥ 5 for a given species indicates it is likely to be found in remnant areas similar to pre-settlement habitats (Rothrock 2004; Rothrock and Homoya 2005). The relatively high percentage of species in Fogwell with a C-value ≥ 5 suggests that the understory plant community has recovered or simply persisted from limited anthropogenic disturbances in the 1930s (i.e., more species are adapted to less disturbance). Inversely, the lower percentage of species at IPFW and Mengerson with a C-value ≥ 5 suggests that the recent disturbances in forest management are still evident in the understory communities, which is likely related to the later canopy closure in these forests. While C_{mean} was not significantly different between the three forests, the FQI for Fogwell was substantially greater than it was for IPFW and Mengerson. Again, the difference is related to the time that has elapsed since the most recent disturbance and to the percentage of canopy closure within the three forests, Fogwell having experienced little or no disturbance since the 1930s.

The density of the midstory is likely related to the time of canopy closure (e.g., Mengerson had the most recent canopy closure and the highest density in midstory individuals), and likely was the driver in accumulation of forest litter. Although IPFW has had some anthropogenic disturbance related to forest management, the canopy appears to have been much denser in the 1930s than the canopy at Mengerson. The greater canopy density may have been an important factor in the greater similarity in both the species observed at Fogwell and IPFW and the midstory and overstory densities in those two forests. Because active forest management has essentially stopped at IPFW and Mengerson, the overstory density in both forests has reached similar values as that of Fogwell. While the similarity in overstory species between forests is relatively high, several of the top five and top ten most important species are unique to a single forest. Those most important species are providing the physical structure of the forest. In addition to being the most important species in the overstory, *Acer saccharum* was the most frequent midstory species pooled across the three forests. Due to the ability to maintain small stature individuals for decades in the shade (Marks and Gardescu 1998), *A. saccharum* is a common midstory species in the region. Once canopy gaps form, *A. saccharum* responds and can quickly be recruited into larger size classes (Marks and Gardescu 1998), leading to inclusion in the canopy.

The location of each forest has likely been an additional factor that has influenced the development of understory communities in these forests. In other urban forests, there has been clear increase in non-native plant species (Dolan et al. 2011). Fogwell, which has the richest understory and the greatest FQI value among the forests, is a rural forest. Although there is a small subdivision to the north of Fogwell, it is not surrounded by urban and suburban development, unlike IPFW and Mengerson, each of which were lower in species richness and FQI values. We did not encounter any non-native understory species at Fogwell. In contrast, non-native species accounted for 16% of the understory individuals counted at IPFW and 26% at Mengerson. Again, this is likely related to the proximity of a forest to urban and suburban development and to the time that has elapsed since canopy closure.

While these three forests had similarities in midstory and overstory species, their importance to the region may exist more in their lack of similarity in understory species. Most of the forest fragments in northeastern Indiana and the surrounding region are small privately owned properties that have undergone a broad range of protection and use over the past century. Allowing forests to undergo canopy closure and long-term minimized anthropogenic disturbance may increase understory plant species richness and FQI, as seen in Fogwell. However, as is apparent in the case of IPFW and Mengerson, proximity to urban development may be just as important a factor as time in promoting colonization of understory communities by non-native species.

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APPENDIX I. List of understory species collected at each of the forests studied. Frequency is the number of 2 m^2 plots (out of 17 at Fogwell and 20 at each of IPFW and Mengerson) in which they were encountered. Count is the mean number of individuals (standard deviation in parentheses). Nomenclature follows ITIS (2013). An asterisk (*) indicates non-native species (USDA NRCS 2013). Collection numbers are in parentheses after each species name..

	Fogwell		IPFW		Mengerson	
Species	Frequency	Count	Frequency	Count	Frequency	Count
Acer saccharum Marsh. (1314)	7	4.7 (3.1)	1	1.0		
Ageratina altissima (L.) King & H. Rob. (1267)	2	3.0 (0.0)			1	1.0
Agrimonia parviflora Aiton (1299)					2	4.0 (1.4)
Allium tricoccum Aiton (1243)					2	7.0 (1.4)
Amelanchier arborea (F. Michx.) Fernald (1300)			2	1.0 (0.0)		
Asarum canadense- L. (1277)	12	42.2 (33.1)	3	3.7 (2.1)		
Asimina triloba (L.) Dunal (1282)			1	1.0		
Bidens connata Muhl. ex Willd. (1269)	1	1.0				
Bidens frondosa L. (1270)			1	1.0		
Boehmeria cylindrical (L.) Sw. (1329)			2	39.5 (51.6)	1	3.0
Botrychium dissectum Spreng. (1288)	1	1.0				
Carex cryptolepis Mack. (1337)					1	6.0
Carex spp. (1338)	5	2.8 (0.8)	4	7.0 (5.0)		
Carpinus caroliniana Walter (1264)	1	2.0			1	1.0
Carya cordiformis (Wangenh.) K. Koch (1253)			4	6.3 (3.9)		
Carya ovata (Mill.) K. Koch (1252)	3	1.3 (0.6)				
Cinna arudinacea L. (1283)					2	10.5 (10.5)
Circaea alpina L. (1290)			2	3.5 (0.7)		
Circaea lutetiana L. (1291)			1	3.0		
Cornus florida L. (1256)					9	4.1 (4.1)
Erigeron annuus (L.) Pers. (1271)	3	17.0 (21.9)			4	2.5 (1.0)
Erigeron strigosus Muhl. ex Willd. (1274)					2	12.5 (16.3)
Euonymus atropurpureus Jacq. (1258)	3	3.3 (2.5)				
**Euonymus fortunei* (Turcsz.) Hand.-Maz. (1257)					1	8.0
Fragaria virginiana Duchesne (1302)					4	7.5 (8.2)

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APPENDIX I. (Continued).

Species	Fogwell		IPFW		Mengerson	
	Frequency	Count	Frequency	Count	Frequency	Count
Fraxinus americana L. (1240)	13	10.1 (9.1)				
Fraxinus pennsylvanica Marsh. (1238)	1	1.0	9	7.8 (12.6)		
Fraxinus quadrangulata Michx. (1293)			2	3.5 (2.1)		
Galium circaezans Michx. (1313)	11	9.7 (8.0)				
Galium triflorum Michx. (1231)					1	8.0
Geranium maculatum L. (1250)	1	1.0				
Geum aleppicum Jacq. (1341)					1	1.0
Geum canadense Jacq. (1303)					9	11.3 (11.9)
Geum vernum (Raf.) Torr. & A. Gray (1305)					2	3.0 (2.8)
Geum virginianum L. (1306)			2	1.0 (0.0)		
Gleditsia triacanthos L. (1254)			1	1.0		
Glyceria striata (Lam.) Hitchc. (1284)	1	24.0				
Hydrophyllum canadense L. (1259)	3	9.3 (11.0)				
Laportea canadensis (L.) Wedd. (1330)	6	6.8 (4.4)				
Leersia virginica Willd. (1285)			3	38.0 (36.0)		
Lemna minor L.			1	200.0		
**Leucanthemum vulgare* Lam. (1275)			1	1.0		
Lindera benzoin (L.) Blume (1246)			4	2.0 (2.0)		
**Lonicera maackii* (Rupr.) Herder (1232)			5	3.2 (3.3)	16	13.3 (12.4)
**Lysimachia nummularia* L. (1237)					1	26.0
Maianthemum racemosum ssp. *racemosum* (L.) Link (1244)					1	3.0
**Malva neglecta* Wallr. (1242)			5	5.2 (7.8)		
Menispermum canadense L. (1241)	1	7.0				
Ostrya virginiana (Mill.) K. Koch (1261)	1	1.0				
Oxalis stricta L. (1289)			1	15.0		
Parthenocissus quinquefolia (L.) Planch. (1333)	5	8.0 (2.7)	5	5.6 (9.2)	10	4.1 (3.1)
Penstemon digitalis Nutt. ex Sims (1317)					1	1.0

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APPENDIX I. (Continued).

Species	Fogwell		IPFW		Mengerson	
	Frequency	Count	Frequency	Count	Frequency	Count
Persicaria virginiana (L.) Gaertn. (1295)			1	2.0	4	6.0 (1.4)
Phlox divaricata L. (1294)					1	1.0
Phytolacca americana L. (1340)			2	1.5 (0.7)		
**Plantago major* L. (1287)			1	3.0		
**Poa compressa* L. (1286)					5	5.8 (4.4)
Polygonatum pubescens (Willd.) Pursh (1245)	3	2.0 (1.0)				
Prunella vulgaris L. (1249)					1	1.0
Prunus americana Marshall (1308)			1	3.0		
Prunus serotina Ehrh. (1307)			4	2.0 (1.4)	1	1.0
Quercus rubra L. (1339)	2	1.0 (0.0)			3	2.0 (1.7)
Rosa blanda Aiton (1311)					4	2.5 (1.0)
Rubus spp. (1312)					1	6.0
Sanicula odorata (Raf.) K.M. Pryer & L.R. Phillippe (1279)	11	12.2 (12.0)			2	1.5 (0.7)
Scutellaria nervosa Pursh (1248)					1	7.0
Smilax ecirrhata (Engelm. ex Kunth) S. Watson (1319)	1	1.0				
Smilax tamnoides L. (1320)	3	4.0 (4.4)	1	2.0		
Symphyotrichum praealtum (Poir.) G.L. Nesom (1268)	1	2.0				
Teucrium canadense L. (1247)			1	3.0		
Tilia americana L. (1322)	3	1.3 (0.6)				
Toxicodendron radicans (L.) Kuntze	2	6.5 (3.5)	2	3.0 (2.8)	14	11.3 (6.2)
Ulmus americana L. (1324)			1	1.0		
Ulmus rubra Muhl. (1327)	5	3.6 (2.4)	1	1.0	2	1.0 (0.0)
Viburnum acerifolium L. (1233)	1	1.0				
Viola canadensis L. (1331)	1	1.0				

APPENDIX II. List of midstory species collected at each of the forests studied. Frequency is the number of 25 m^2 plots (out of 17 at Fogwell and 20 at each of IPFW and Mengerson) in which they were encountered. Count is the mean number of individuals (standard deviation in parentheses). Nomenclature follows ITIS (2013). An asterisk (*) indicates non-native species (USDA NRCS 2013).

	Fogwell		IPFW		Mengerson	
Species	Frequency	Count	Frequency	Count	Frequency	Count
Acer saccharinum L.					2	15.0 (0.7)
Acer saccharum Marsh.	12	3.5 (2.2)	10	2.0 (0.8)		
Carpinus caroliniana Walter					1	3.0
Carya ovata (Mill.) K. Koch					2	1.0 (0.0)
Cornus florida L.					2	4.0 (2.8)
Fagus grandifolia Ehrh.	1	1.0			2	2.5 (0.7)
Fraxinus americana L.			1	1.0	2	1.0 (0.0)
Fraxinus pennsylvanica Marsh.			1	1.0		
Lindera benzoin (L.) Blume	1	2.0	1	1.0		
**Lonicera japonica* Thunb.					1	1.0
**Lonicera maacki* (Rupr.) Herder			2	3.0 (2.8)	5	5.8 (3.0)
Ostrya virginiana (Mill.) K. Koch	2	1.5 (0.7)	1	1.0	6	1.0 (0.0)
Prunus serotina Ehrh.			2	2.0 (1.4)		
Quercus macrocarpa Michx.					1	1.0
Ulmus americana L.	3	1.3 (0.6)	1	1.0	8	2.5 (2.3)
Ulmus rubra Muhl.	4	1.3 (0.5)			1	1.0

APPENDIX III. List of overstory species collected at each of the forests studied. Frequency is the number of 500 m^2 plots (out of 17 at Fogwell and 20 at each of IPFW and Mengerson) in which they were encountered. Count is the mean number of individuals (standard deviation in parentheses). Nomenclature follows ITIS (2013).

	Fogwell		IPFW		Mengerson	
Species	Frequency	Count	Frequency	Count	Frequency	Count
Acer nigrum F. Michx.	3	1.3 (0.5)	2	1.5 (0.7)		
Acer rubrum L.	1	1.0			4	2.0 (1.4)
Acer saccharinum L.					10	2.5 (1.7)
Acer saccharum Marsh.	15	4.9 (2.9)	18	14.7 (7.6)	10	6.9 (5.2)
Aesculus glabra Willd.	1	1.0			1	2.0
Carpinus caroliniana Walter	2	1.5 (0.7)			3	1.7 (0.6)
Carya cordiformis (Wangenh.) K. Koch	2	1.0 (0.0)	2	1.0 (0.0)	6	2.2 (1.5)
Carya glabra (Mill.) Sweet	1	1.0				
Carya laciniosa (Michx. f.) G. Don			1	1.0		
Carya ovata (Mill.) K. Koch	12	1.7 (0.9)				
Celtis occidentalis L.			5	2.0 (1.7)		
Cornus florida L.					6	2.8 (2.5)
Crataegus mollis Scheele					4	6.0 (6.9)
Fagus grandifolia Ehrh.	13	2.2 (2.2)	1	5.0	5	3.0 (2.8)
Fraxinus americana L.			2	1.5 (0.7)	3	5.0 (4.6)
Fraxinus nigra Marshall					1	1.0
Fraxinus pennsylvanica Marshall					4	1.7 (0.9)
Juglans nigra L.	3	1.0 (0.0)	8	2.1 (1.6)	4	2.5 (1.3)
Liriodendron tulipifera L.			1	1.0		
Malus sp.	1	2.0				
Morus rubra L.			1	1.0		
Ostrya virginiana (Mill.) K. Koch	1	1.0			8	2.5 (1.6)
Platanus occidentalis L.			3	1.3 (0.6)	1	1.0
Populus deltoides W. Bartram ex Marshall			1	5.0		
Prunus serotina Ehrh.			5	2.0 (1.7)	1	1.0
Quercus alba L.	4	1.8 (1.0)			6	1.5 (0.8)
Quercus bicolor Willd	1	1.0			6	1.8 (0.8)
Quercus macrocarpa Michx.	1	1.0			1	1.0
Quercus nigra L.					1	2.0
Quercus palustris Munchh.					4	1.5 (0.6)
Quercus rubra L.	7	1.9 (1.9)	4	2.0 (0.8)	12	3.0 (1.7)
Quercus velutina Lam.	1	4.0	5	1.6 (0.9)		
Tilia americana L.	12	1.8 (0.9)	11	2.4 (1.9)	7	4.0 (2.6)
Ulmus americana L.	3	1.7 (1.2)	11	2.8 (2.5)	10	3.8 (2.4)
Ulmus rubra Muhl.	7	1.9 (1.8)	11	2.4 (1.7)	3	2.0 (1.0)