

Major changes in tree community composition and structure over 86 years in an old-growth beech-maple-hemlock forest¹

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Abstract. Old-growth forests dominated by shade-tolerant tree species are among the plant communities most likely to be in equilibrium. However, the assumption that these forests show long-term stability has rarely been tested. In this study, we resurveyed plots established 86 yr before in an old-growth beech-maple-hemlock forest in northeast Ohio to examine changes in tree community composition, diversity, and structure. Species richness and diversity remained constant from 1932 to 2018, but we found dramatic shifts in the relative abundances of species and the size structure of populations. *Fagus grandifolia* remained the most frequent and abundant tree species in the forest, while changing dramatically in size structure; larger *Fagus grandifolia* trees died and were replaced by large numbers of root suckers, increasing the overall stem density of the forest by 50%. *Tsuga canadensis* declined in frequency and stem density, shifted away from smaller size classes, and had almost no saplings. Plots dominated by *Tsuga canadensis* in 1932 showed the greatest magnitude of compositional change over time, shifting toward dominance by *Acer saccharum*, which along with *Acer rubrum*, increased greatly in frequency, stem density, and basal area. Eight species including *Castanea dentata* and *Sassafras albidum* were lost from the plots. In sum, *Fagus grandifolia* and *Acer saccharum* are displacing *Tsuga canadensis* in this stand. Tree diseases, pests, and deer herbivory likely contributed to these compositional shifts. Given the time scale of the directional changes we observed, even relatively undisturbed communities such as old-growth forests might be best viewed as not in equilibrium.

Key words: *Acer saccharum*, beech-maple, *Fagus grandifolia*, forest, long-term, Ohio, old-growth, resurvey, *Tsuga canadensis*

Many important ecological processes shaping species composition and diversity operate over time scales of decades to hundreds of years. The consequences of human actions such as climate change, habitat destruction, and species introductions ramify over long time scales as well. To understand environmental drivers of community composition, we therefore need a long-term perspective (Wiens *et al.* 2012, Vellend *et al.* 2013a). We particularly need data sources with a temporal resolution of tens to hundreds of years to allow us to see how communities respond to slow processes and ongoing changes (Jackson and Blois 2015). Among the most valuable data for this purpose come from resurveying permanent plots, because this approach directly measures change in

local diversity and abundance over time (Sax and Gaines 2003, Hédli *et al.* 2017). Now that ecologists have been quantitatively surveying vegetation for about a century, a number of recent studies have tested hypotheses about species compositional changes by combining legacy data with resurveys (e.g., Anderson and Inouye 2001; Taverna, Peet, and Phillips 2005; Rogers *et al.* 2008; Damschen, Harrison, and Grace 2010). However, very few have spanned long enough to examine forest tree community dynamics (but see European studies by Keith *et al.* 2009, Šebesta *et al.* 2011, Kokarēviča *et al.* 2016 spanning up to 80 yr).

Protected old-growth forests are particularly interesting to resurvey because, of all ecosystems, we might expect them to exhibit the greatest long-term stability. Roughly 12,000 yr after the Wisconsin glaciation, tree distributions in eastern North America might have reached an equilibrium with climate, topography, and soils (Delcourt and Delcourt 2000). Although most vegetation of this region underwent radical transformations due to land use (Flinn and Vellend 2005), forests that escaped clearing and that remain as today's protected old-growth stands remained relatively undisturbed. These forests should therefore undergo self-replacement via gap dynamics rather than the directional change of succession (Runkle

¹ We thank Baldwin Wallace University for supporting this project. We thank Shanon Donnelly for georeferencing plot locations, Ryan Trimbath for facilitating collaborations, and Wendy Wasman for providing access to archives. Constance Hausman gave thoughtful comments on the manuscript. Thanks to Cleveland Metroparks for permission to conduct the research.

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doi: 10.3159/TORREY-D-18-00041.1

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Received for publication July 17, 2018, and in revised form September 9, 2018; first published May 8, 2019.

1981). Furthermore, the long lifespans of trees, coupled with a turnover rate among canopy trees of only about 1% per year, can result in stasis in forest canopy composition for hundreds of years (Runkle 2000, Busing 2005). However, these long-held assumptions about old-growth forest stability have rarely been tested and are open to question. Even protected stands that seemingly experience minimal human impact might be affected by many ecological changes. First, most old-growth remnants are very small and surrounded by contrasting habitats; they might continue to lose species to extinction debt (Vellend *et al.* 2006), and some species might suffer from edge effects (Jules and Rathcke 1999). Other important region-wide changes over the last hundred years include the introduction of exotic species, especially tree diseases and pests, and the dramatic increase in deer populations. These factors could lead to substantial changes in forest structure and composition over time, despite the lack of major disturbance.

Here we resurvey plots established in 1932 in an old-growth beech-maple-hemlock forest in northeast Ohio called A.B. Williams Woods. The timespan of 86 yr allows us to discern changes in tree community composition, diversity, and structure. Arthur Baldwin Williams (1936), who conducted the original survey, predicted that *Fagus grandifolia* Ehrh. and *Acer saccharum* Marshall would displace *Tsuga canadensis* (L.) Carrière. He based this prediction on his observations of large numbers of standing dead *Tsuga canadensis*, dead *Tsuga canadensis* logs lying in areas occupied by *Fagus grandifolia* and *Acer saccharum*, and a lack of *Tsuga canadensis* reproduction. We also expected a further decline in *Castanea dentata* (Marshall) Borkh. due to blight (most *Castanea dentata* trees were already dead in 1932) and a paucity of regeneration due to deer herbivory.

Materials and Methods. **STUDY AREA.** A.B. Williams Woods is a 26-ha stand of old-growth forest located in Cleveland Metroparks's North Chagrin Reservation, Mayfield, OH (41°33'40"N, 81°25'39"W, 274 m elevation). The land lies on the glaciated Allegheny Plateau and on the western border of the Chagrin River valley. Topography is mostly level, with elevation change of < 30 m and one small stream. Cleveland shale underlies somewhat poorly drained clay loam soils (Williams 1936). The region has a humid continental

climate with a mean annual temperature of 10.8 °C, mean annual precipitation of 99.4 cm (including 173 cm of snow), and a median frost-free season of 189 days (Midwestern Regional Climate Center 2017). The study area has remained forested throughout the historical period (Flinn, Mahany, and Hausman 2018). In 1871, a few large trees of *Quercus* L. spp., *Carya* Nutt. spp., *Liriodendron tulipifera* L., and *Castanea dentata* were cut (Williams 1936). No other logging is known to have occurred, and the forest contains many trees 250–300 yr old (Williams 1936). Cleveland Metroparks acquired the land in 1925.

HISTORICAL DATA. A.B. Williams (1932, 1936) collected three datasets in 1932. In a belt transect, he counted, identified, and measured the diameter at breast height (dbh) of all trees and shrubs ≥ 0.8 cm dbh in 44 adjacent 8 m \times 10 m plots. He also established 10, 30 m \times 30 m plots throughout the study area in which he counted and identified all trees and shrubs at least knee high, divided into stems ≤ 5 cm dbh and > 5 cm dbh. Third, he sampled 4, 15 m \times 15-m plots in which he counted, identified, and measured the dbh of all trees and shrubs at least 2 m tall. Williams drew detailed maps showing the location of all plots. For the belt transect and the 4, 15 m \times 15-m plots, he left hand-drawn maps showing the location, size, and identity of every tree. Williams (1936) also conducted a complete floristic survey of the study area.

FIELD SAMPLING. We relocated Williams's plots by georeferencing his maps to obtain GPS coordinates. In the field, we were able to locate the plots more precisely by finding many individual trees that were still extant. We are confident that we relocated all plots within ± 20 m and many plots more precisely. Kopecky and Macek (2015) showed that vegetation resurvey is robust to this level of plot location uncertainty. We replicated Williams's sampling methods exactly, measuring dbh at 1.37 m. Nomenclature follows Voss and Reznicek (2012).

STATISTICAL ANALYSES. We calculated the species richness and Shannon diversity of each plot and compared them between years using paired *t* tests. We calculated the frequency of each species as the percentage of plots in which it occurred, considering only trees ≥ 5 cm dbh. To assess differences in frequency between 1932 and 2018, we used *G* tests of independence to compare the proportions

of plots where species were present and absent between the two years.

For each plot and for each species in each plot, we calculated stem density (stems/ha) and basal area (m^2/ha) of trees (i.e., ≥ 5 cm dbh) and of saplings (i.e., < 5 cm dbh). We compared them between years using paired t tests for plot totals and for species found in at least 10% of plots in either year. For the three most frequent species, we compared the proportions of stems in each size class between years using G tests of independence, with the classes 5–14.9, 15–24.9, 25–34.9, 35–44.9, 45–54.9, and ≥ 55 cm dbh.

To describe shifts in tree community composition, we performed a nonmetric multidimensional scaling (NMS) ordination on stem density of trees ≥ 5 cm dbh in PC-ORD (McCune and Grace 2002, McCune and Mefford 2006). The ordination used Sørensen (Bray-Curtis) distance, a random starting point, 50 runs with real data, and 249 runs with randomized data. We found a two-dimensional solution and varimax-rotated it.

To test whether species composition differed between years, we used a multiresponse permutation procedure (MRPP) based on Sørensen (Bray-Curtis) distance. We tested whether 1932 and 2018 differed along each ordination axis using paired t tests on axis scores. We also conducted an indicator species analysis to identify species associated with each year (Dufrêne and Legendre 1997). This method combines information on species' concentration of abundance in each year and their faithfulness of occurrence in each year. We used a Monte Carlo test with 4,999 randomizations to evaluate the significance of the indicator values.

We tested whether initial composition and diversity affected compositional change over time in two ways. First, we calculated species turnover rate for each plot as $100 \times (1 - [\text{number of species present in both years}/\text{mean number of species present in both years}])$ (Johnson, Mudrak, and Waller 2014). We tested the effects of initial species richness and ordination axis scores on species turnover using regression analysis. Second, we used the length of vectors between plot positions on ordination axes in the two years to quantify the magnitude of compositional change over time (Taverna, Peet, and Phillips 2005). Again we tested the effects of initial species richness and ordination axis scores on compositional change using regression analysis.

Results. Overall we found 18 species of trees and shrubs, of which 15 were shared with the 1932 sample. *Carya cordiformis* (Wang.) K. Koch occurred in our sample and not in the 1932 sample, but it was included in Williams's complete flora of the study area. We found two species that were not included in Williams's complete flora: *Malus coronaria* (L.) Mill. and *Smilax rotundifolia* L. Eight species found in the plots in 1932 were missing in 2018: *Carya ovata* (Mill.) K. Koch, *Castanea dentata*, *Cornus florida* L., *Sambucus racemosa* L., *Sassafras albidum* (Nutt.) Nees, *Tilia americana* L., *Ulmus americana* L., and *Viburnum acerifolium* L. No exotic species of trees or shrubs were found in either 1932 or 2018.

Species richness and Shannon diversity were similar between 1932 and 2018, with a mean of 2.5 woody plant species in an 80 m^2 plot (species richness: $t = -0.8465$, d.f. = 57, $P = 0.4008$; Shannon diversity: $t = -1.2642$, d.f. = 57, $P = 0.2113$).

In 1932, the most frequent tree species were *Fagus grandifolia*, *Tsuga canadensis*, *Acer saccharum*, and *Acer rubrum* L. (Table 1). In 2018, *Fagus grandifolia* had a similar frequency as before, but *Tsuga canadensis* had declined by 30%, and *Acer saccharum* and *Acer rubrum* had increased by over 50%. *Acer saccharum* displaced *Tsuga canadensis* as the second-most-frequent species. Both *Castanea dentata* and *Sassafras albidum* showed declines as they were lost entirely from the plots.

The stem density of trees ≥ 5 cm dbh in A.B. Williams Woods increased by 50%, from 530 stems/ha in 1932 to 795 stems/ha in 2018 ($t = 3.943$, d.f. = 57, $P < 0.0001$). However, basal area remained similar at 55 m^2/ha ($t = 0.562$, d.f. = 47, $P = 0.576$). In 1932, *Tsuga canadensis* had the highest stem density, comprising 30% of all trees in the forest, followed by *Fagus grandifolia* (29%) and *Acer saccharum* (24%; Table 2, Fig. 1A). By 2018, *Fagus grandifolia* and *Acer saccharum* had supplanted *Tsuga canadensis* as the most abundant species. In 2018, *Fagus grandifolia* represented 43% of all trees in the forest, *Acer saccharum* 29%, and *Tsuga canadensis* only 12%.

Individual species showed dramatic changes in stem density from 1932 to 2018; the stem densities of *Fagus grandifolia* and *Acer saccharum* more than doubled (Table 2, Fig. 1A). The stem density of *Acer rubrum* tripled; *Fraxinus americana* L. increased five-fold; and *Nyssa sylvatica* Marshall

Table 1. Frequency of tree species in A. B. Williams Woods, Mayfield, OH in 1932 and 2018, expressed as the percentage of plots in which the species occurred. The table includes all species that occurred in at least 5% of the 58 plots in either year and considers only trees ≥ 5 cm diameter at breast height (dbh). Species are listed in descending order of their frequency in 1932. The P values are for G tests of independence comparing the proportions of plots where species were present and absent between the 2 yr. Significant differences in frequency between 1932 and 2018 are indicated as increases (+) or decreases (-). Marginally significant differences ($0.05 < P < 0.10$) are shown in parentheses.

Species	Freq. in 1932	Freq. in 2018	P	Change
<i>Fagus grandifolia</i> Ehrh.	0.72	0.79	0.3848	
<i>Tsuga canadensis</i> (L.) Carrière	0.62	0.43	0.0402	-
<i>Acer saccharum</i> Marshall	0.48	0.74	0.0040	+
<i>Acer rubrum</i> L.	0.22	0.38	0.0675	(+)
<i>Liriodendron tulipifera</i> L.	0.14	0.26	0.1009	
<i>Castanea dentata</i> (Marshall) Borkh.	0.10	0	0.0033	-
<i>Magnolia acuminata</i> (L.) L.	0.05	0.07	0.6961	
<i>Nyssa sylvatica</i> Marshall	0.05	0.12	0.1801	
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.05	0.03	0.6465	
<i>Prunus serotina</i> Ehrh.	0.05	0.09	0.4615	
<i>Quercus alba</i> L.	0.05	0.05	1	
<i>Quercus rubra</i> L.	0.05	0.09	0.4615	
<i>Sassafras albidum</i> (Nutt.) Nees	0.05	0	0.0395	-
<i>Fraxinus americana</i> L.	0.03	0.10	0.1344	

twenty-fold. Meanwhile, the stem density of *Tsuga canadensis* declined by half, and the stem density of *Castanea dentata* declined to zero. Despite its increase in stem density (Table 2), the basal area of *Fagus grandifolia* declined from 1932 to 2018 (Fig. 1B), indicating a preponderance of smaller trees. *Acer saccharum* had an increase in basal area consistent with its increase in stem density.

The density of saplings < 5 cm dbh decreased by 22% from 1932 to 2018 ($t = 1.831$, d.f. = 57, $P = 0.0361$). In 1932, *Acer saccharum* had the most saplings, representing 59% of all saplings, followed by *Tsuga canadensis* with 17%, whereas in 2018, *Fagus grandifolia* represented 70% of all saplings (Fig. 2). The density of *Fagus grandifolia*

saplings quadrupled from 1932 to 2018 ($t = 5.787$, d.f. = 57, $P < 0.0001$; Fig. 2). In contrast, the density of *Acer saccharum* saplings decreased threefold ($t = 5.284$, d.f. = 57, $P < 0.0001$), and *Tsuga canadensis* saplings decreased from 229 to only 1.1 stems/ha ($t = 4.883$, d.f. = 57, $P < 0.0001$).

The size structure (diameter distribution) of the *Fagus grandifolia* population changed significantly from 1932 to 2018, with a shift toward smaller trees ($G = 66.88$, d.f. = 5, $P < 0.0001$; Fig. 3B). In 1932, only 29% of all *Fagus grandifolia* trees were 5–15 cm dbh, whereas in 2018, 80% of all *Fagus grandifolia* trees belonged to this smallest size class. The propor-

Table 2. Stem density and basal area of tree species in A.B. Williams Woods, Mayfield, OH in 1932 and 2018. The table includes all species that occurred in at least 10% of the 58 plots in either year and considers only trees ≥ 5 cm diameter at breast height (dbh). Species are listed in descending order of their stem density in 1932. The P values are for paired t tests comparing stem density between 1932 and 2018. Significant differences in stem density between 1932 and 2018 are indicated as increases (+) or decreases (-). Marginally significant differences ($0.05 < P < 0.10$) are shown in parentheses.

Species	Stem density (stems/ha)		Basal area (m ² /ha)		P	Change
	1932	2018	1932	2018		
<i>Tsuga canadensis</i> (L.) Carrière	210	109	13.0	7.3	0.0010	-
<i>Fagus grandifolia</i> Ehrh.	142	319	22.2	17.9	< 0.0001	+
<i>Acer saccharum</i> Marshall	108	235	2.4	9.6	< 0.0001	+
<i>Acer rubrum</i> L.	16	48	2.0	2.0	0.0120	+
<i>Liriodendron tulipifera</i> L.	15	25	7.1	6.8	0.1830	
<i>Castanea dentata</i> (Marshall) Borkh.	6	0	0.6	0	0.0530	(-)
<i>Fraxinus americana</i> L.	4	23	0.6	0.2	0.0590	(+)
<i>Nyssa sylvatica</i> Marshall	0.6	12	0	2.4	0.0230	+

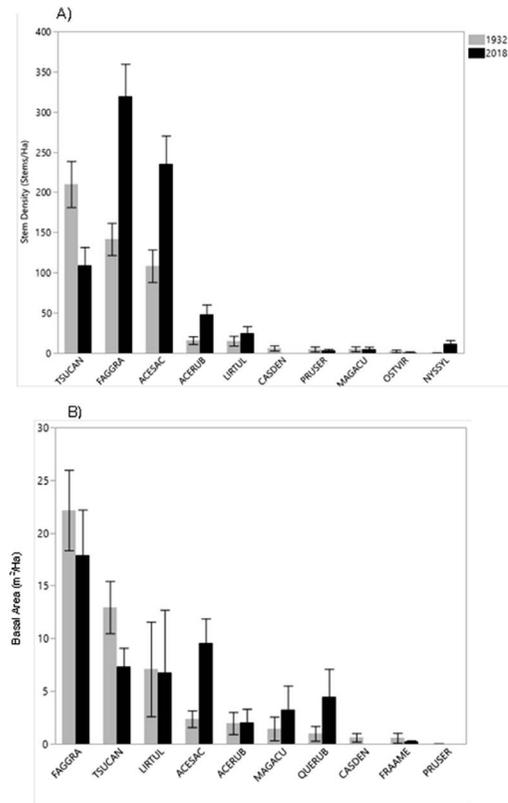


FIG. 1. (A) Stem density and (B) basal area (mean \pm SE) of tree species in A.B. Williams Woods, Mayfield, OH in 1932 and 2018, for trees ≥ 5 cm diameter at breast height (dbh). Each graph shows the top ten species in descending order of their importance in 1932. Species abbreviations are the first three letters of genus and species names, listed in Table 1. $N = 58$ plots for stem density and 48 plots for basal area.

tion of *Fagus grandifolia* trees ≥ 55 cm dbh also decreased by half. The size structure of *Tsuga canadensis* shifted in the opposite direction, toward larger trees ($G = 21.86$, d.f. = 5, $P = 0.0006$; Fig. 3C). In 1932, 55% of all *Tsuga canadensis* trees were 5–15 cm dbh; by 2018, only 21% of *Tsuga canadensis* trees belonged to this smallest size class. The size structure of *Acer saccharum* remained unchanged ($G = 7.393$, d.f. = 5, $P = 0.1930$; Fig. 3A).

By using NMS ordination, we explained 82% of the variation in tree community composition. Axis 1 described a gradient from *Acer saccharum* to *Tsuga canadensis* (Fig. 4A). *Quercus rubra* L. was also associated with *Tsuga canadensis*, whereas *Acer rubrum* and *Fraxinus americana* were

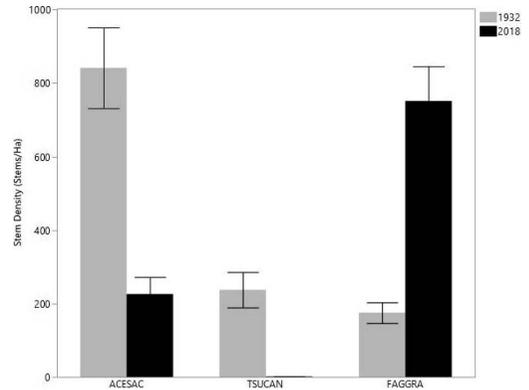


FIG. 2. Stem density (mean \pm SE) of saplings (< 5 cm diameter at breast height [dbh]) in A.B. Williams Woods, Mayfield, OH in 1932 and 2018, by species. The graph shows the top three species in descending order of their importance in 1932: *Acer saccharum* Marshall, *Tsuga canadensis* (L.) Carrière, and *Fagus grandifolia* Ehrh. $N = 58$ plots.

associated with *Acer saccharum*. Tree communities in 1932 and 2018 differed along this axis, with greater dominance by *Tsuga canadensis* in 1932 and greater dominance by *Acer saccharum* in 2018 ($t = 5.162$, d.f. = 57, $P < 0.0001$; Fig. 4B). Axis 2 described a gradient from low to high abundance of *Fagus grandifolia* (Fig. 4A). Tree communities in 1932 and 2018 differed along this axis as well, with greater *Fagus grandifolia* dominance in 2018 ($t = 2.498$, d.f. = 57, $P = 0.150$; Fig. 4B). Overall, plant communities in 1932 and 2018 differed significantly according to MRPP ($A = 0.0345$, $P < 0.0001$).

The strongest indicator species for 1932 (according to the magnitude of indicator values; Dufrene and Legendre 1997) were *Tsuga canadensis* and *Castanea dentata*, whereas the strongest indicator species for 2018 were *Fagus grandifolia*, *Acer saccharum*, *Acer rubrum*, and *Nyssa sylvatica* (all $IV > 10$, $P < 0.05$).

Plots with greater species richness in 1932 had higher rates of species turnover from 1932 to 2018 ($F = 6.3707$, d.f. = 1, 56, $P = 0.0145$). Species composition in 1932 did not affect species turnover rate. Plots with higher scores on ordination axis 1 in 1932 (i.e., greater dominance of *Tsuga canadensis*) showed greater compositional change from 1932 to 2018 ($F = 5.5004$, d.f. = 1, 56, $P = 0.0226$). Species richness and axis 2 scores did not affect the magnitude of compositional change.

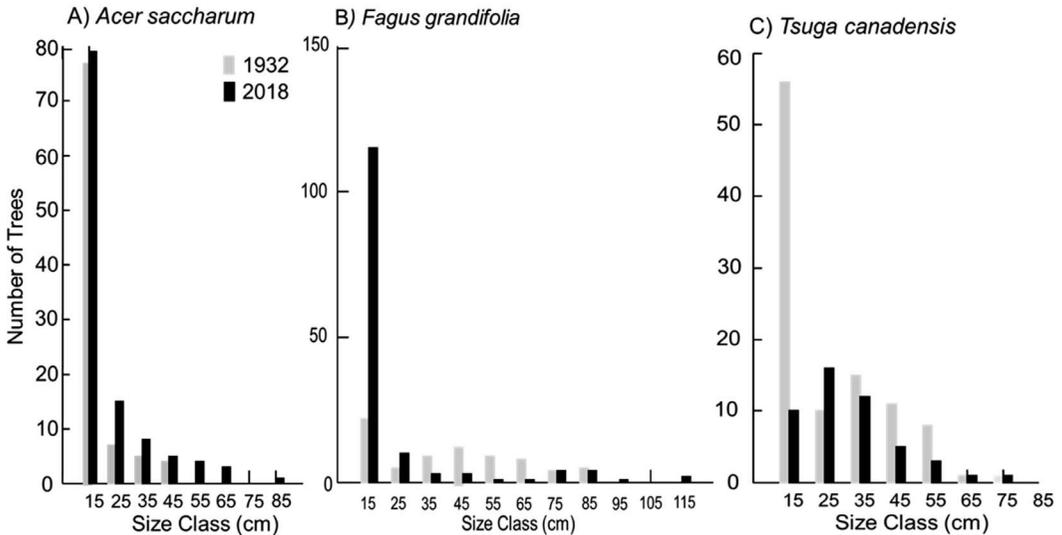


FIG. 3. Size structure (diameter distribution) of (A) *Acer saccharum* Marshall, (B) *Fagus grandifolia* Ehrh., and (C) *Tsuga canadensis* (L.) Carrière in A.B. Williams Woods, Mayfield, OH in 1932 and 2018, for trees ≥ 5 cm dbh. The X axis shows the upper limit of each size class for diameter at breast height (dbh) in cm.

Discussion. For an old-growth forest thought to represent “climax” vegetation and long protected from many human impacts such as logging, A.B. Williams Woods showed surprisingly major changes

in composition and structure. Species richness and diversity remained the same, which is consistent with global meta-analyses of resurvey studies (Vellend *et al.* 2013b, Bernhardt-

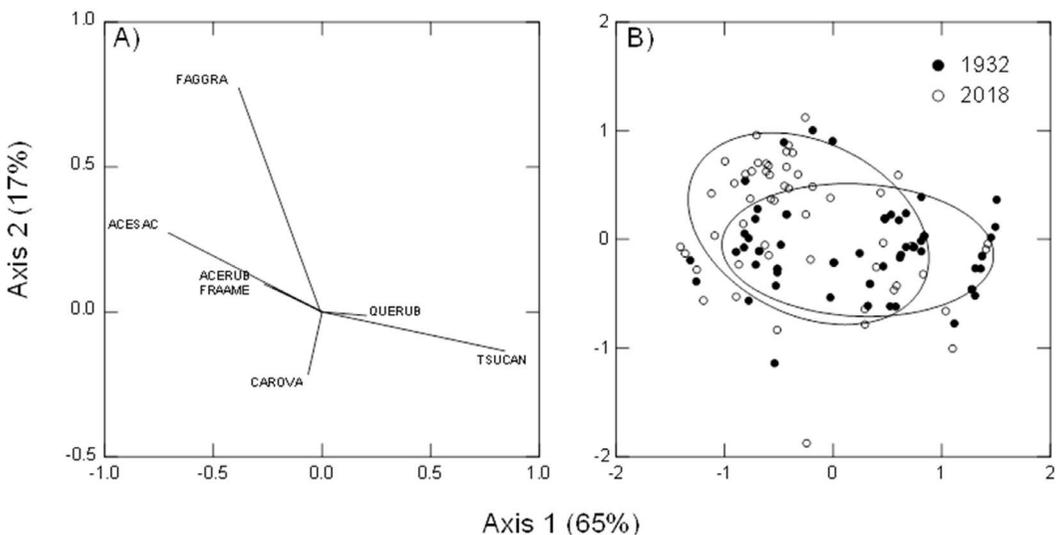


FIG. 4. Nonmetric multidimensional scaling (NMS) ordination of tree community composition (stem density of trees ≥ 5 cm diameter at breast height [dbh] in 1932 and 2018 in A.B. Williams Woods, Mayfield, OH. Axis labels indicate how much variation is explained by each axis. (A) Joint plot showing relationships between ordination axes and individual tree species. The angles and lengths of the vectors indicate the direction and strength of Pearson correlations between species’ axis scores and their stem density. The graph shows only species with correlations $|r| > 0.20$. Species abbreviations are the first three letters of genus and species names, listed in Table 1. (B) Locations of plots ($N = 58$) on ordination axes in 1932 and 2018, with 68% confidence ellipses for each year.

Römermann *et al.* 2015). As in several other studies, compositional changes were not driven by the introduction of exotic plant species (Keith *et al.* 2009; McCune and Vellend 2013; Johnson, Mudrak, and Waller 2014). However, native species abundances and community structure shifted dramatically.

The tree community changed exactly as Williams (1936) had predicted, with *Fagus grandifolia* and *Acer saccharum* displacing *Tsuga canadensis*. *Tsuga canadensis* declined in frequency and stem density, shifted away from smaller size classes, and had almost no saplings, continuing the pattern of decline and the lack of reproduction that Williams had observed in 1932. *Tsuga canadensis* comprised 30% of the forest's stems in 1932, 12% in 2018, and, given the lack of reproduction, it should continue to disappear. Plots dominated by *Tsuga canadensis* in 1932 showed the greatest magnitude of compositional change over time, with individual plots shifting from *Tsuga canadensis* to *Acer saccharum* dominance. The causes of this pronounced, long-term, and ongoing decline of *Tsuga canadensis* are unknown. Williams (1936) noted the presence of hemlock borer (*Phaenops fulvoguttata* Harris), but typically this beetle only attacks trees weakened by other pests or stresses (Evans 2000). Hemlock woolly adelgid (*Adelges tsugae* Annand) has not been observed in the area (Ohio Department of Natural Resources 2018). In Ohio, *Tsuga canadensis* occurs primarily in ravines (Black and Mack 1976), which border the study area, and it appears to be disappearing from the uplands bordering the ravines (K.M. Flinn, personal observation). Based on its restricted occurrence and association with other northern species, *Tsuga canadensis* in Ohio has been considered a relict of vegetation that moved north as the glaciers retreated, and might be in decline for this reason (although this view is controversial; Black and Mack 1976). The loss of *Tsuga canadensis* from this forest could have far-reaching implications for bird assemblages associated with *Tsuga canadensis* and other wildlife that eat its foliage and cones (Tingley *et al.* 2002).

Fagus grandifolia remained the most frequent and abundant tree species in the forest, while changing dramatically in size structure. Larger *Fagus grandifolia* trees died and were replaced by large numbers of root suckers. Therefore *Fagus grandifolia* is primarily responsible for the overall increase of the stem density of the stand, without

any concomitant increase in basal area. The vast majority of *Fagus grandifolia* trees now belong to the smallest size classes; the density of *Fagus grandifolia* saplings quadrupled, and 70% of all saplings belong to this species. Individual plots shifted toward *Fagus grandifolia* dominance due to the increase in density of small root suckers. This change in size structure might have resulted from larger trees suffering from fungal diseases. Although not as extreme, the stand might be approaching the thicket condition known as “beech hell” that characterizes forests impacted by beech bark disease (Cogbill 2005). However, beech bark disease has not affected this stand (MacKenzie and Iskra 2005). Beech leaf disease was discovered in northeast Ohio in 2012 (Pogancik and Macy 2016) and is now heavily impacting the stand (K.M. Flinn, personal observation), but this new disease cannot have been responsible for the shift in size structure. In fact, it kills small trees and can help to thin the *Fagus grandifolia* population. Alternatively, the death of larger trees and subsequent sprouting might have simply resulted from a cohort reaching advanced age at the same time.

In addition, *Fagus grandifolia* is less palatable to deer than *Tsuga canadensis* or *Acer saccharum*, which might contribute to its success with prolific sprouting (USDA Natural Resources Conservation Service 2018). As predicted, we observed a decline in saplings of more palatable species such as *Tsuga canadensis* and *Acer saccharum*. In fact, the abundance of small *Tsuga canadensis* trees in 1932 might have resulted from the lack of deer at that time. Deer were extirpated from Ohio by 1900; their populations began to rebound in the 1920s and 1930s. The subsequent increase in deer densities might have led to the current lack of *Tsuga canadensis* and *Acer saccharum* regeneration.

The other major “winner” over time was *Acer saccharum*, which increased greatly in frequency, stem density, and basal area, and came to dominate individual plots. This trend could reflect a pulse of *Acer saccharum* regeneration Williams observed in 1932, and it might not continue, because there are currently three times fewer *Acer saccharum* saplings than in 1932. *Acer rubrum* likewise increased in frequency and stem density. In fact, *Acer* species have increased dramatically in frequency and dominance throughout the region over the past 200 yr (Flinn, Mahany, and Hausman 2018). Similar increases in *Acer* have been

documented in the hemlock-hardwood forests of the Allegheny Plateau (Whitney 1990) and throughout the northeast and upper midwest United States (Schulte *et al.* 2007, Thompson *et al.* 2013). The present results suggest that this regional increase in *Acer* is caused not only by stand-replacing disturbances such as clear-cutting or conversion to postagricultural forests, but also by shifts within existing stands.

Prior to the arrival of chestnut blight in the early 1900s, *Castanea dentata* had been an important constituent of the forest, comprising 15% of trees in some areas, based on standing dead trees in 1932 (Williams 1936). By 1932, living *Castanea dentata* represented only 1% of stem density, and by 2018, it had disappeared. Williams (1936) hypothesized that *Castanea dentata* would have been eliminated even without blight, because *Fagus grandifolia* and *Acer saccharum* were invading the area dominated by *Tsuga canadensis*, *Quercus rubra*, and *Castanea dentata*, and because *Castanea dentata* had a lack of reproduction.

In sum, the composition and structure of this old-growth forest have been far from stable during the past century. Several species were lost or gained from the woody flora, but no exotic species arrived, and species richness and diversity remained constant. However, the relative abundances of species and the size structure of populations changed dramatically. In this way our study contrasts with studies of old-growth beech-maple forests that concluded the forests remained in a “climax” or equilibrium state (Abrell and Jackson 1977, Brewer and Merritt 1978). Rather, the changes we observed might be more consistent with a pattern of reciprocal replacement seen in other beech-maple forests (Woods 1979). Our study adds support to other studies of old-growth forests that reject the expectation of self-replacement (Runkle 2013, Schumacher and Carson 2013, Chapman and McEwan 2016). We provide a long-term, baseline estimate of compositional turnover in a plant community in the relative absence of anthropogenic disturbance, which is useful for comparison with changes caused by human impacts. Given the time scale of the directional changes we observed, even relatively undisturbed communities might be best viewed as not in equilibrium.

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