

Two decades of compositional and structural change in deciduous old-growth forests of Indiana, USA

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Abstract

Aims

Using a network of permanent plots, we determined how multiple old-growth forests changed over an 18–19-year period at a state-wide scale. This examination of change allowed us to assess how the compositional and structural stability of each forest varied with site characteristics (topography, physiography and productivity) and stochastic disturbance.

Methods

In 2011, we resampled 150 plots distributed across five old-growth hardwood forests in Indiana, USA that were originally sampled in 1992–1993. Within each plot, we relocated and remeasured the diameter at breast height (dbh) of all trees (≥ 10.0 cm) present during the 1992–1993 sample, which allowed us to track their individual fates through time for growth and mortality calculations. Trees that grew to ≥ 10.0 cm dbh since plot establishment were designated as ingrowth. The dbh and species of all saplings (stems ≥ 2.0 cm but < 10.0 cm dbh) were also recorded. For each forest, we calculated density (stems ha^{-1}), basal area (BA; $\text{m}^2 \text{ha}^{-1}$) and importance value (relative density + relative BA)/2 of trees by species. For saplings, density per ha was calculated by species for each forest. We also calculated annual mortality rate (AMR) for three diameter classes (10–29.9, 30–59.9 and ≥ 60 cm) and species richness (S), evenness (E) and Shannon–Weiner diversity (H') for the tree and sapling layers. Differences between years were compared for each forest using paired t -tests and Wilcoxon signed rank tests.

Important Findings

Although we observed commonality in changes across some sites, our results suggest that these forests differ in their rates and trajectories of change. Changes in total stand BA and density varied across sites and were influenced by past disturbance and mortality rates. We observed a general increase in the overstory dominance of *Acer saccharum* coupled with a general decrease in the dominance of *Quercus* section *Lobatae* (red oak group) species. Mortality of overstory trees present in 1992–1993 ranged from 27 to 49% over the study period (mean AMR 1.6–3.7%). Most sites experienced greater mortality of early and mid-successional species, but one site experienced heavy mortality of *Fagus grandifolia*, a shade-tolerant late-successional species. Shade tolerant species, *A. saccharum* in particular, dominated the sapling layer at most sites. However, recruitment of this species into larger size classes did not occur uniformly across all sites and the species was comparatively uncommon at one site. Overall, our results suggest that old-growth remnants, even within a single state, cannot be viewed as equivalent units with regard to research or management. Stochastic disturbance events and surrounding land use may have amplified effects on small scattered remnants. Therefore, continued monitoring of these rare, but biologically important forests is critical to their long-term management and protection.

Keywords: forest remnants, forest structure, long-term data, mortality, species diversity, stand development.

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INTRODUCTION

The definition of old-growth forest has evolved through time from as simple a definition as natural forests where no harvests have occurred (first growth; [Pinchot 1905](#)) to more contemporary definitions based on stand structure, species composition and ecosystem processes ([Frelich and Reich 2003](#); [Martin 1992](#); [Parker 1989](#); [Wirth *et al.* 2009](#)). Many modern process-based definitions or conceptual models of old-growth have centered upon concepts of structural and compositional stability, with old-growth offered as a relatively stable phase of forest development that will generally remain stable until altered by major disturbance ([Bormann and Likens 1979](#); [Frelich 2002](#); [Oliver and Larson 1996](#)). However, as concepts related to old-growth development and stability have been applied across geographic regions, debate has ensued about how these concepts apply across divergent species pools, physiography, edaphic characteristics and disturbance regimes. These debates have led to definitions of old-growth specific to a forest type or region ([Greenberg *et al.* 1997](#); [Spies 2004](#); [Tyrrell *et al.* 1998](#)), and have highlighted the need to monitor the variability and rates of change in structure and composition within and across regions. Such assessments are needed to identify commonalities and unique differences among these rare, but biologically important forests. While this type of information is critical to a scientific understanding of long-term forest dynamics, such knowledge may also have important practical ramifications considering the ability of old-growth forests to continually accumulate carbon and serve as critical long-term carbon sinks ([Luyssaert *et al.* 2008](#)) and serve as critical habitat for rare and threatened species ([Vandekerckhove *et al.* 2011](#)).

In landscapes fragmented by agriculture, urbanization and industrial development, old-growth forests typically exist as small isolated remnants that lack connectivity to other forests ([Spetich *et al.* 1997](#)). Consequently, these isolated remnants are more susceptible to wind storms, surrounding land use, invasive species, edge-influenced variation in vegetation and microclimate, and browsing by overabundant ungulate populations ([Frelich 2002](#); [Hurley *et al.* 2012](#); [Palik and Murphy 1990](#); [Schumacher and Carson 2013](#); [Wales 1972](#)). Within North America, the Central Hardwood Forest Region (CHFR) is an archetype example of a landscape fragmented by agricultural land use, expanding urban centers, industrial development and surface mining ([Hart 1968](#)). Within this region, old-growth forests are a rare occurrence ([Whitney and Somerlot 1985](#)) due to historical patterns of anthropogenic disturbances ([Den Uyl 1954](#)). For example, [Parker \(1989\)](#) estimated that only 607 ha of old-growth forests occur in Indiana, out of a total state-wide forest area of 2.06 million ha ([Indiana Department of Natural Resources 2010](#)). Although rare, these forests serve as critical reference conditions for comparison with actively managed and anthropogenically disturbed forests that dominate the contemporary forest landscape ([Whitney 1987](#); [McCarthy *et al.* 2001](#); [Frelich and](#)

[Reich 2003](#)). In addition, while little old-growth forest exists on the contemporary landscape of the CHFR, land management agencies across the region have set aside forest reserves with the expressed purpose of allowing their development into mature late-successional forests. For example, the forest plans for national forests in Illinois, Indiana, and Ohio call for nearly 50 000 ha to be set aside as future old or mature forest ([USDA Forest Service 2006a, 2006b, 2006c](#)). Also, over the past four decades silvicultural management has declined on many public lands, and if this trend continues, many of these forests will enter the old-growth stage of development ([Parker 1989](#); [Parker and Ruffner 2004](#); [Shifley *et al.* 2012, 2014](#)). Therefore, understanding how structure, composition, mortality and stand development vary within and among old-growth remnants is critical to understand the potential developmental trajectories of these maturing forests.

While old-growth forests in fragmented landscapes have garnered considerable attention from researchers, thereby greatly increasing our understanding of these forests, most long-term plot-based studies have focused on an individual forest ([Lin and Augspurger 2008](#); [McCune *et al.* 1988](#); [Morrissey *et al.* 2012](#); [Parker *et al.* 1985](#); [Runkle 2007, 2013](#); [Spetich and Parker 1998](#)), and few studies have tracked long-term changes across multiple sites ([Runkle 1998, 2000](#)). However, understanding long-term changes in these forests at broader spatial scales requires repeated sampling using standardized methodology applied across multiple forests. Data collected with such a design would better identify concurrent trends across a region and better illustrate the inherent variability of scattered forest remnants.

[Parker \(1989\)](#) defined old-growth forests within the CHFR as possessing: (i) trees greater than 150 years of age with little or no understory disturbance for the past 80–100 years, (ii) uneven age structure with multilayered canopies and (iii) stand structure consisting of multiple canopy gaps, dead snags, and large diameter down deadwood. Using these selection criteria, researchers from Purdue University and the USDA Forest Service established permanent vegetation plots across five old-growth forests in Indiana in 1992 and 1993 ([Table 1](#)). Thirty plots were established systematically in each forest (150 total) using a grid and sampled using a consistent and well-documented protocol ([Spetich 1995](#)). In 2011, we resampled all 150 plots to examine changes in these forests over an 18–19-year period. This standardized, unbiased sample design avoided many of the limitations of old-growth studies identified by [McCune and Menges \(1986\)](#), namely inadequate sample size, ‘big tree’ or other sampling bias and poorly documented sampling design that hinders subsequent resampling.

Based upon this resampling, we addressed the following questions:

- (1) How has the structure, species composition and species diversity of these forests changed over time?
- (2) How has annual mortality varied by species and size class across the five forests; how has this mortality influenced shifts in structure and composition?

Table 1: location and site descriptions of five remnant old-growth forests in Indiana, USA

Site	Location (lat/long)	Size (ha)	Geology/topography	Physiographic class	Tree ages	Potential site productivity ^a (m ³ ha ⁻¹ year ⁻¹)	Dominant cohort
Davis-Purdue	40°15' N, 85°9' W	21	Till plain with wet depressions	Mesic, wet-mesic to wet upland forest	132–300 ^b	5.5	<i>Quercus alba</i> , <i>Q. rubra</i>
Donaldson Woods	38°45' N, 86°25' W	27	Unglaciated karst	Mesic to dry-mesic upland forest	173–185 ^b	5.5	<i>Q. alba</i> , <i>Liriodendron tulipifera</i>
Hemmer Woods	38°14' N, 87°22' W	17	Driftless, glacial outwash	Mesic upland forest	141–208 ^b	4.5	<i>Q. alba</i> , <i>Q. velutina</i>
Laughery Bluff	39°3' N, 85° 12' W	15	Dissected ridges, karst	Mesic upland forest	132–292 ^b	6.0	<i>L. tulipifera</i> , <i>Fagus grandifolia</i>
Pioneer Mothers	38°32' N, 86° 27' W	15	Unglaciated sandstone over limestone karst	Mesic to dry-mesic upland forest	152–296 ^c	5.5	<i>F. grandifolia</i> , <i>L. tulipifera</i> , <i>Q. alba</i>

Abbreviations: dominant cohort = most common species for stems ≥ 60 cm dbh.

^aPotential site productivity values from Hansen et al. (1992), as presented in Spetich et al. (1999).

^bAge values from Spetich (1995) were determined in 1993 based upon limited sampling ranging from two trees at Donaldson Woods to 18 trees at Davis-Purdue.

^cAge values from Maxwell et al. (2014) were determined in 2012 based upon the sampling of 64 trees.

(3) What local environmental and/or disturbance factors have influenced differences observed among forests?

METHODS

Site descriptions

Between May 4 and September 18 2011, we resampled 150 permanent plots originally established in 1992–1993 in five old-growth forests across Indiana (Davis-Purdue, Donaldson Woods, Hemmer Woods, Laughery Bluff, and Pioneer Mothers; Table 1). All forests were in the old-growth stage of development as defined by Parker (1989). The forests varied in glacial history, parent material, potential productivity and dominant overstory species (Table 1). Potential productivity (as derived by Hansen et al. 1992) ranged from a low of 4.5 m³ ha⁻¹ year⁻¹ at Hemmer Woods, a forest dominated by *Quercus alba* and *Q. velutina*, to 6.5 m³ ha⁻¹ year⁻¹ at Laughery Bluff, a forest dominated by *Liriodendron tulipifera* and *Fagus grandifolia*. Davis-Purdue is managed by the Department of Forestry and Natural Resources at Purdue University and is surrounded on all sides by agricultural fields. Donaldson Woods is a nature preserve located within Spring Mill State Park, which buffers the old-growth forest on all sides. Hemmer Woods is also a state nature preserve, but the forest is surround by surface mining and agricultural fields. A third nature preserve, Laughery Bluff, is located within Versailles State Park. A wind storm occurred at this site two weeks prior to sampling in 1993, affecting approximately 30% of the site by creating gaps and taking down scattered mature trees, mostly *F. grandifolia* (M. Spetich, personal observation). As a result, Laughery Bluff had the lowest basal area (BA) of trees ≥ 60 cm dbh (8.8 ± 1.2 m² ha⁻¹; Table 2) during the 1993 sampling. Pioneer Mothers is part of the Hoosier National Forest and is managed by the USDA Forest Service as a Research Natural Area.

Each of the five forests contained 30 nested plots distributed on a pre-established grid. Grid dimensions were proportional to stand area, resulting in inter-plot distances ranging from 45 to 74 m. Each nested circular plot consisted of a 0.1 ha (17.84 m radius) plot and a concentric 0.01 ha subplot (5.64 m radius).

Field methods

Within each 0.1 ha plot, the diameter at breast height (dbh; 1.37 m above the ground) and species of all living and dead trees (≥ 10.0 cm dbh) were recorded. Trees present during the 1992–1993 sample were relocated based upon plot maps derived from distance and azimuth measurements from plot center collected during the original sampling. Relocating individual trees allowed us to track their fate through time for growth and mortality calculations. Trees that grew to ≥ 10.0 cm dbh since plot establishment were designated as ingrowth. Within the 0.01 ha subplot, the dbh and species of all saplings (stems ≥ 2.0 cm but < 10.0 cm dbh) were recorded.

Table 2: changes in mean (± 1 SE) density (stems ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$) of all stems, overstory, saplings and trees in three diameter classes (10–29.9 cm dbh, 30–59.9 cm dbh and ≥ 60 cm dbh) across five old-growth forests in Indiana between 1992–1993 and 2011

	Davis-Purdue		Donaldson Woods		Hemmer Woods		Laughery Bluff		Pioneer Mothers	
	1992	2011	1992	2011	1993	2011	1993	2011	1992	2011
All stems (≥ 2.0 cm dbh)										
Density (stems ha^{-1})	1360 \pm 72	1270 \pm 81	1232 \pm 133	1349 \pm 135	1485 \pm 142	1134 \pm 131	983 \pm 100	1307 \pm 132	1140 \pm 115	813 \pm 74
% Δ 1992–1993 (<i>P</i> value)		–7 (0.28)		9 (0.41)		–24 (0.02)		33 (0.07)		–29 (0.02)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	32.1 \pm 1.3	31.1 \pm 1.8	32.3 \pm 1.3	32.8 \pm 1.6	25.0 \pm 1.3	23.8 \pm 1.2	21.1 \pm 1.7	24.3 \pm 1.6	28.3 \pm 1.1	28.5 \pm 1.4
% Δ 1992–1993 (<i>P</i> value)		–3 (0.37)		2 (0.48)		–5 (0.23)		15 (0.01)		1 (0.54)
Overstory (≥ 10.0 cm dbh)										
Density (stems ha^{-1})	314 \pm 11	293 \pm 10	239 \pm 11	192 \pm 9	259 \pm 12	224 \pm 9	219 \pm 14	314 \pm 15	260 \pm 14	226 \pm 10
% Δ 1992–1993 (<i>P</i> value)		–7 (0.06)		–20 (<0.001)		–14 (0.01)		43 (<0.001)		–13 (0.003)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	30.3 \pm 1.3	28.7 \pm 1.9	31.1 \pm 1.3	31.3 \pm 1.6	22.7 \pm 1.3	21.9 \pm 1.2	19.6 \pm 1.7	22.7 \pm 1.7	27.2 \pm 1.1	27.5 \pm 1.5
% Δ 1992–1993 (<i>P</i> value)		–5 (0.21)		1 (0.54)		–4 (0.38)		16 (0.01)		1 (0.54)
Saplings (2.0–9.9 cm dbh)										
Density (stems ha^{-1})	1047 \pm 73	977 \pm 82	993 \pm 135	1157 \pm 140	1227 \pm 143	907 \pm 131	763 \pm 102	993 \pm 138	880 \pm 121	587 \pm 79
% Δ 1992–1993 (<i>P</i> value)		–7 (0.36)		17 (0.33)		–26 (0.04)		30 (0.21)		–33 (0.04)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	1.8 \pm 0.1	2.2 \pm 0.2	1.2 \pm 0.1	1.4 \pm 0.2	2.3 \pm 0.3	1.8 \pm 0.3	1.5 \pm 0.2	1.6 \pm 0.2	1.1 \pm 0.1	1.0 \pm 0.1
% Δ 1992–1993 (<i>P</i> value)		22 (0.06)		17 (0.28)		–22 (0.10)		7 (0.48)		–9 (0.41)
Trees (10–29.9 cm dbh)										
Density (stems ha^{-1})	228 \pm 10	212 \pm 9	143 \pm 11	95 \pm 8	185 \pm 10	152 \pm 10	152 \pm 11	236 \pm 14	162 \pm 14	130 \pm 10
% Δ 1992–1993 (<i>P</i> value)		–7 (0.17)		–34 (<0.001)		–18 (0.03)		55 (<0.001)		–20 (0.004)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	5.3 \pm 0.3	5.2 \pm 0.2	4.2 \pm 0.3	3.0 \pm 0.3	3.7 \pm 0.3	3.4 \pm 0.2	3.7 \pm 0.3	5.8 \pm 0.3	4.3 \pm 0.4	3.8 \pm 0.3
% Δ 1992–1993 (<i>P</i> value)		–2 (0.50)		–29 (0.001)		–8 (0.3)		57 (<0.001)		–12 (0.07)
Trees (30–59.9 cm dbh)										
Density (stems ha^{-1})	52 \pm 6	51 \pm 7	58 \pm 5	62 \pm 4	46 \pm 4	47 \pm 5	48 \pm 5	59 \pm 6	69 \pm 5	68 \pm 5
% Δ 1992–1993 (<i>P</i> value)		–2 (0.57)		7 (0.25)		2 (0.58)		23 (0.047)		–1 (0.57)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	7.9 \pm 0.8	7.4 \pm 0.9	8.7 \pm 0.8	9.2 \pm 0.7	7.3 \pm 0.6	6.6 \pm 0.7	7.2 \pm 0.6	7.9 \pm 0.8	9.6 \pm 0.7	9.8 \pm 0.8
% Δ 1992–1993 (<i>P</i> value)		–6 (0.35)		6 (0.30)		–10 (0.33)		10 (0.24)		2 (0.55)
Trees (≥ 60 cm dbh)										
Density (stems ha^{-1})	34 \pm 4	30 \pm 4	37 \pm 3	35 \pm 3	28 \pm 3	25 \pm 2	19 \pm 3	19 \pm 3	30 \pm 3	28 \pm 3
% Δ 1992–1993 (<i>P</i> value)		–12 (0.18)		–5 (0.25)		–11 (0.23)		0 (0.60)		–7 (0.42)
Basal area ($\text{m}^2 \text{ha}^{-1}$)	17.1 \pm 1.8	16.3 \pm 3.3	18.2 \pm 1.4	19.1 \pm 1.7	11.8 \pm 1.3	11.9 \pm 1.2	8.8 \pm 1.2	8.9 \pm 1.6	13.3 \pm 1.3	13.8 \pm 1.6
% Δ 1992–1993 (<i>P</i> value)		–5 (0.48)		5 (0.34)		1 (0.59)		1 (0.58)		4 (0.49)

Means between sample intervals were compared with paired *t*-tests. *P* values were adjusted for multiple comparisons with a graphically sharpened procedure to control the false discovery rate (Benjamini and Hochberg 1995).

Data preparation and analysis

For each forest, we grouped woody vegetation into three broad classes: (i) all stems (≥ 2.0 cm dbh), (ii) overstory trees (≥ 10.0 cm dbh) and (iii) saplings (2.0–9.9 cm dbh). Overstory trees were

further divided into three diameter classes: (i) 10–29.9 cm dbh, (ii) 30–59.9 cm dbh and (iii) ≥ 60 cm dbh for examinations of structure and mortality. For all classes, we calculated density (trees ha^{-1}) and BA ($\text{m}^2 \text{ha}^{-1}$) by species, using mean plot

values ($n = 30$) for each forest. For each overstory species, we calculated relative density (total density of a species on a plot/total density of all species on a plot) and relative BA (total BA of a species on a plot/total BA of all species on a plot) and used those values to derive importance value [IV; (relative density + relative BA)/2]. For saplings within each forest, we calculated density per ha by species, using the mean plot values. Because we did not include data for stems <2 cm dbh, we were unable to examine changes in seedling-size individuals. Species nomenclature follows the USDA Natural Resource Conservation Service Plants Database nomenclature (USDA NRCS 2015). For each forest, we calculated annual mortality rate (AMR) for the three overstory diameter classes (10–29.9 cm, 30–59.9 cm, and ≥ 60 cm) with the formula: $AMR = 1 - [1 - (M_1/N_0)]^{1/t}$ where N_0 is the number of trees alive in the 1992–1993 census, M_1 is the number of trees that died between 1992–1993 and 2011, and t is the time between censuses in years (Lutz and Halpern 2006). We also calculated species richness (S), evenness (E) and Shannon–Weiner diversity (H') for the overstory and sapling layers (McCune and Mefford 2006), using IV and relative density, respectively, as input data. Mean plot values ($n = 30$) were calculated for each forest.

Changes in total BA and total density of all stems between 1992–1993 and 2011 at each forest were analyzed using paired t -tests. Changes in the BA and density of trees (stems ≥ 10 cm dbh) from the five most dominant species across the five forests (*Acer saccharum*, *L. tulipifera*, *Q. rubra*, *Q. alba* and *F. grandifolia*) were compared for each forest using Wilcoxon signed rank tests. Wilcoxon signed rank tests were also used to compare changes in IV and sapling density of selected focal species at selected sites. This test was used because our individual species data did not respond to transformations used to improve normality due to a large number of zero values. Means ± 1 standard error are presented in tables and figures for ease of interpretation. Because of the large number of statistical tests performed, we used the spreadsheet provided by Pike (2011) to adjust P values (q values, Pike 2011) with a graphically sharpened procedure based on control of the false discovery rate (FDR; Benjamini and Hochberg 1995, 2000). In recent years, multiple comparison techniques based upon FDR have been used more frequently in ecological studies as an alternative to traditional controls of family-wise error rate because FDR-based techniques retain statistical power while keeping the proportion of false discoveries small relative to all significant results (Pike 2011; Verhoeven et al. 2005). Overstory and sapling S, E and H' were compared using paired t -tests because these data conformed better to assumptions of normality.

RESULTS

Stand density and BA

In 2011, over 5100 live stems, consisting of 54 different species, were measured on 150 plots (15 ha total sampled area) distributed across the five Indiana old-growth forests, compared to over 5300 live stems from 52 species in 1992–1993.

In these forests, mean density of all stems (≥ 2.0 cm dbh) in 1992–1993 ranged from 983 ± 100 stems ha^{-1} (mean \pm SE) at Laughery Bluff to 1485 ± 142 stems ha^{-1} at Hemmer Woods. In 2011, density (stems ha^{-1}) ranged from 813 ± 74 at Pioneer Mothers to 1349 ± 135 stems at Donaldson Woods (Table 2). Two forests, Hemmer Woods and Pioneer Mothers, experienced significant decreases ($P = 0.013$ for both forests) in density of all stems between sampling events, 24 and 29%, respectively (Table 2). In 1992–1993, mean BA of all stems ranged from 21.1 ± 1.7 $m^2 ha^{-1}$ at Laughery Bluff to 32.3 ± 1.3 $m^2 ha^{-1}$ at Donaldson Woods. In 2011, BA ranged from 23.8 ± 1.2 $m^2 ha^{-1}$ at Hemmer Woods to 32.8 ± 1.6 $m^2 ha^{-1}$ at Donaldson Woods (Table 2). Only Laughery Bluff experienced a significant change in BA (15% increase, $P = 0.001$; Table 2).

In 1992–1993, mean density of overstory trees (≥ 10.0 cm dbh) ranged from 219 ± 14 stems ha^{-1} at Laughery Bluff to 314 ± 11 stems ha^{-1} at Davis-Purdue. In 2011, overstory density (stems ha^{-1}) ranged from 192 ± 9 at Donaldson Woods to 314 ± 15 at Laughery Bluff (Table 2). Four of the forests, Davis-Purdue, Donaldson Woods, Hemmer Woods and Pioneer Mothers, exhibited significant decreases in density ranging from 7 to 20%. In contrast, Laughery Bluff experienced a 43% increase ($P \leq 0.001$) in overstory density (Table 2).

In 1992–1993, mean overstory BA ranged from 19.6 ± 1.7 $m^2 ha^{-1}$ at Laughery Bluff to 31.1 ± 1.3 $m^2 ha^{-1}$ at Donaldson Woods. In 2011, overstory BA ranged from 21.9 ± 1.2 $m^2 ha^{-1}$ at Hemmer Woods to 31.3 ± 1.6 $m^2 ha^{-1}$ at Donaldson Woods (Table 2). Between sampling events, overstory BA changed little in most forests; Laughery Bluff was the only forest to exhibit a significant change in overstory BA, increasing 16% (from 19.6 ± 1.7 to 24.3 ± 1.6 $m^2 ha^{-1}$; $P = 0.001$).

Observed changes in overstory density were largely driven by changes in the density of trees 10–29.9 cm dbh. Donaldson Woods (-34% ; $P < 0.001$), Hemmer Woods (-18% ; $P = 0.03$) and Pioneer Mothers (-20% ; $P = 0.004$) all exhibited significant decreases in density of this size class, while Laughery Bluff exhibited a 55% ($P < 0.001$) increase. BA also decreased at Donaldson Woods (-29% ; $P = 0.001$) and Pioneer Forest (-12% ; $P = 0.07$), but increased 57% at Laughery Bluff ($P < 0.001$). Density of stems 30–59.9 cm dbh increased 23% at Laughery Bluff ($P = 0.047$). We observed no significant changes in density or BA of trees >60 cm dbh.

In 1992–1993, mean sapling (stems 2.0–9.9 cm dbh) density ranged from 763 ± 102 stems ha^{-1} at Laughery Bluff to 1227 ± 143 stems ha^{-1} at Hemmer Woods. In 2011, sapling density ranged from 587 ± 79 stems ha^{-1} at Pioneer Mothers to 1157 ± 140 stems ha^{-1} at Donaldson Woods (Table 2). Between 1992–1993 and 2011, sapling density decreased significantly at Hemmer Woods and Pioneer Mothers (26%, $P = 0.04$ and 33%, $P = 0.04$, respectively; Table 2).

Overstory BA, density and importance of dominant species

Changes in the BA and density of individual overstory species highlighted changes in the composition of these forests

(Fig. 1). Across all five forests, the BA of *A. saccharum* increased between sampling events. These increases in BA corresponded to increases in *A. saccharum* density in three forests: Davis-Purdue, Hemmer Woods and Laughery Bluff. Density of *A. saccharum* decreased at the other two forests. Changes in *A. saccharum* BA and density were greatest at Laughery Bluff, where BA of the species increased by 73% and density increased by 78%. These changes in BA and density drove a general increase in the importance value (IV) of this species across the five sites. This increase was most pronounced at Hemmer Woods (64%), Davis-Purdue (56%) and Laughery Bluff (30%; Table 3). However, even with this increase, the

IV of *A. saccharum* at Hemmer Woods was still only 7.4 ± 2.0 in 2011.

Quercus species exhibited a general decline in BA and density across the five forests (Fig. 1). *Quercus rubra* BA declined 47% ($P = 0.004$) and density declined 20% ($P = 0.012$) at Davis-Purdue. The density of *Q. rubra* also declined significantly at Hemmer Woods (45%, $P = 0.048$). The IV of this species declined at Davis-Purdue ($P = 0.02$, Table 3). *Quercus alba* BA did not change significantly across sites, but density of this species declined significantly at Davis-Purdue (23%, $P = 0.04$), Donaldson Woods (21%, $P < 0.001$) and Hemmer Woods (22%, $P < 0.001$). We observed decreases in the IV

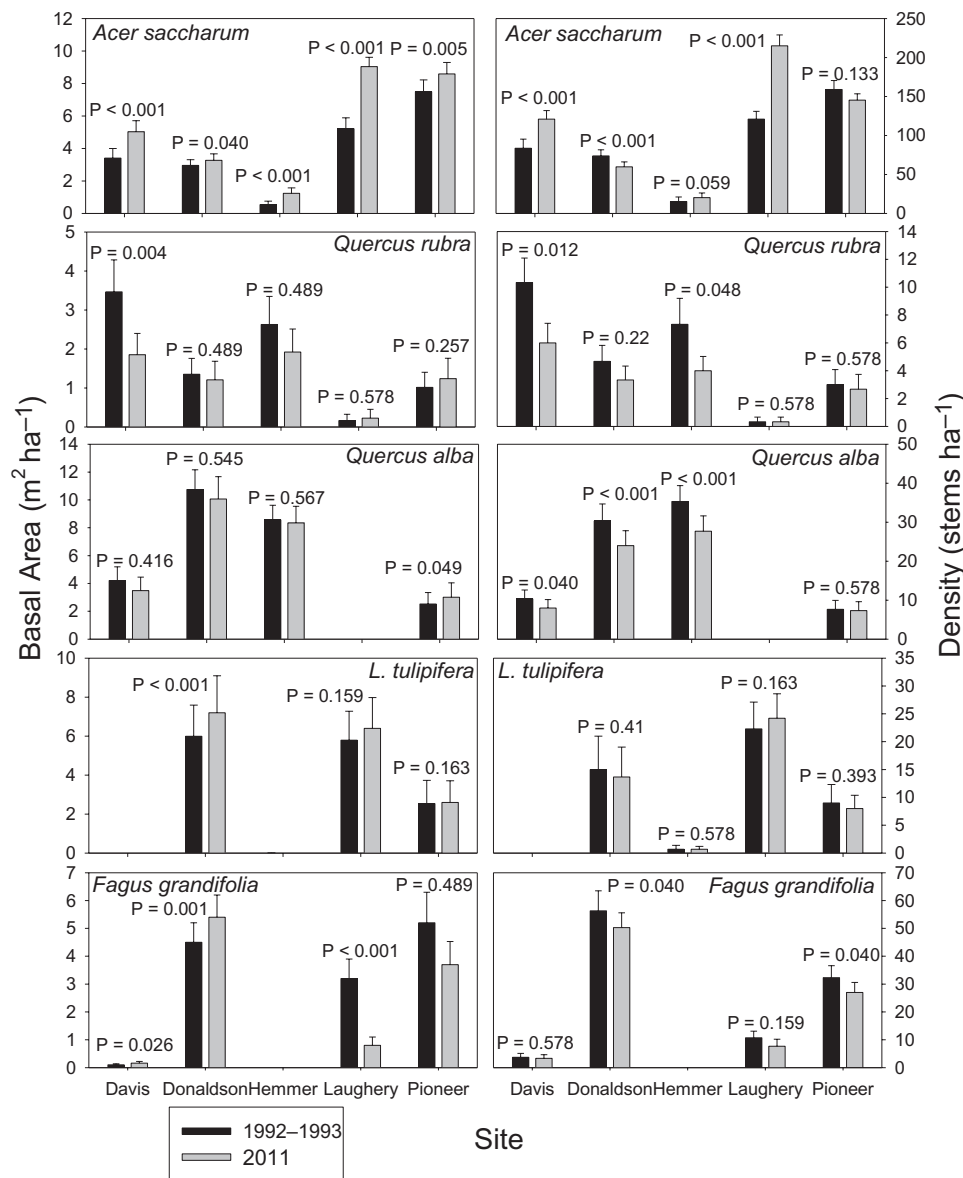


Figure 1: changes in mean (± 1 SE) basal area (m² ha⁻¹) and density (stems ha⁻¹) of five common trees species (stems ≥ 10 cm dbh) across five old-growth forest in Indiana between 1992-1993 and 2011. Means between sample intervals were compared with Wilcoxon signed rank tests. P values were adjusted for multiple comparisons with a graphically sharpened procedure to control the false discovery rate (Benjamini and Hochberg 1995).

Table 3: importance value (mean \pm 1 SE for stems ≥ 10 cm dbh) of common tree species across five old-growth forest remnants in Indiana, USA in 1992–1993 and 2011

Species	Davis-Purdue		Donaldson Woods		Hemmer Woods		Laughery Bluff		Pioneer Mothers	
	1992/1993	2011	1992/1993	2011	1992/1993	2011	1992/1993	2011	1992/1993	2011
<i>Acer rubrum</i>	0.3 \pm 0.2	0.6 \pm 0.4	4.0 \pm 1.1	3.0 \pm 1.1	0.1 \pm 0.1	0.5 \pm 0.2	0.1 \pm 0.1	—	—	—
<i>A. saccharum</i>	20.4 \pm 2.9	31.8 \pm 3.4	20.4 \pm 2.2	21.2 \pm 2.4	4.5 \pm 1.6	7.4 \pm 2.0	43.3 \pm 3.1	56.2 \pm 2.4	44.7 \pm 2.5	49.1 \pm 2.5
<i>Aesculus glabra</i>	2.8 \pm 0.7	2.6 \pm 0.5	—	—	—	—	—	—	—	—
<i>Carya cordiformis</i>	2.2 \pm 0.6	1.9 \pm 0.6	0.7 \pm 0.4	1.0 \pm 0.6	1.0 \pm 0.7	1.2 \pm 0.8	—	0.1 \pm 0.1	0.6 \pm 0.3	0.6 \pm 0.4
<i>C. glabra</i>	1.5 \pm 0.5	1.5 \pm 0.5	2.5 \pm 0.7	1.5 \pm 0.6	2.3 \pm 0.8	2.3 \pm 0.8	—	—	1.3 \pm 0.7	1.6 \pm 0.9
<i>C. laciniosa</i>	—	—	—	—	2.9 \pm 1.0	3.2 \pm 1.2	0.2 \pm 0.2	0.2 \pm 0.2	3.8 \pm 0.9	3.9 \pm 0.9
<i>C. ovata</i>	5.6 \pm 1.1	5.0 \pm 1.1	2.4 \pm 0.7	1.9 \pm 0.7	2.7 \pm 0.8	3.5 \pm 1.2	—	—	—	—
<i>C. tomentosa</i>	0.2 \pm 0.1	0.2 \pm 0.2	0.1 \pm 0.1	0.1 \pm 0.1	2.1 \pm 0.6	2.7 \pm 0.9	—	—	—	—
<i>Celtis occidentalis</i>	3.2 \pm 0.9	3.2 \pm 1.1	0.2 \pm 0.2	0.2 \pm 0.2	1.6 \pm 0.5	3.1 \pm 0.6	2.2 \pm 0.8	2.5 \pm 0.8	0.8 \pm 0.3	0.7 \pm 0.4
<i>C. canadensis</i>	—	—	—	—	1.3 \pm 0.7	2.6 \pm 0.8	—	0.1 \pm 0.1	—	—
<i>Cornus florida</i>	—	—	0.7 \pm 0.2	0.1 \pm 0.1	16.8 \pm 1.5	5.1 \pm 1.0	1.7 \pm 0.6	0.2 \pm 0.1	0.3 \pm 0.1	0.6 \pm 0.6
<i>Fagus grandifolia</i>	0.8 \pm 0.3	1.0 \pm 0.4	20.5 \pm 2.9	23.8 \pm 3.1	—	—	11.2 \pm 2.2	2.9 \pm 0.9	16.8 \pm 3.0	13.5 \pm 2.3
<i>Fraxinus americana</i>	1.7 \pm 0.6	1.7 \pm 0.7	2.3 \pm 0.6	2.3 \pm 0.7	3.3 \pm 1.2	2.7 \pm 1.2	—	6.3 \pm 1.6	2.5 \pm 0.7	2.0 \pm 0.7
<i>F. pennsylvanica</i>	4.7 \pm 1.5	4.5 \pm 1.5	0.1 \pm 0.1	0.4 \pm 0.4	—	—	—	—	—	—
<i>Juglans nigra</i>	3.4 \pm 0.8	3.0 \pm 0.9	0.1 \pm 0.1	—	—	—	5.0 \pm 1.6	4.3 \pm 1.4	4.7 \pm 1.3	3.7 \pm 1.2
<i>Liriodendron tulipifera</i>	—	—	11.6 \pm 3.2	13.0 \pm 3.3	0.1 \pm 0.1	0.2 \pm 0.1	16.3 \pm 3.3	14.2 \pm 2.7	5.7 \pm 2.2	5.9 \pm 1.8
<i>Nyssa sylvatica</i>	—	—	1.8 \pm 0.6	1.3 \pm 0.6	0.1 \pm 0.1	0.1 \pm 0.1	2.7 \pm 1.4	1.7 \pm 0.8	0.2 \pm 0.1	0.1 \pm 0.1
<i>Prunus serotina</i>	1.3 \pm 0.4	0.6 \pm 0.2	—	—	1.6 \pm 0.6	1.5 \pm 0.6	1.4 \pm 0.5	2.2 \pm 0.6	0.5 \pm 0.3	0.3 \pm 0.3
<i>Quercus alba</i>	7.9 \pm 1.7	6.4 \pm 1.7	23.7 \pm 3.0	21.6 \pm 3.2	25.8 \pm 2.9	24.7 \pm 3.1	—	—	5.6 \pm 1.6	6.1 \pm 1.9
<i>Q. bicolor</i>	3.0 \pm 1.6	0.8 \pm 0.4	—	—	—	—	—	—	—	—
<i>Q. macrocarpa</i>	5.5 \pm 1.8	5.4 \pm 1.8	—	—	—	—	—	—	—	—
<i>Q. muehlenbergii</i>	3.4 \pm 0.9	3.9 \pm 1.1	0.2 \pm 0.2	0.1 \pm 0.1	—	—	—	—	—	—
<i>Q. rubra</i>	7.5 \pm 1.6	4.5 \pm 1.2	3.3 \pm 0.9	2.8 \pm 1.0	7.2 \pm 1.8	5.3 \pm 1.5	0.4 \pm 0.4	0.4 \pm 0.4	2.5 \pm 1.0	2.8 \pm 1.2
<i>Q. shumardii</i>	4.4 \pm 1.5	4.1 \pm 1.6	—	—	—	—	0.2 \pm 0.2	0.3 \pm 0.3	—	—
<i>Q. velutina</i>	—	—	4.2 \pm 1.3	3.2 \pm 1.4	11.2 \pm 2.1	8.9 \pm 2.0	—	—	4.1 \pm 1.4	2.9 \pm 1.0
<i>Sassafras albidum</i>	—	—	0.3 \pm 0.2	0.1 \pm 0.1	5.4 \pm 1.7	8.1 \pm 2.0	0.6 \pm 0.4	1.2 \pm 0.6	0.4 \pm 0.2	0.3 \pm 0.2
<i>Ulmus americana</i>	6.0 \pm 1.0	4.7 \pm 0.9	0.1 \pm 0.1	0.5 \pm 0.3	2.7 \pm 0.9	2.8 \pm 1.0	0.5 \pm 0.3	0.4 \pm 0.2	—	—
<i>U. rubra</i>	5.4 \pm 1.0	3.2 \pm 0.6	0.3 \pm 0.2	1.2 \pm 0.5	6.1 \pm 1.1	12.0 \pm 1.8	5.7 \pm 1.5	4.3 \pm 1.0	0.8 \pm 0.4	1.3 \pm 0.7

Values were calculated from data collected on 30 plots at each site.

of *Q. bicolor* at Davis-Purdue (3.0 \pm 1.6 to 0.8 \pm 0.4, $P = 0.08$) and *Q. velutina* at Hemmer Woods (11.2 \pm 2.1 to 8.9 \pm 2.0, $P = 0.08$).

While *L. tulipifera* was an important species at three of the forests, it displayed little change in BA and density (Fig. 1). BA of this species increased 20% ($P < 0.001$) at Donaldson Woods, but displayed no other significant changes. Importance value of this species changed little across sites (Table 3). Changes in the BA and density of *F. grandifolia* varied across the five forests. BA of *F. grandifolia* increased at Davis-Purdue (from 0.1 \pm 0.04 to 0.16 \pm 0.06 m² ha⁻¹, $P = 0.026$), although the species was uncommon across the forest (Table 3). *F. grandifolia* BA also increased at Donaldson Woods (from 4.5 \pm 0.7 to 5.4 \pm 0.8 m² ha⁻¹, 20%, $P = 0.001$), but density declined slightly (11%, $P = 0.04$), driving a small increase in IV (Table 3). Laughery Bluff exhibited a dramatic decrease in the BA of this species (75%, $P < 0.001$), but density did not change ($P = 0.159$). Importance value of *F. grandifolia* declined

dramatically at Laughery Bluff (from 11.2 \pm 2.2 to 2.9 \pm 0.9, $P = 0.001$, Table 3).

Mortality

Many of the trees present in these forests in 1992–1993 died by 2011. Total mortality of overstory trees in these forests ranged from 27 to 49% over this 18–19-year study period. Hemmer Woods experienced the greatest AMR for overstory trees (3.7%), which was much greater than Davis-Purdue (2.1%), Donaldson Woods (1.7%), Laughery Bluff (1.8%) and Pioneer Mothers (1.6%).

Annual mortality differed among size classes and species across the five forests (Fig. 2). Among stems 10–29.9 cm dbh, mortality was highest for *Cornus florida*, which experienced 10.4% annual mortality at Hemmer Woods, where its high density resulted in an IV second only to *Q. alba* in 1992–1993. This species experienced 100% mortality at Donaldson Woods and Pioneer Mothers, but sampled plots only contained a

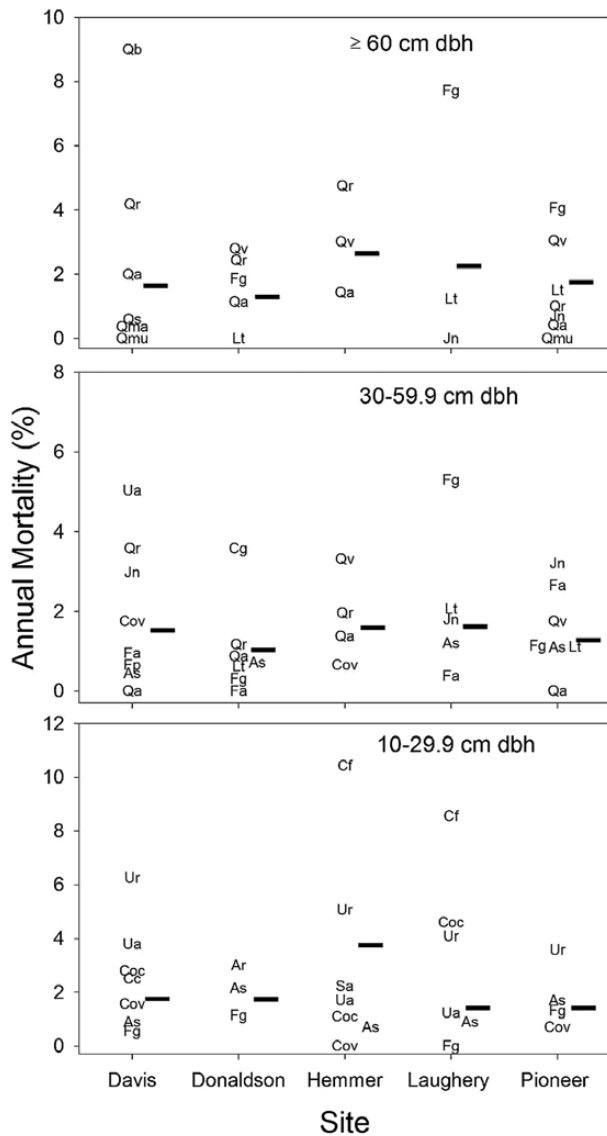


Figure 2: annual mortality of woody species in three diameter classes: (1) 10–29.9, (2) 30–59.9 and (3) ≥ 60 cm dbh. Mortality calculated from individual tree data collected in 1992–1993 and 2011. Class 1 includes species with at least 30 stems at one or more sites. Classes 2 and 3 include species with at least seven stems at one or more sites. Horizontal bars represent mean mortality across all species at a site within each diameter class. Mortality of *Cornus florida* was 100% across the study period at Hemmer Woods and Pioneer Mothers. Ar = *Acer rubrum*, As = *Acer saccharum*, Cc = *Carya cordiformis*, Cf = *Cornus florida*, Cg = *Carya glabra*, Coc = *Celtis occidentalis*, Cov = *Carya ovata*, Fa = *Fraxinus americana*, Fp = *Fraxinus pennsylvanica*, Fg = *Fagus grandifolia*, Jn = *Juglans nigra*, Lt = *Liriodendron tulipifera*, Qa = *Quercus alba*, Qb = *Quercus bicolor*, Qma = *Quercus macrocarpa*, Qmu = *Quercus muehlenbergii*, Qr = *Quercus rubra*, Qs = *Quercus shumardii*, Qv = *Quercus velutina*, Sa = *Sassafras albidum*, Ua = *Ulmus americana*, Ur = *Ulmus rubra*

total of 10 and five *C. florida* trees ≥ 10 cm dbh, respectively (data not shown). At four out of five sites (Davis-Purdue, Hemmer Woods, Laughery Bluff and Pioneer Mothers), overstory *Ulmus rubra* trees experienced annual mortality ranging

from 3.6% at Pioneer Mothers to 6.4% at Davis-Purdue. Mortality among *U. rubra* stems 10–29.9 cm dbh was greatest at Hemmer Woods (4.6%), which was double that of the forest with the next greatest annual mortality for this diameter class (Davis-Purdue, 2.3%).

Among stems 30–59.9 cm dbh, we observed more variability in annual species mortality across forests (Fig. 2). At Davis-Purdue, *U. americana*, *Q. rubra* and *Juglans nigra* experienced the greatest annual mortality. At Donaldson Woods, *Carya glabra* exhibited the greatest annual mortality (3.6%); mortality of all other common species was less than 2%. *Q. velutina* exhibited the greatest mortality at Hemmer Woods (3.3%), followed by *Q. rubra* (2.0%), and *Q. alba* (1.4%). *F. grandifolia* annual mortality was greatest of all species at Laughery Bluff (5.3%), followed by *L. tulipifera* (2.1%) and *J. nigra* (1.8%). At Pioneer Mothers, annual mortality was greatest for *J. nigra* (3.2%), followed by *Fraxinus americana* (2.7%) and *Q. velutina* (1.8%). Overall mortality in this diameter class (30–59.9 cm dbh) was low compared to other classes and similar between forests, ranging from 1.2% at Pioneer Mothers to 1.7% at Laughery Bluff.

With the exception of Laughery Bluff, mortality in the largest (≥ 60 cm dbh) diameter class was greatest among *Quercus* species (Fig. 2). *Quercus bicolor* annual mortality was 9% (based upon 10 original trees) at Davis-Purdue, followed by *Q. rubra* (4.2%) and *Q. alba* (2.1%). At Donaldson Woods, we observed the greatest mortality for *Q. velutina* (2.8%), followed closely by *Q. rubra* (2.4%). At Hemmer Woods, *Q. rubra* exhibited 4.7% mortality, followed by *Q. velutina* (3.0%) and *Q. alba* (1.4%). As observed also in the smaller 30–59.9 cm dbh class, *F. grandifolia* mortality was high at Laughery Bluff (7.7%). Overall mortality of trees ≥ 60 cm diameter ranged from 1.2% at Donaldson Woods to 2.6% at Hemmer Woods.

Species diameter distributions

Observed differences in mortality among the five forests were exemplified by changes in the diameter distributions of dominant species (Figs 3–5). Across the four sites with a large component of *Quercus* species (Davis-Purdue, Donaldson Woods, Hemmer Woods and Pioneer Mothers), we observed a general decrease in the density of *Q. rubra* across 5-cm diameter classes (Fig. 3), resulting in a flattening of the roughly bell-shaped curves. While Pioneer Mothers exhibited some recruitment of individual *Q. rubra* stems into larger classes, the other three forests showed a decline in most classes. In particular, the decline in *Q. rubra* abundance across diameter classes was highly pronounced at Hemmer Woods. While the bell-shaped diameter distributions of *Q. alba* showed overall reductions in abundance across classes, progression into larger diameter classes was also evident. Across forests, our results showed little or no ingrowth of *Quercus* species from the sapling layer.

For shade-tolerant *A. saccharum*, our results showed the expected reverse-j diameter distributions for the five forests

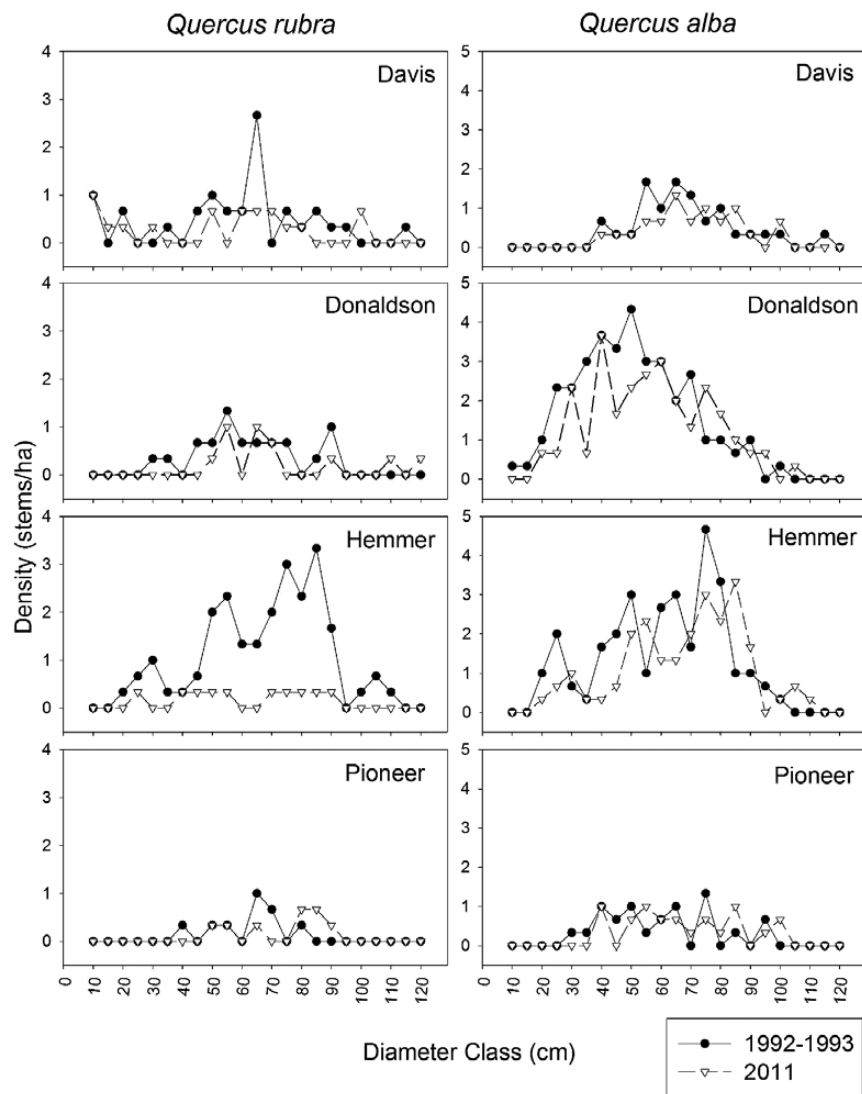


Figure 3: diameter distributions (stems ha^{-1}) of *Quercus rubra* and *Q. alba* across four old-growth forests in Indiana between 1992–1993 and 2011. Data are not shown for Laughery Bluff because *Q. alba* IV was <1 at the site. Trees are grouped in 5 cm diameter classes.

(Fig. 4). However, we observed a lower abundance of *A. saccharum* in smaller diameter classes at Donaldson Woods and Hemmer Woods than at the other three sites. We observed an increase in abundance in diameter classes <20 cm at Laughery Bluff and Davis-Purdue, suggesting ingrowth from the sapling layer. Conversely, we observed a decline in abundance within these classes at Donaldson Woods and Pioneer Mothers. *F. grandifolia* also exhibited a reverse-j shaped distribution (Fig. 5). Abundance of this species in smaller diameter classes declined sharply at Donaldson Woods, while the abundance of stems in the larger diameter classes declined at Laughery Bluff.

The generally bell-shaped distributions of *L. tulipifera* were similar to those of *Quercus* species (Fig. 5). Recruitment into larger size classes was evident, but there was little or no ingrowth from the sapling layer. At Laughery Bluff, a

reduction in abundance within intermediate diameter classes was evident.

Sapling density

Sapling-layer density of common species suggests that *A. saccharum* will continue to be an important species across the five forests (Table 4). In 2011, *A. saccharum* was the most abundant sapling species at Davis-Purdue, Donaldson Woods and Pioneer Mothers, and was second only to *Asimina triloba* in abundance at Laughery Bluff. Densities of *A. saccharum* saplings were similar between sample years at Davis-Purdue, Hemmer Woods and Pioneer Mothers, but more than doubled at Donaldson Woods (113 ± 21 to 287 ± 53 stems ha^{-1} ; $P = 0.004$) and declined by half at Laughery Bluff (477 ± 96 to 237 ± 54 stems ha^{-1} ; $P = 0.001$). The density of *F. grandifolia* saplings nearly

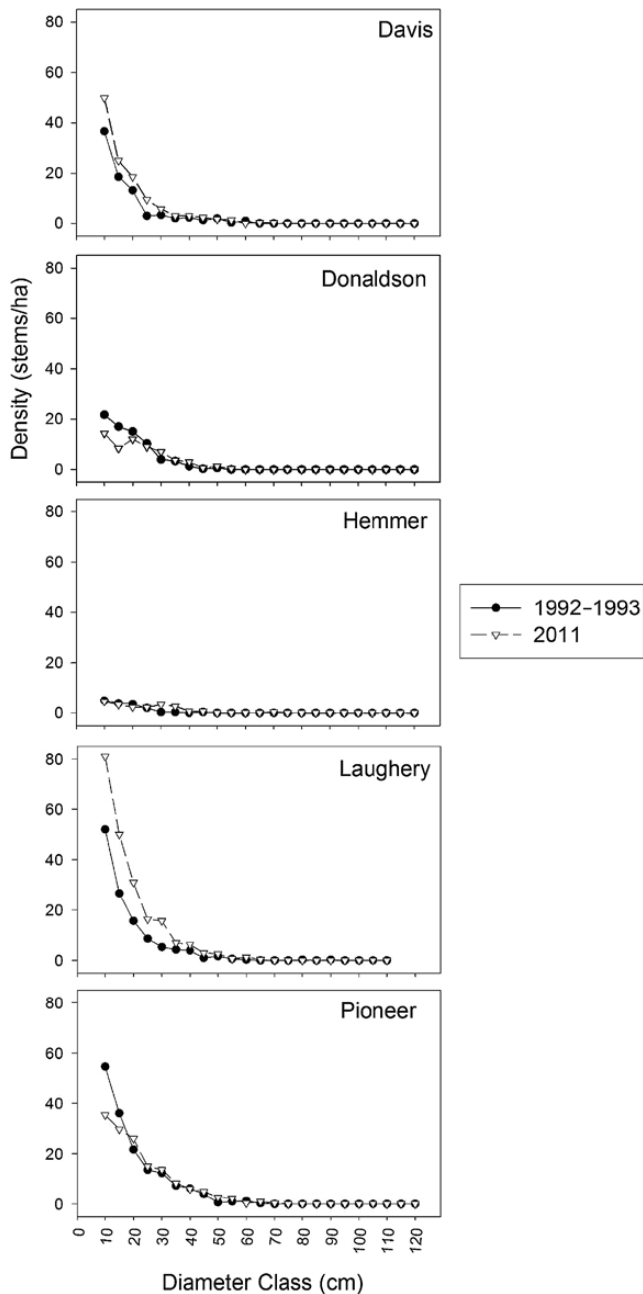


Figure 4: diameter distributions of *Acer saccharum* across five old-growth forest in Indiana between 1992–1993 and 2011. Trees are grouped in 5 cm diameter classes.

tripled at Donaldson Woods (27 ± 13 to 73 ± 22 stems ha^{-1} ; $P = 0.004$). Also notable was a fourfold increase in the density of *Vitis* spp. at Laughery Bluff (40 ± 18 to 160 ± 52 stems ha^{-1} ; $P = 0.004$). Supporting the high mortality observed for *C. florida* among stems 10–29.9 cm dbh, we observed significant reductions in sapling density for this species at all four sites where it occurred, ranging from 89% at Hemmer Woods (420 ± 51 to 47 ± 15 stems ha^{-1} ; $P = 0.001$) to 96% at Laughery Bluff (70 ± 22 to 3 ± 3 stems ha^{-1} ; $P = 0.004$).

Declines in the density of *U. rubra* saplings also paralleled the high mortality observed in the 10–29.9 cm diameter class. Sapling densities of this species declined at four out of five sites (Davis-Purdue 50%, $P = 0.06$; Hemmer Woods 58%, $P = 0.005$; Laughery Bluff 100%, $P = 0.08$ and Pioneer Mothers 77%, $P = 0.02$).

Species richness, evenness and diversity

In the overstory, we observed significant reductions in both species richness and diversity at three out of the five forests (Davis-Purdue, Donaldson Woods and Pioneer Mothers; Table 5). Two forests (Davis-Purdue and Laughery Bluff) exhibited significant reductions in species evenness. Trends were less evident in the sapling layer. We observed a significant increase in species richness and diversity at Donaldson Woods. However, sapling diversity significantly decreased at Davis-Purdue and richness significantly decreased at Pioneer Mothers.

DISCUSSION

Our results suggest a general trend of structural stability in the five old-growth forests we sampled. Between the 1992–1993 and 2011 sampling events, we observed significant decreases ($P < 0.05$) in the density of all stems ≥ 2.0 cm dbh in two of the five forests (Hemmer Woods and Pioneer Mothers) and a significant increase in BA in one of the five forests (Laughery Bluff). However, when only trees ≥ 10 cm dbh were considered, structural changes were more evident. Four of the five forests (Davis-Purdue, Donaldson Woods, Hemmer Woods and Pioneer Mothers) exhibited significant declines in overstory density, while the remaining forest, Laughery Bluff, exhibited a 43% increase in density. Laughery Bluff was the only forest to experience a significant increase in BA (16%) of trees in this size class. The stability of BA in these forests, despite the decreases in density, suggests that the growth of remaining trees compensated for the loss of BA resulting from decreased density. The contrary trend observed at Laughery Bluff likely resulted from damage caused by straight line winds two weeks prior to initial establishment of our sample plots in 1993 (Spetich 1995). As a result of this disturbance, the forest underwent a period of accelerated regeneration and canopy recruitment during which both surviving and newly established stems were able to take advantage of increased growing space (Oliver and Larson 1996), thereby increasing both density and BA. It is worth noting that our study consisted to two sampling intervals that were 19 years apart, and thus did not capture shorter term fluctuations in forest structure. In addition, while our 19-year interval between inventories did allow us to identify trends in structure and composition, 19 years is a short time within the multicentury timespan of forest development. Therefore, continued monitoring is needed to fully understand and predict development in these forests.

According to Oliver and Larson (1996), a shift from a dominant cohort initiated by allogenic processes to one developed via small-scale autogenic processes occurs as forests enter

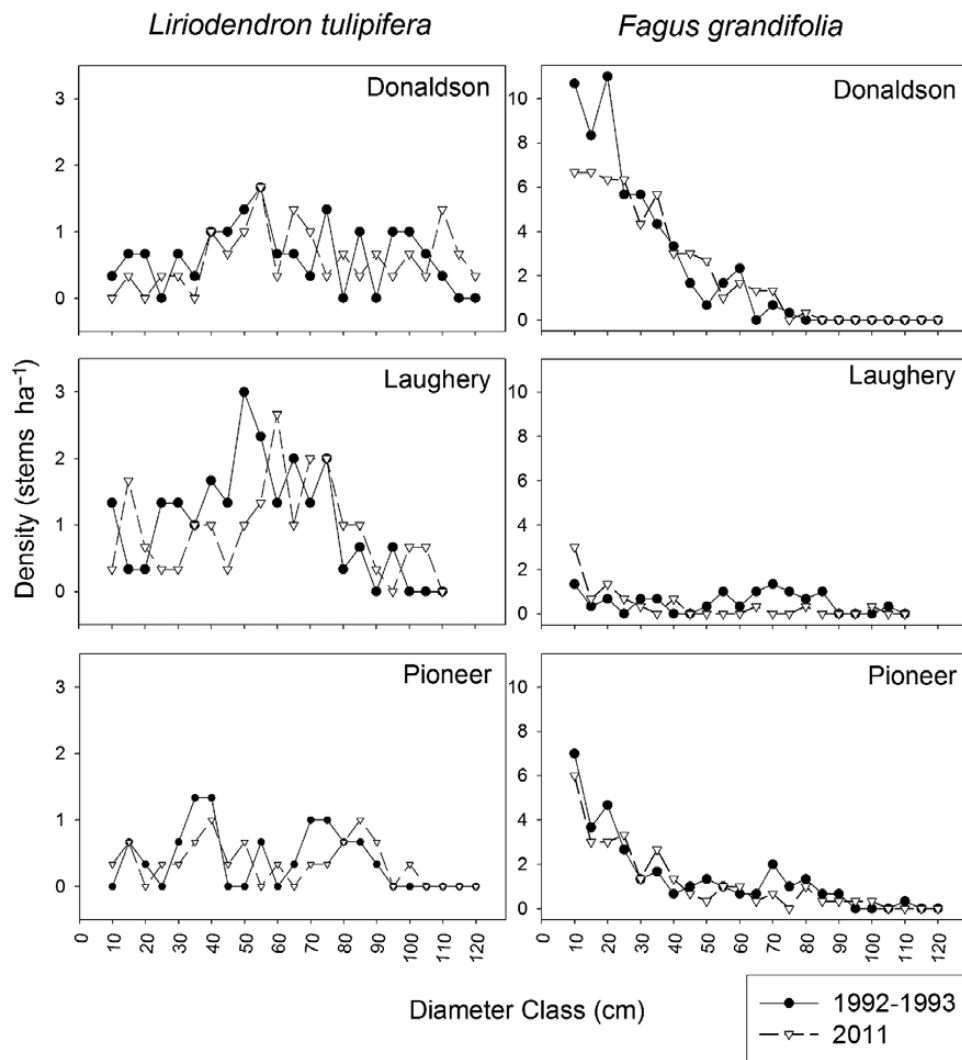


Figure 5: diameter distributions of *Liriodendron tulipifera* and *Fagus grandifolia* across three old-growth forests in Indiana between 1992–1993 and 2011. Data are not shown for Davis-Purdue and Hemmer Woods because IVs of both species were ≤ 1 at both sites. Trees are grouped in 5 cm diameter classes.

the old-growth stage of development. In the forests we sampled, observed mortality of early and mid-seral species and ingrowth of shade-tolerant species suggests that this transition is underway. For example, *Quercus* species displayed the greatest rates of mortality among trees ≥ 60 cm dbh in the three *Quercus*-dominated forests (Davis-Purdue, Donaldson Woods and Hemmer Woods). However, our results suggest that this transition is occurring at different rates, and with potentially different trajectories. Mortality of overstory trees measured in the original 1992–1993 survey ranged from 27 to 49% over the 18–19-year study period, resulting in different rates of overstory turnover. Likewise, the shift towards canopy-replacement by shade-tolerant species differed in intensity between sites, suggesting variability in trajectories of forest development. For example, Davis-Purdue and Laughery Bluff exhibited high and increasing densities of

understory and subcanopy *A. saccharum*, while Donaldson Woods and Hemmer Woods exhibited low densities with no increase through time. In addition, we observed a decline in the importance of overstory *F. grandifolia* at two out of three forests where it was a common species (Laughery Bluff and Pioneer Mothers). At these two sites, we observed AMRs of large (>60 cm dbh) *F. grandifolia* trees (4.1% at Pioneer Mothers and 7.7% at Laughery Bluff) that exceeded published values for large trees in other old-growth forests unaffected by beech bark disease (3.8%, Forrester and Runkle 2000; $\approx 2.4\%$, Runkle 2000; 3.8%, Olano and Palmer 2003). Many *F. grandifolia* trees at Pioneer Mothers exhibited signs of stress during the first survey, and many *F. grandifolia* trees at Laughery Bluff were leaning following the windstorm (M. Spetich, personal communication). Although *F. grandifolia* is a shade-tolerant late-successional species, it is likely to have

Table 4: mean (± 1 SE) density (stems ha^{-1}) of saplings (stems ≥ 2.0 cm but <10.0 cm dbh) by species across five old-growth forest remnants in Indiana, USA in 1992–1993 and 2011

Species	Davis-Purdue		Donaldson Woods		Hemmer Woods		Laughery Bluff		Pioneer Mothers	
	1992	2011	1992	2011	1993	2011	1993	2011	1992	2011
<i>Acer rubrum</i>	7 \pm 5	3 \pm 3	30 \pm 15	17 \pm 8	7 \pm 5	7 \pm 5	—	—	3 \pm 3	3 \pm 3
<i>A. saccharum</i>	610 \pm 79	650 \pm 81	113 \pm 21	287 \pm 53	33 \pm 13	40 \pm 18	477 \pm 96	237 \pm 54	357 \pm 67	307 \pm 55
<i>Asimina triloba</i>	43 \pm 43	40 \pm 33	283 \pm 129	487 \pm 118	367 \pm 158	487 \pm 124	67 \pm 39	323 \pm 77	130 \pm 53	90 \pm 30
<i>Carpinus caroliniana</i>	57 \pm 14	30 \pm 11	—	—	—	—	—	—	—	—
<i>Carya cordiformis</i>	27 \pm 13	7 \pm 5	—	3 \pm 3	—	3 \pm 3	7 \pm 5	7 \pm 5	—	—
<i>C. glabra</i>	10 \pm 6	—	—	—	—	3 \pm 3	—	—	—	—
<i>Celtis occidentalis</i>	30 \pm 17	20 \pm 11	—	10 \pm 6	10 \pm 7	33 \pm 12	3 \pm 3	—	70 \pm 35	27 \pm 23
<i>C. canadensis</i>	—	—	—	7 \pm 7	57 \pm 22	27 \pm 14	—	—	10 \pm 10	3 \pm 3
<i>Cornus florida</i>	—	—	337 \pm 56	20 \pm 7	420 \pm 51	47 \pm 15	70 \pm 22	3 \pm 3	60 \pm 26	3 \pm 3
<i>Fagus grandifolia</i>	3 \pm 3	3 \pm 3	27 \pm 13	73 \pm 22	—	—	20 \pm 17	30 \pm 17	60 \pm 18	93 \pm 22
<i>Fraxinus americana</i>	—	—	13 \pm 6	30 \pm 10	7 \pm 5	—	3 \pm 3	3 \pm 3	7 \pm 7	3 \pm 3
<i>F. pennsylvanica</i>	3 \pm 3	—	10 \pm 7	7 \pm 5	—	—	—	—	—	—
<i>Lindera benzoin</i>	7 \pm 5	—	—	13 \pm 8	7 \pm 7	3 \pm 3	17 \pm 11	170 \pm 73	3 \pm 3	7 \pm 5
<i>Liriodendron tulipifera</i>	—	—	—	—	—	—	10 \pm 7	3 \pm 3	—	—
<i>Ostrya virginiana</i>	13 \pm 6	7 \pm 5	3 \pm 3	17 \pm 7	—	—	10 \pm 6	7 \pm 7	—	3 \pm 3
<i>Prunus serotina</i>	7 \pm 5	10 \pm 7	—	—	—	13 \pm 8	10 \pm 6	7 \pm 7	13 \pm 13	—
<i>Sassafras albidum</i>	—	—	—	—	60 \pm 22	70 \pm 25	7 \pm 5	23 \pm 23	—	—
<i>Tilia americana</i>	—	—	—	—	13 \pm 6	—	3 \pm 3	3 \pm 3	—	—
<i>Ulmus americana</i>	27 \pm 10	20 \pm 10	13 \pm 8	13 \pm 6	10 \pm 7	10 \pm 7	—	—	—	—
<i>U. rubra</i>	113 \pm 36	57 \pm 21	163 \pm 55	170 \pm 37	220 \pm 46	93 \pm 25	17 \pm 7	—	163 \pm 51	37 \pm 16
<i>Vitis</i> spp.	—	—	—	—	7 \pm 5	10 \pm 7	40 \pm 18	160 \pm 52	—	—

Values were calculated from data collected on 30 plots at each site. Only species with at least 10 stems ha^{-1} at one or more sites were included.

Table 5: species richness, evenness and Shannon–Wiener diversity (mean \pm 1 SE) of over story (≥ 10 cm dbh) species across five old-growth forest remnants in Indiana, USA in 1992–1993 and 2011

Species	Davis-Purdue		Donaldson Woods		Hemmer Woods		Laughery Bluff		Pioneer Mothers	
	1992–1993	2011	1992–1993	2011	1992–1993	2011	1992–1993	2011	1992–1993	2011
Trees										
Richness	11.13 \pm 0.44	9.73 \pm 0.47***	7.06 \pm 0.41	6.00 \pm 0.37***	8.30 \pm 0.36	8.47 \pm 0.35	5.63 \pm 0.36	6.13 \pm 0.38	6.07 \pm 0.37	5.43 \pm 0.27*
Evenness	0.85 \pm 0.01	0.81 \pm 0.02**	0.82 \pm 0.02	0.83 \pm 0.02	0.85 \pm 0.01	0.85 \pm 0.01	0.78 \pm 0.02	0.68 \pm 0.02**	0.79 \pm 0.02	0.78 \pm 0.02
S-W diversity	2.03 \pm 0.06	1.84 \pm 0.07***	1.56 \pm 0.06	1.44 \pm 0.06**	1.77 \pm 0.05	1.80 \pm 0.04	1.30 \pm 0.07	1.20 \pm 0.05	1.38 \pm 0.06	1.31 \pm 0.06*
Saplings										
Richness	3.27 \pm 0.44	2.63 \pm 0.33	2.77 \pm 3.0	3.67 \pm 0.24**	3.33 \pm 0.31	2.97 \pm 0.34	2.50 \pm 0.23	2.73 \pm 0.27	2.87 \pm 0.28	2.17 \pm 0.26*
Evenness	0.61 \pm 0.06	0.51 \pm 0.07	0.69 \pm 0.06	1.77 \pm 0.05	0.66 \pm 0.06	0.68 \pm 0.08	0.58 \pm 0.07	0.67 \pm 0.06	0.65 \pm 0.07	0.53 \pm 0.08
S-W diversity	0.77 \pm 0.10	0.58 \pm 0.10*	0.75 \pm 0.08	1.00 \pm 0.07*	0.86 \pm 0.10	0.78 \pm 0.09	0.63 \pm 0.09	0.70 \pm 0.08	0.76 \pm 0.09	0.58 \pm 0.10

Values were calculated from data collected on 30 plots at each site. Means between sample intervals were compared with paired *t*-tests. *P* values were adjusted for multiple comparisons with a graphically-sharpened procedure to control the false discovery rate (Benjamini and Hochberg 1995). ****P* < 0.001; ***P* < 0.01; **P* < 0.05.

diminished importance in the future canopies of these two forests. Reductions in *F. grandifolia* importance have been reported in some studies of old-growth forests within the region (Abrell and Jackson 1977; Runkle 2000) but not in others (Cowell *et al.* 2010; Pinheiro *et al.* 2008).

As with many other studies in eastern hardwood forests (Cho and Boerner 1991; Johnson *et al.* 2002; Lorimer 1984; Nowacki and Abrams 2008), we observed few *Quercus* spp. stems in smaller overstory size classes or in the sapling layer (<10 stems ha^{-1}) at all sites. This lack of oak recruitment

suggests a shift in the disturbance regime of these forests, which many authors have attributed to a decrease in the frequency of surface fires (Abrams 1992; Dey and Guyette 2000; Nowacki and Abrams 2008). Many fire history studies have identified periods of frequent burning intermixed with long fire-free periods often associated with the movements of human populations (Dey and Guyette 2000; McCarthy et al. 2001; McClain et al. 2010). How these shifting fire regimes, in combination with other allogenic disturbances, promoted the regeneration and canopy recruitment of *Quercus* species is not well understood and warrants continued study.

Although published values are rare for old-growth hardwood forests, AMRs at Davis-Purdue (2.1%), Donaldson Woods (1.7%), Laughery Bluff (1.8%) and Pioneer Mothers (1.6%) were similar to those observed for old-growth forests elsewhere in the CHFR, where annual mortality ranged between 0.7 and 2.5% (Busing 2005; Cowell et al. 2010; Foré et al. 1997; Runkle et al. 2005; Runkle 2013) for overstory stems (minimum dbh ranged from 10 to 25 cm). AMRs in these four forests were also similar to published values for secondary hardwood forests in Texas (1.6% for stems ≥ 4.5 cm dbh; Harcombe et al. 1983), New York (1.7% for stems ≥ 5 cm dbh; Fahey 1998), and New Hampshire (1.1% for stems ≥ 10 cm dbh; Siccamo et al. 2007). However, annual mortality at Hemmer Woods (3.7%) was higher than these published values. Large numbers of dead trees were reported for this forest by McCune et al. (1988), who observed that the mortality of most standing dead trees could not be attributed to disease or insects. For trees ≥ 30 cm dbh in our study, *Quercus* species exhibited the highest rates of mortality in this forest, with two *Quercus* section *Lobatae* species (red oak group species; *Q. rubra* and *Q. velutina*) exhibiting the highest rates of mortality. In even-aged secondary forests, section *Lobatae* species are prone to stand-level dieback and mortality associated with episodic droughts and secondary attacks by insects and disease (Fan et al. 2008; Jenkins and Pallardy 1995). Similar stand-level mortality has not been observed in old-growth forests, and our results and those of McCune et al. (1988) suggest the high mortality at Hemmer Woods has been a long-term occurrence. *Q. velutina* and *Q. rubra* are not as long lived (typical lifespan 200–250 years for both species; Johnson and Abrams 2009) as *Q. alba* (over 400 years; Black et al. 2008), the dominant species at Hemmer Woods. Therefore, observed mortality for section *Lobatae* species may be a result of natural senescence augmented by the environmental stress produced by the low productivity conditions of Hemmer Woods compared to our other study sites (Table 1). Furthermore, Hemmer Woods is surrounded on three sides by a surface coal mining operation that has been active since 1993 (Indiana Geological Survey 2008). During the first inventory, mining operations were approximately one mile from the forest, however during the second inventory mining operations had progressed up to the edge of Hemmer Woods. Surface mining and post-mining reclamation may compact soil and alter subsurface geologic structure, leading to disrupted surface and subsurface hydrologic regimes (Negley and Eshleman 2006; Starnes and Gasper

1995), which could have negatively affected water flow into Hemmer Woods. In August 2012 (after our 2011 resampling), Hemmer Woods experienced a severe windstorm that reduced the density of standing trees by 30–50% across the forest (Abrell 2013), further altering the composition and structure of this forest.

Over the 19 years of our study, we observed mortality of *C. florida* stems 10–29.9 cm dbh ranging from 80% at Laughery Bluff to 100% at Donaldson Woods and Pioneer Mothers. Although once one of the most abundant understory species in the eastern United States (Holzmueller et al. 2010), the abundance of this species has been greatly reduced across its range due to dogwood anthracnose (Holzmueller et al. 2006; Wyckoff and Clark 2002) and changes in microenvironment associated with stand development (Pierce et al. 2008). Research has shown that the loss of this species in hardwood forests results in reduced cycling of calcium from deeper soils to biota-rich surface horizons (Holzmueller et al. 2010; Jenkins et al. 2007). A similar reduction may have occurred in the forests we studied, particularly at Hemmer Woods where the abundance of *C. florida* ≥ 10 cm dbh declined from 76 ± 7 stems ha^{-1} in 1992–1993 to 20 ± 4 stems ha^{-1} in 2011.

Like *C. florida*, we observed heavy mortality of *U. rubra* stems 10–29.9 cm dbh, combined with large decreases in sapling densities of this species. Beginning in the 1930s, *U. americana* experienced severe declines in abundance across its range as a result of Dutch elm disease and phloem necrosis (Castello et al. 1995), and this wave of mortality was noted at two of our sites (McCune et al. 1988; Parker and Leopold 1983). *U. rubra* is thought to be more resistant to Dutch elm disease than *U. americana* (Schlarbaum et al. 1997), and McCune et al. (1988) identified an increase in *U. rubra* reproduction after 1946, which coincided with heavy mortality of *U. americana*. However, the cause of the *U. rubra* mortality we observed decades later is unknown, but warrants investigation.

Over a 20-year period that included our 19-year study interval, two of the five forests (Laughery Bluff and Hemmer Woods) experienced substantial canopy disturbance as a result of wind events. The effects of the 1993 wind event at Laughery Bluff were highly evident and included reduced overstory BA and density, increased *A. saccharum* recruitment into the overstory, and a 30% increase in sapling density. While the response of vegetation at Hemmer Woods to a 2012 wind event remains to be seen, the effects of the windstorm, in combination with overstory mortality, will likely have pronounced and lasting effects on the vegetation structure and composition of the forest. In this region, the estimated return interval of catastrophic stand-replacing wind events range from one hundred to over 1000 years (Canham and Loucks 1984; Foster 1988), but less is known about localized winds associated with storm fronts and thunderstorms. However, these localized events are likely a more important disturbance agent than large-scale storms because they occur with much greater frequency and, when considered in mass, probably affect a larger total area (Bormann and Likens 1979). The effects of these

localized wind events are likely amplified in old-growth remnants within agricultural landscapes due to both the high contrast edge between the forest and adjacent land use (Saunders *et al.* 1991) and the higher susceptibility of larger trees in older forests to uprooting (Busing *et al.* 2009; Xi *et al.* 2008).

CONCLUSIONS

While many models of stand development view old-growth forest as a relatively stable endpoint in a sequence of change, our results support the view that old-growth forests are in a dynamic equilibrium where episodic disturbance counteracts the autogenic processes of senescence and succession (Huston 1994, McCarthy *et al.* 2001). A gradual shift in species composition away from dominant *Quercus* species toward shade tolerant *A. saccharum* is in progress. The variability we observed in mortality, structure, and species composition suggests that old-growth remnants, even within a single state, cannot be viewed as equivalent units with regard to research or management. Because old-growth remnants within fragmented landscapes are often small and widely scattered, stochastic disturbance events and surrounding land use may have amplified effects on an individual remnant, or on the summed old-growth resource across a region. Therefore, continued monitoring of these rare, but biologically important forests is critical to their long-term management and protection. Furthermore, long-term monitoring of these forests provides critical information to guide the management of other forests that have been set aside to develop old-growth structure.

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