



Overstory species response to clearcut harvest across environmental gradients in hardwood forests

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ABSTRACT

Despite their long history as a forest dominant, the importance of *Quercus* (oak) species is declining under contemporary disturbance regimes in many parts of the world. This is cause for concern considering the great economic and ecological value of this genus. While many chronosequence studies have shown that clearcutting has accelerated the loss of *Quercus* species in forests of eastern North America, long-term repeated measures studies are needed to understand how topo-edaphic variables and disturbance history influence the persistence of the genus in post-harvest stands. In 1988, a study was implemented on the Hoosier National Forest (HNF) in southern Indiana, USA to examine the fate of *Quercus* species and their competitors within developing stands following clearcut harvests. Permanent plots were established in six harvest units in *Quercus-Carya* (oak-hickory) forests using a stratified design to capture a variety of physiographic and edaphic conditions. Pre-harvest plot data were collected in 1988 and plots were resampled in 2011, allowing documentation of shifts in species composition over a 23-year period (1988–2011). Aerial photos from the 1930s were used to determine canopy cover and likely historic land-use within each stand prior to incorporation into the HNF. To characterize edaphic conditions, soil samples were collected and analyzed for chemical characteristics in 2011. Non-metric multi-dimensional scaling (NMS) and multiple linear regression using fixed and mixed-effect models were used to examine species composition along topo-edaphic and historic canopy cover gradients. We observed drastic declines in the importance of *Quercus alba* (white oak), *Quercus velutina* (black oak), and *Quercus prinus* (chestnut oak) across all stands following harvest. During the same time period, we observed large increases in the importance of other species, with *Acer rubrum* (red maple) showing large increases on the driest sites and *Liriodendron tulipifera* (tulip-poplar) displaying the greatest increase across all sites. In pre-harvest stands, *Q. prinus* was confined to the poorest sites and displayed the strongest association of all species with historically closed canopies in both pre and post-harvest stands. In post-harvest stands, the diminished importance of *Q. alba* was associated with low soil nitrogen levels and historically open canopies. *L. tulipifera* and *Prunus serotina* (black cherry) were associated with more nutrient-rich mesic sites in post-harvest stands. *Populus grandidentata* (big-tooth aspen) in post-harvest stands was associated with historically closed canopies and low cation exchange capacity.

1. Introduction

Quercus (oak) is an ecologically important genus in temperate forests throughout the world, with 32 overstory species in eastern North America, 21 in eastern Asia, 11 in Europe, and 5 in Pacific North America (Latham and Ricklefs, 1993). However, the sustainability of *Quercus* species across forest landscapes is threatened by climate-related

mortality of mature trees (Jenkins and Pallardy, 1995; Demchik and Sharpe, 2000; Allen et al., 2010; Levanič et al., 2011), and wide-spread regeneration failure resulting from shifting disturbance regimes (Shrestha, 2003; Zavaleta et al., 2007; Plieninger et al., 2010; McEwan et al., 2011; Dey, 2014). Observed and predicted declines in *Quercus* species importance have caused great concern because significant reductions in oak abundance will likely have profound effects on forest

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ecosystems throughout the global range of the genus (Fei et al., 2011; Dey, 2014). *Quercus* is often considered a foundation genus because member species drive trophic interactions and influence population and community dynamics by providing hard mast and shelter for numerous vertebrate species (Ellison et al., 2005) and serving as habitat for large numbers of insect species (Opler, 1974; Futuyma and Gould, 1979; Vodka et al., 2009), often several times more than other co-occurring hardwood species (Southwood, 1961; Ranius and Jansson, 2000).

Many presettlement forests of eastern North America were pyrogenic as structure and composition was dependent on the recurrent use of fire by Native Americans (Nowacki and Abrams, 2008). During early European settlement, fire frequencies increased and forests were cleared for row agriculture and livestock grazing, perpetuating disturbance-adapted *Quercus* species across the landscape (Guyette et al., 2005). In many eastern hardwood forests, the loss of *Castanea dentata* (American chestnut) also resulted in increased importance of *Quercus* species, particularly in the southern Appalachian Mountains (Nelson, 1955; Woods and Shanks, 1959). Starting in the early 20th century, fire suppression created drastic reductions in *Quercus* regeneration, especially on more productive sites (Dey, 2002). Although *Quercus* species remain dominant in the overstory of many forests, the lack of fire or surrogate disturbances have allowed them to be replaced by shade-tolerant and fire-sensitive species.

The desire to perpetuate *Quercus*-dominated forests fostered extensive research to identify silvicultural systems best suited to regenerating and sustaining the genus. In the eastern United States, even-aged reproduction systems in the form of clearcutting were deemed suitable and widely implemented throughout the range of *Quercus* species (McGee, 1987). Clearcut harvests were considered the most efficient and economically advantageous form of silviculture due to greater yields per hectare, lower harvesting costs, and simplified management (Clark and Watt, 1971; Sander and Clark, 1971). This technique was frequently viewed as a panacea for regenerating *Quercus* species and was implemented across much of the eastern United States from the 1960s through the 1980s (Roach and Gingrich, 1968; Sander and Clark, 1971).

Subsequent observations in post-harvest stands often found composition shifting away from *Quercus* domination towards a mix of hardwood species, raising concerns about the efficacy of clearcutting (George, 1988). Early research in clearcuts suggested that site conditions determined the distribution and importance of *Quercus* species, with *Quercus* reproduction in greatest abundance on the poorest site, but rarely occurring on more productive sites where *L. tulipifera*, *Acer* spp., *P. serotina*, *Populus* spp., and *Fraxinus* spp. (ash species) dominated (Trimble and Hart, 1961; Hilt, 1985).

Understanding the post-harvest persistence of *Quercus* species requires a fine-scale examination of how the silvics of the genus interact with disturbance and environmental gradients. Several physiological and morphological characteristics give *Quercus* species an advantage under xeric conditions including the rapid development of a long taproot, the ability to photosynthesize and conduct water under high drought stress, and the maintenance of high root:shoot ratios through recurrent shoot dieback (Abrams, 1990; Pallardy and Rhoads, 1993; Parker and Dey, 2008; Johnson et al., 2009). However, these characteristics are associated with greater investment in belowground growth and may create a competitive disadvantage on more mesic sites with greater water availability.

The Central Hardwood Region (CHR) of the United States is the archetype of a region whose forests have experienced declines in *Quercus* species importance in response to shifting disturbance regimes. The Hoosier National Forest (HNF) in southern Indiana used clearcutting as its dominant harvesting prescription for approximately 20 years, ending in the late 1980s. As with much of the southern portion of the CHR, forests of HNF are underlain by bedrock (nonglaciated) substrate that creates gradients of moisture availability, microclimate, and soil fertility (Van Kley et al., 1995). Throughout the CHR, the forests that

developed after clearcutting are now entering the understory re-initiation stage (Oliver and Larson, 1996), and more research is needed to understand how these forests developed across physiographic gradients as they enter later stages of stand development. In a chronosequence study of 9–27 year-old clearcuts, Jenkins and Parker (1998) found that clearcuts on mesic slopes contained greater importance of *L. tulipifera* than dry-mesic slopes where *Quercus* species competed better. While such chronosequence studies have provided valuable information, they may fail to capture ecological patterns and processes across environmental gradients that are better assessed by the resampling of long-term monitoring plots. Consequently, long-term datasets are critical to understanding forest development in post-harvest stands where a diverse array of overstory species and high inter-site variability may limit the use of a chronosequence (Walker et al., 2010).

In 1988, a long-term, repeated measure study was implemented on the HNF by the USDA Forest Service North-Central Experiment Station to examine the competitive ability of *Quercus* species after clearcutting and the post-harvest development of forest stands. In 2011, we resampled 55 plots that were established prior to harvesting in 1988 and used these data to examine the importance of *Quercus* species and their competitors in pre- and post-harvest stands. We also examined how species were distributed across gradients created by historical land use and topo-edaphic characteristics. Based upon these examinations, we address three primary questions:

1. How do the distributions of species differ between pre- and post-harvest stands in relation to underlying environmental gradients?
2. How have land-use practices prior to the creation of the HNF (represented by canopy cover in 1938–1940 aerial photos) influenced the pre- and post-harvest composition of sampled stands?
3. Where across contemporary environmental and disturbance gradients are *Quercus* species best able to persist in post-harvest stands?

2. Methods

2.1. Harvest treatments

In 1988, six mature *Quercus-Carya* dominated stands ranging in size from 4.5 to 12.1 ha were harvested on the HNF. Three of the stands were located on the Brownstown Ranger District and three stands were located on the Tell City Ranger District (Table 1). All stands were clearcut for merchantable timber between the months of April and August 1988. After removal of merchantable timber, all remaining live and cull trees ≥ 5.1 cm dbh (diameter at breast height) were felled. No herbicide treatments or additional site preparation treatments were performed.

2.2. Study sites

Stand 1 is located in the Brown County Hills Section of the Highland Rim Natural Region (Homoya et al., 1985). This section is characterized by deeply dissected uplands underlain by siltstone, sandstone, and shale. Soils are Brownstone channery silt loams, which are moderately deep and well drained soils formed in residuum from siltstone. Steep slopes and narrow hollows are typical topographic features of this section (Van Kley et al., 1995). There is little disparity in forest composition, with *Quercus-Carya* dominated uplands often consisting of nearly pure stands of *Q. prinus* on upper slopes and ridge tops. Mesic ravines harbor species such as *Fagus grandifolia* (American beech), *Quercus rubra* (northern red oak), *Acer saccharum* (sugar maple), and *Fraxinus americana* (white ash).

Stands 2, 3, and 6 are located in the Crawford Upland Section of the Shawnee Hills Natural Region (Homoya et al., 1985). The broad ridge tops and flats of this section contrast with the narrow ridges and steep terrain of the Brown County Hills Section. Stand 2 is underlain by Wellston-Tipsaw-Adyeville Complex (Ultic Hapludalfs, Typic

Table 1 Location, site, and soil chemical descriptions of six study stands on the Hoosier National Forest in southern Indiana. *Total across all species (m²ha⁻¹); mean ± 1 standard error.

Stand	Location lat/long (N/W)	Size (ha)	# of plots	Pre-harvest basal area*	Post-harvest basal area*	Hist. canopy cover (%)	Trans. aspect range	Slope (%) range	Soil pH range	CEC range	Ca (%) range	K (%) range	Mg (%) range	Total N (%) range	Total C (%) range
1	38.9984 -86.1810	12.1	12	27.3 ± 1.3	18.7 ± 0.9	100	0.3-2.0	25-44	4.8-5.9	3.0-7.7	33.3-54.4	2.4-5.5	7.7-25.2	0.16-0.32	2.3-6.4
2	38.6208 -86.8039	7.6	10	23.5 ± 2.3	21.1 ± 0.8	84	0.4-1.8	15-28	4.9-5.5	2.1-6.7	36.5-51.7	2.7-7.1	10.9-20.3	0.18-0.32	2.4-4.9
3	38.6503 -86.6737	8.1	10	22.0 ± 0.9	18.8 ± 1.0	50	0.1-0.7	10-30	5.0-5.9	3.0-5.6	39.6-59.0	3.4-5.0	12.3-22.6	0.20-0.32	2.4-4.5
4	38.4807 -86.4067	7.6	10	15.7 ± 0.8	17.8 ± 0.8	48	0.1-1.3	2-15	5.0-5.9	4.5-7.4	51.3-63.2	2.0-4.3	6.0-22.2	0.17-0.25	2.1-3.5
5	38.4772 -86.4067	4.5	6	16.0 ± 2.0	18.2 ± 1.0	48	0.2-2.0	8-25	5.3-6.1	3.8-7.8	57.8-71.2	2.3-3.7	8.4-14.1	0.20-0.32	2.0-3.8
6	38.2292 -86.5615	9.3	7	22.7 ± 1.6	17.2 ± 0.6	63	1.7-2.0	8-21	5.2-5.8	3.4-11.2	50.0-63.3	2.1-3.5	11.3-20.4	0.19-0.41	2.4-5.2

Dystrudepts, and Typic Hapludults, respectively) soils, which are moderately deep, well to excessively well-drained and were formed in loamy residuum from sandstone interbedded with shale and siltstone (Soil Survey Staff, 2017). Soils in Stand 3 include the Apalona-Zanesville Complex (Oxyaquic Fragiudults) and the Adyeville-Wellston Complex (Typic Hapludults and Ultic Hapludalfs), which formed in residuum from interbedded sandstone, siltstone, and shale (Soil Survey Staff, 2017). These soils are moderately deep to deep and vary from moderately well to excessively drained. The Apalona and Zanesville soils have a fragipan that restricts rooting and impedes drainage. Stand 6 is underlain by Adyeville (Typic Hapludults) and Wellston (Ultic Hapludalfs) silt loams, which are moderately deep, well drained to excessively well drained, and formed in residuum from interbedded sandstone, siltstone, and shale (Soil Survey Staff, 2017). Species composition on upper slopes often consists of mixed *Quercus* and *Carya* species including *Q. velutina*, *Q. alba*, *Q. prinus*, *Quercus coccinea* (scarlet oak), *Carya glabra* (pignut hickory), and *Carya ovata* (shagbark hickory). Cove forests of the section typically consist of mesophytic species such as *F. grandifolia*, *L. tulipifera*, *Q. rubra*, *A. saccharum*, and *Juglans nigra* (black walnut).

Stands 4 and 5 are located in the Escarpment Section of the Shawnee Hills Natural Region (Homoya et al., 1985). The rugged hills of this section are situated along the eastern boundary of the region and are characterized by soils from the Wellston-Adyeville Complex (Typic Hapludults and Ultic Hapludalfs), which are moderately deep, well drained to excessively drained, and formed in residuum from interbedded sandstone, siltstone, and shale (Soil Survey Staff, 2017). Dry-mesic and mesic forest types are common and similar to those of the Crawford Upland Section, although *Q. prinus* is often absent and replaced by *Q. velutina* and *Quercus stellata* (post oak).

2.3. Plot establishment and sampling

Prior to harvest, between April 20 and June 22, 1988, data were collected from sixty-one 809 m² fixed circular plots across the six stands. Within each stand, between 6 and 14 permanent overstory plots were located using a stratified random design based upon topographic positions. Plots centers were located a minimum of 28.2 m from the edge of the clearcut, in order to reduce edge effects from surrounding mature stands, and situated within each stand to encompass as many aspect-slope combinations as possible. Study plots were established by personnel from the USDA Forest Service, North-Central Research Station and the HNF. During the summer of 2011, 55 of the original 61 plots were relocated and remeasured. Two plots in Stand 1 were never harvested and, therefore, not resampled in 2011. Four plots in Stand 6 could not be relocated.

All trees ≥ 4.1 cm dbh were measured by species in each 809 m² overstory plot. Advanced reproduction at the time of harvest was assessed in three 16.2 m² circular subplots within each overstory plot. Each overstory plot was divided into thirds using a randomly chosen azimuth to locate the first dividing line. One hundred twenty degrees were added to this azimuth to locate the second line, and another 120 degrees added to locate the third line. Within each third, a 16.2 m² circular plot was randomly located by adding a random number from between 1 and 120 to the azimuth of the dividing line. These plots were permanently marked with a length of metal conduit. The 16.2 m² subplots were not allowed to overlap, so they were spaced at least 4.3 m apart. Subplots were also spaced so they were at least 2.1 m from the center and outside edge of the main plot. All woody stems in these plots were tallied into nine diameter classes ranging from 0 to 17.78 cm dbh and nine height classes ranging from < 30.48 cm to > 243.84 cm.

In 2011, overstory plots and regeneration subplots were both re-sampled. We collapsed height and diameter classes from the original sampling protocol to define seedlings as woody stems ≤ 0.91 m height and saplings as stems > 0.91 m height but less than ≤ 5.1 cm dbh. Site variables measured, at the scale of the overstory plot, included aspect

(with compass), percent slope (with clinometer), and slope position, which was visually assessed as a relative proportion in relation to a ridge summit (=100) or drainage (=0). Soil samples were also collected from each plot to examine how soil characteristics are correlated with species composition and the importance of *Quercus* species. Subsamples were collected from the top 10 cm of the upper horizon at ~10 m from plot center in each cardinal direction. Subsamples were pooled and analyzed by overstory plot.

2.4. Data preparation

Summary statistics calculated for each overstory plot included density (stems/ha), basal area (m²/ha), relative density, relative basal area, and importance value [IV; (relative basal area + relative density)/2] of each species present in 1988 (pre-harvest) and 2011 (post-harvest) stands. Pre and post-harvest regeneration subplot data were used to calculate relative density of seedlings and saplings by species. Overstory plot and regeneration subplot data were not combined for analysis as some stems were counted in both plot types (i.e., stems 4.1–5.1 cm dbh).

Soil samples were frozen immediately after field collection until they were processed for analysis. Samples were analyzed for pH (in a 2:1 slurry of deionized water using a pH meter), concentrations of Melich-III extractable cations (P, K, Mg, and Ca; ppm), organic matter (%; ignition loss method), and cation exchange capacity (CEC; barium chloride method) by A&L Analytical Laboratories (Memphis, TN). Percent saturation of K, Mg, and Ca was calculated as the percentage of respective cation that contributed to total CEC. A subset of all samples were dried at 60 °C for 24 h and then ground to a fine texture with mortar and pestle. Carbon (mg absolute), nitrogen (mg absolute), % carbon, and % nitrogen were determined from these samples using an ECS 4010 CHNSO Analyzer (Costech Analytical Technologies, Inc).

To more efficiently relate aspect to site productivity, aspect was transformed to a linear scale ranging from 0 to 2, with zero value at southwest using the following formula: transformed aspect = cos(45-aspect) + 1 (Beers et al., 1966). Percent historical canopy cover for each study site was estimated to the nearest 4% using a stereoscope and dot grid on 1:20,000 aerial photos of the HNF flown between 1938 and 1940. This allowed assessment of likely historic land-use in each stand prior to incorporation into the HNF.

2.5. Data analysis

Non-metric multidimensional scaling (NMS) was conducted using PC-ORD Version 5 (McCune and Mefford, 2011) to examine species composition along topo-edaphic and historical canopy cover gradients. We used data from both 1988 and 2011 to examine compositional changes in the overstory following harvest and 2011 data to examine the distribution of seedling and saplings in contemporary stands 23 years after harvest. NMS was utilized due to the relaxed assumption of normality and because it does not assume a linear response of species to site-related gradients (McCune et al., 2002). The main matrices contained overstory IV, sapling relative density, and seedling relative density data, while the secondary matrix for all analyses included 20 environmental variables consisting of all previously described soil chemical analyses, in addition to transformed aspect, slope position, percent slope, and percent historical canopy cover. Autopilot mode (slow and thorough) was selected using the Sorensen (Bray-Curtis) distance measurement, with 1.0×10^{-7} stability criterion, 250 runs with real data, 250 runs with randomized data, and 500 maximum iterations for each. According to Clarke (1993), NMS ordination analyses with a final stress > 20 are likely to yield plots which could be dangerous to interpret. Our NMS analysis of sapling data yielded a stress = 25. Because of this high stress value and the resulting problematic interpretation, the results of this analysis are not presented.

Correlations between environmental variables and ordination axes

were evaluated based on Pearson's correlation coefficients. Overstory *A. saccharum* and *A. rubrum* were not separated in Stands 4, 5, and 6 during pre-harvest sampling, but were instead grouped by genus. Therefore, we combined *Acer* species in the 2011 data prior to running NMS ordination for overstory IV data from all six stands. Successional vectors were created for the overstory NMS ordination to allow visual comparison of temporal shifts in species composition. Vectors of environmental gradients were assessed with Pearson's correlation analysis and overlaid onto species biplots to examine species/site relationships. Because topography and edaphic characteristics influence land use, we also used Pearson's correlation analysis to examine relationships between historic canopy cover and all other variables. Bubble plots were created to illustrate overstory species importance on individual plots and shifts in distribution along environmental gradients following harvest.

To confirm the results of the NMS analysis and more directly examine the relationships between the importance of individual species and environmental variables, we used multiple linear regression with fixed and mixed-effects models to analyze the relationship between overstory species IVs (response variables) and environmental variables (independent variables; Table 2). Square root and natural log transformations of response variables were used as needed to homogenize error variance. Full models of all environmental variables were fit to the data with multiple linear regression, and then reduced to include only significant environmental variables with a backwards stepwise procedure. Criteria for a variable to stay in the model was set at $P < 0.05$. Variance inflation factors (VIF) were then used to detect whether independent variables in the final models had strong linear associations. Models with mean VIFs considerably greater than 1 were considered to contain significantly collinear variables (Neter et al., 1996); variables were removed as needed to reduce overall VIF to less than 3. These models were then used in a mixed-effects framework to account for the sample design of plots within stands. Stand was added as a random effect that would adjust the overall y-intercept of the model. Significance of random effects was assessed using a maximum likelihood test of the mixed effects model against the fixed effects model. In many cases, random effects could not be estimated (i.e., variance equal to 0), and were subsequently dropped from the model. For all final models, plots of studentized residuals versus fitted values were used to assess the assumption of constant variance, and residual plots and standard techniques were used to evaluate influence of potential outliers (Neter et al., 1996). All predictors in the final models, except in some cases the intercept and random effects, were significant at $P < 0.05$. Regression analysis was performed in R 3.5.0 (R Core Team 2018) using packages *stat* and *lme4* (Bates et al., 2015). The package *lmerTest* (Kuznetsova et al., 2017) was used to assess significance of all models and provide summary statistics such as R².

3. Results

3.1. Overstory ordination analysis

The species data from all six stands were best described by a 3-dimensional solution in NMS, which displayed a final stress of 14.9 and instability criterion of < 0.000001. Overall, the ordination explained 82% of variance in overstory community composition, with the dominant axes 1 and 2 explaining 30% and 28% of variation, respectively. Overstory (trees ≥ 4.1 cm dbh) species compositions of pre- and post-harvest stands were strongly separated in ordination space and shifts in composition were largely unidirectional (Fig. 1a). In ordination space, pre-harvest plots were strongly associated with greater importance of *Cornus florida* (flowering dogwood), *Q. alba*, *Q. prinus*, *Q. rubra*, and *Q. velutina*, while post-harvest plots were associated with *Acer* spp., *L. tulipifera*, *Ostrya virginiana* (eastern hophornbeam), *P. grandidentata*, and *P. serotina* (Fig. 1b).

NMS results for all stands indicated that slope position, percent

Table 2
Pearson's correlation coefficients between NMS ordination axes scores and environmental variables and individual overstory and seedling species.

Variable	Symbol	Overstory			Seedlings		
		Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
		<i>r</i>	<i>r</i>	<i>r</i>	<i>r</i>	<i>r</i>	<i>R</i>
Transformed aspect	ASP	0.088	-0.222	0.105	-0.331	-0.090	-0.096
Slope position	SP	0.055	-0.333	-0.115	-0.072	0.066	-0.278
Percent slope	%SL	-0.270	-0.488	-0.033	0.141	0.286	-0.286
Soil pH	pH	0.412	0.232	0.277	-0.273	-0.595	0.040
Soil phosphorus (ppm)	P	0.180	-0.153	-0.23	-0.353	0.229	-0.121
Soil potassium (ppm)	K	0.007	-0.332	0.040	-0.277	0.053	0.124
Soil calcium (ppm)	Ca	0.347	0.156	0.094	-0.375	-0.475	0.113
Soil magnesium (ppm)	Mg	0.211	-0.049	0.053	-0.280	-0.309	0.195
Percent organic matter	%OM	0.216	-0.153	0.213	-0.345	0.005	0.122
Cation exchange capacity (meq/100 g)	CEC	0.259	0.063	0.154	-0.349	-0.358	0.179
Percent soil potassium saturation	%K	-0.295	-0.362	-0.074	0.123	0.419	-0.099
Percent soil calcium saturation	%Ca	0.470	-0.361	-0.109	-0.298	-0.565	-0.004
Percent soil magnesium saturation	%Mg	0.016	-0.146	-0.125	0.010	-0.082	0.145
Percent soil hydrogen saturation	%H	-0.439	-0.242	0.198	0.288	0.565	-0.056
Soil nitrogen (mg)	N	0.248	-0.123	0.168	-0.331	-0.133	-0.095
Soil carbon (mg)	C	-0.086	-0.182	0.201	-0.035	0.119	0.083
Percent soil nitrogen	%N	0.255	-0.115	0.165	-0.339	-0.167	-0.067
Percent soil carbon	%C	-0.083	-0.182	0.207	-0.035	0.119	0.083
Percent historical canopy closure	%CC	-0.441	-0.552	0.094	0.111	0.428	-0.033
Species							
<i>Acer rubrum</i>	Ar	-	-	-	0.742	0.234	-0.459
<i>A. saccharum</i>	As	-	-	-	-0.367	-0.124	-0.116
<i>Acer</i> spp.	Asp	0.336	-0.468	0.537	-	-	-
<i>Ailanthus altissima</i>	Aa	-	-	-	-0.383	-0.079	0.128
<i>Amelanchier arborea</i>	Aar	-	-	-	0.032	0.120	0.011
<i>Asimina triloba</i>	At	-	-	-	-0.220	-0.128	0.015
<i>Carpinus caroliniana</i>	Cc	0.350	0.087	-0.224	-0.140	-0.397	-0.344
<i>Carya</i> spp.	Cs	-0.010	0.667	0.351	0.146	0.115	0.370
<i>Celtis occidentalis</i>	Co	-	-	-	-0.001	-0.339	0.292
<i>Cercis canadensis</i>	Cec	0.293	0.174	-0.171	0.131	-0.307	0.552
<i>Cornus florida</i>	Cf	-0.580	0.201	-0.013	-0.108	-0.093	0.044
<i>Fagus grandifolia</i>	Fg	0.007	-0.124	0.100	-0.343	-0.239	0.147
<i>Fraxinus americana</i>	Fa	0.324	-0.098	-0.028	-0.299	-0.620	0.134
<i>Liriodendron tulipifera</i>	Lt	0.358	-0.200	-0.802	-0.009	-0.338	0.106
<i>Morus rubra</i>	Mr	-	-	-	0.100	-0.141	-0.170
<i>Nyssa sylvatica</i>	Ns	-0.107	0.126	-0.145	0.055	-0.084	-0.088
<i>Ostrya virginiana</i>	Ov	0.560	0.057	-0.206	-0.560	0.047	-0.457
<i>Populus grandidentata</i>	Pg	0.191	-0.563	-0.190	-0.196	0.229	-0.006
<i>Prunus sylvatica</i>	Ps	0.685	-0.389	-0.197	-0.579	0.549	0.172
<i>Quercus alba</i>	Qa	-0.377	0.484	0.440	0.021	0.141	0.060
<i>Q. coccinea</i>	Qc	-0.154	0.216	-0.138	-0.154	0.186	0.014
<i>Q. muehlenbergii</i>	Qm	0.223	-0.003	-0.127	-0.051	-0.048	-0.040
<i>Q. prinus</i>	Qp	-0.761	-0.280	0.155	0.351	0.272	0.121
<i>Q. rubra</i>	Qr	-0.016	0.125	0.217	-0.086	0.347	0.043
<i>Q. velutina</i>	Qv	-0.328	0.590	0.031	0.048	0.015	0.366
<i>Rhus</i> spp.	Rs	-	-	-	0.269	0.161	0.165
<i>Sassafras albidum</i>	Sa	0.050	0.411	-0.225	0.487	-0.106	0.530
<i>Ulmus</i> spp.	Us	0.396	-0.073	-0.060	-0.373	-0.574	-0.081

slope, soil pH, soil potassium, percent soil calcium saturation, percent soil potassium saturation, percent soil hydrogen, and percent historical canopy cover were the environmental variables most correlated with the distribution of overstory species across axes 1 and 2 (Table 2). Variables showing strong correlations with Axis 1 included: percent soil calcium ($r = 0.47$), percent historical canopy cover ($r = -0.44$), percent soil hydrogen ($r = -0.44$), pH ($r = 0.41$), and soil calcium concentration ($r = 0.35$). Variables showing strong correlations with Axis 2 included: transformed aspect ($r = -0.23$), slope position ($r = -0.33$), percent slope ($r = -0.49$), soil potassium ($r = 0.33$), percent soil potassium saturation ($r = -0.33$), and percent historical canopy cover ($r = -0.55$). Percent historical canopy cover displayed the strongest correlation of any variable with axis 2 and the second strongest correlation with axis 1 (Table 2). However, plots with high historic canopy cover also had steep slopes, low pH, and low CEC, making it difficult to distinguish gradients resulting for past disturbance from gradients resulting from topo-edaphic conditions. Generally, edaphic variables

were most strongly correlated with the gradients represented by axis 3, although the variables we measured displayed poor correlations compared to axes 1 and 2 (max $r = 0.28$ for pH). Percent historic canopy cover was significantly correlated with nine out of nineteen topographic and edaphic variables, and was most strongly correlated with percent slope ($r = 0.753$) and percent soil calcium saturation ($r = -0.679$; data not shown).

3.2. Site conditions and compositional shifts

The overstory ordinations illustrate that clearcutting has largely reduced the importance of *Quercus* and *Carya* species across study sites (Table 4, Fig. 2). In pre-harvest stands, *Quercus alba* showed a strong correlation with axis 2, which was also correlated with historically open canopies, less steep slopes, and reduced K and Ca availability (Table 2, Fig. 1). While regression analysis displayed poor fits between the importance of *Q. alba* and environmental variables (Table 3; adj.

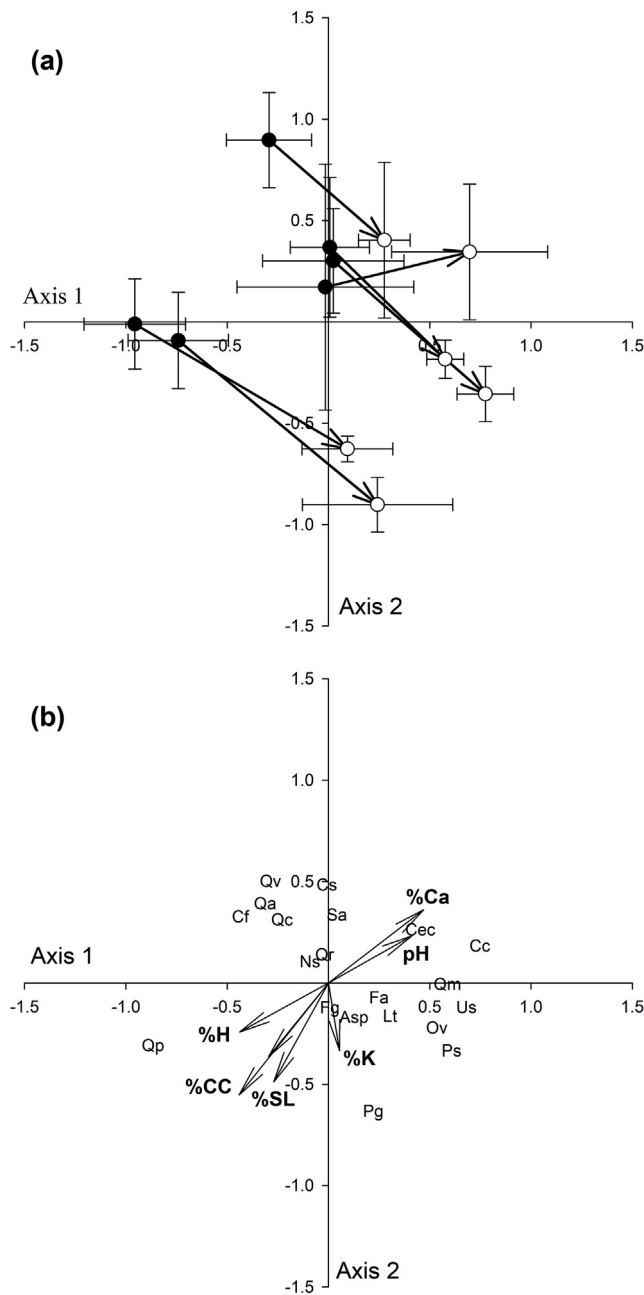


Fig. 1. NMS ordination of overstory species importance across all six stands. (a) Successional vectors indicating change in composition from 1988 (pre-harvest) to 2011 (post-harvest). (b) Biplot of most important overstory species in 2011 and dominant environmental variables ($r \geq 0.35$); %Ca (percent soil calcium saturation), pH (soil pH), %K (percent soil potassium saturation), %SL (percent slope), %CC (percent historical canopy closure), and %H (percent soil hydrogen saturation) are shown as vectors. Explanations of species abbreviations are provided in Table 2.

$R^2 = 0.269$), pre-harvest importance of the species was most strongly, and negatively, related to percent slope and organic matter content. *Quercus prinus* displayed a strong negative correlation with axis 1, which was associated with historically closed canopies, steep slopes, and acidic low calcium soils (Table 2, Fig. 1b). Regression analysis revealed that *Q. prinus* IV in pre and post-harvest stands was strongly associated ($\text{adj. } R^2 = 0.709$ and 0.660 , respectively) with historically closed canopies on xeric sites with poor soils (high C content, low pH, low soil Mg and P content). In post-harvest stands, *Q. alba* nearly disappeared altogether on poor sites (steeper slopes and low pH; Fig. 1b,

Table 2), and was associated with historically open canopies on sites with lower soil nitrogen content and less steep slopes (Table 3). In post-harvest stands, *Q. prinus* retained the greatest importance of any *Quercus* species on plots where it occurred (Table 4).

Quercus velutina and *Q. rubra* largely disappeared across all plots following harvest (Fig. 2) and IVs of these species were weakly related to environmental variables in pre and post-harvest stands (Table 3; $\text{max adj. } R^2 = 0.201$). *Carya* species displayed an ordination pattern similar to *Q. alba* in post-harvest stands; their importance was strongly correlated with historically open canopies, less steep slopes, and reduced K and Ca availability in the NMS ordination (Table 2) and the genus largely disappeared from steeper more nutrient poor sites after harvest (Fig. 2). According to regression analysis, the limited importance of this genus in post-harvest stands was negatively associated with historically closed canopies and positively associated soil hydrogen saturation (Table 3).

As expected, early-successional species, including *L. tulipifera*, *P. serotina*, and *P. grandidentata*, established a strong presence in post-harvest stands (Table 4, Fig. 3). Prior to harvest, *L. tulipifera* was mostly found on mesic plots with high nutrient availability, but in postharvest stands its importance increased across environmental gradients. For example, plots in Stand 1 did not contain a single *L. tulipifera* prior to harvest, but in the post-harvest stand, it was the single most important species (IV = 22.8), more than double that of the most important *Quercus* species (*Q. prinus*, IV = 11.2). According to regression analysis, the importance of *L. tulipifera* in both pre and post-harvest stands was most strongly related to low levels of H saturation. *Populus grandidentata* and *P. serotina* were largely absent prior to harvest, but greatly increased in importance after harvest. *P. grandidentata* established on poor sites (most strongly associated with low CEC; Table 3) and *P. serotina* importance was associated with better sites (Table 2; Figs. 1b and 3). According to regression analysis, *P. serotina* IV was most associated with soils with low carbon content in post-harvest stands (Table 3). Stand 2 saw the largest increase in *P. grandidentata* importance where the species was absent prior to harvest but was the single most important species (IV = 26.9) after harvest displaying an importance three times greater than any *Quercus* species (*Q. prinus*, IV = 8.1; Table 4). *Prunus serotina* was most successful in Stand 6, increasing from an IV less than 1.0 to the second most important species (IV = 20.0) behind *A. saccharum* (IV = 24.8), and sixteen times more important than the most important *Quercus* species (black oak, IV = 1.2) in the postharvest stand (Table 4).

3.3. Contemporary seedling and sapling species composition and abundance

The 2011 seedling species data (stems ≤ 0.91 m in height) from all six stands were best described by a 3-dimensional solution in NMS, resulting in a final stress of 14.4 and instability criterion of < 0.000001 . Overall, the ordination explained 86% of the variance in seedlings species composition with axis 1 explaining the greatest proportion of variance in the ordination (48%), followed by axis 2 (21%) and axis 3 (17%). Soil calcium (ppm; $r = -0.375$), soil phosphorus (ppm; $r = -0.353$), CEC ($r = -0.349$), percent organic matter ($r = -0.345$), and percent nitrogen ($r = -0.339$) were most strongly correlated with axis 1 (Table 2). Transformed aspect displayed the strongest correlation with axis 1 of any non-edaphic variable ($r = -0.331$). Soil pH ($r = -0.595$, percent hydrogen saturation ($r = 0.565$), and percent soil calcium ($r = -0.565$) were most strongly associated with Axis 2. Percent historical canopy cover displayed the strongest correlation with axis 2 of any non-edaphic variable ($p = 0.428$). Two topographic variables, percent slope and slope position, were the variables most strongly associated with axis 3 ($r = -0.286$ and $r = -0.278$, respectively). Overall, axis 3 was poorly correlated with the variables we measured. The relative densities of *C. caroliniana*, *F. grandifolia*, *Ulmus* spp., *F. americana*, and *A. saccharum* were associated with better sites represented by greater pH, percent calcium saturation, soil nitrogen and

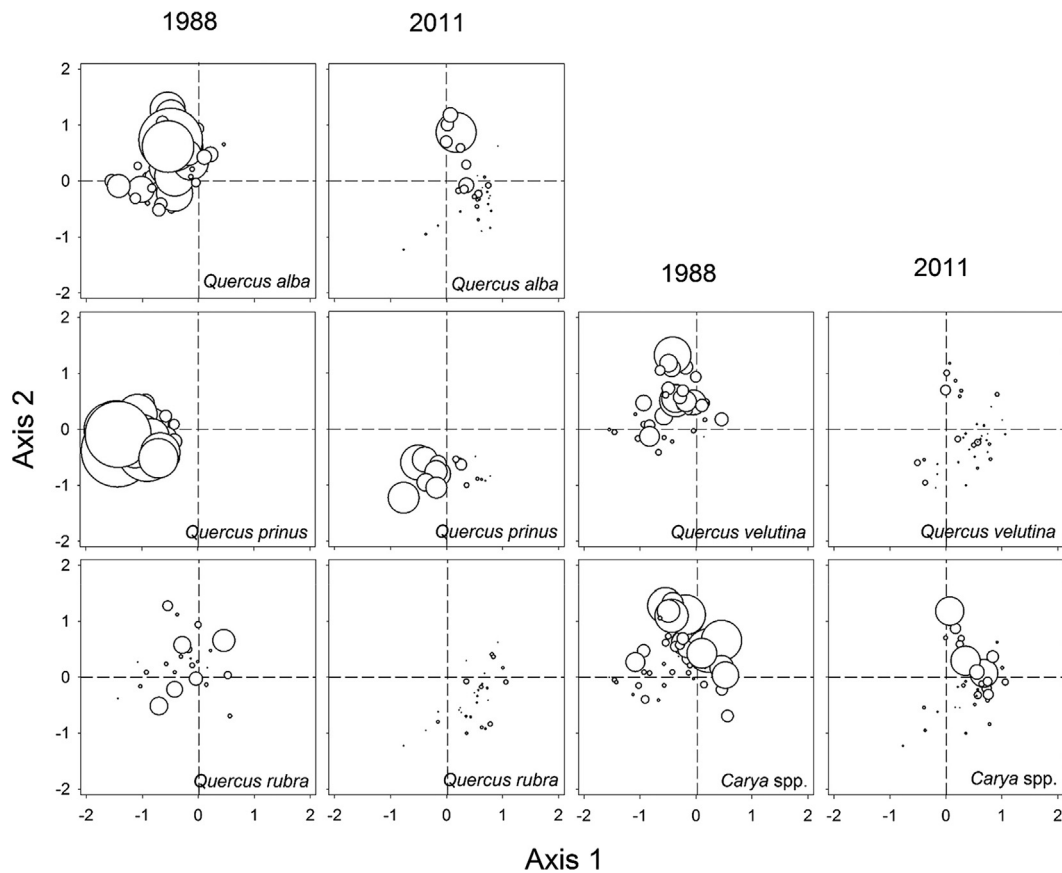


Fig. 2. Bubble plots of *Quercus* species importance overlain onto the NMS sample ordination of all six stands. Importance value of a species on a given plot is proportional to symbol size. (a) Pre-harvest (1988) species importance. (b) Species importance 23 years after harvest (2011).

CEC, while *Q. prinus*, *Q. rubra*, and *A. rubrum* were associated with poorer sites that had lower pH, CEC, soil calcium saturation, and soil nitrogen (Fig. 4).

Twenty-three years post-harvest, *A. rubrum* seedlings had the highest relative density in each stand with the exception of Stand 2, where *P. serotina* was most abundant (Table 5). Between 1988 and 2011, the relative density of *A. rubrum* increased greatly (six to 11-fold) in the three stands where *Acer* species were separated in the 1988 survey. *Cornus florida* was a dominant seedling species in 1988, but was a minor component of the seedling layer in 2011 (Table 5). *Viburnum acerifolium* (mapleleaf viburnum) was an important component of the seedling layer in most stands in 1988, but declined greatly in the 2011 inventory.

In 2011, *A. saccharum* dominated the woody sapling (> 0.91 m height, ≤ 5.1 cm dbh) layer in four out of six stands (Table 6). *Cornus florida* was an important sapling species in 1988 with relative densities ranging from 7.6 to 34.2 (Table 6). In 2011, the relative density of this species declined in all stands, ranging from 0 to 3.3. Three species, *Fagus grandifolia*, *F. americana*, and *O. virginiana* increased in relative density on five out of six stands between 1988 and 2011. Overall, seedlings and saplings of *Quercus* species were relatively scarce in both 1988 and 2011 (Tables 5 and 6).

4. Discussion

4.1. Pre-harvest conditions and historic disturbance

The sites sampled in this study covered a variety of physiographic conditions, including mesic slopes on northern and eastern aspects, dry-mesic slopes on southern and western aspects, and more exposed, xeric ridge tops. The fact that *Quercus* species were once dominant across this

range of site conditions, but were unable to regenerate under contemporary disturbance regimes, suggests that the genus was perpetuated by exogenous factors in pre-harvest stands. Evidence shows that widespread burning in this region created an historical mismatch between the physiographic limits set by climate and the expression of vegetation on the landscape (Nowacki and Abrams, 2008). Native Americans were the primary ignition source in presettlement Indiana, but as Europeans began settlement around 1800, fire frequencies quickly escalated (Guyette et al., 2003; Ponder, 2004). During this post-settlement period, large scale clearing and burning for cropland and open forest grazing by livestock further altered the landscape and helped perpetuate *Quercus* species. Starting in the 1930s, these agricultural lands were largely abandoned and fire was excluded from the system, allowing late-seral species to accumulate in the understories of maturing forests. In our study, we observed high densities of small diameter (sapling) *Acer* species prior to harvest, setting the stage for these forests to transition from early-mid seral *Quercus*-dominated communities to late-seral communities after harvest.

Historical aerial photographs flown between 1938 and 1940 displayed evidence of past disturbances in the stands we studied. In general, stands were much more open compared to the closed canopies that existed in 1988 prior to harvest. While the resolution of the photography did not allow fine-scale identification of individual disturbance agents, the openness of these stands suggests they were subjected to a well-documented array of disturbances (burning, grazing, logging and agriculture) that occurred across southern Indiana in the late 1800s and early 1900s (Sieber and Munson, 1992; Jenkins, 2013). In our study, *Q. prinus* and *Q. alba* showed contrasting affinities for historic canopy cover. As reflected in the NMS axis correlations, *Quercus prinus* was most dominant on plots with the highest historical canopy cover (84–100% pre-harvest cover), while *Q. alba* importance was positively

Table 3

Linear fixed and mixed-effects regression equations relating importance value (IV) of common overstory species in 1998 and 2011 to environmental variables. No model = analyses not run; six or fewer non-zero data points in sample year. Fixed effects regression analyses: VIF = mean of Variance Inflation Factor values for all independent variables. Mixed-effects regression analyses: *Rstand* STD = standard deviation of random effect *stand*; *Rstand* P = p-value of random effect *stand*. Environmental variable abbreviations are provided in Table 2.

Fixed-Effects Regression: Species	F	Adj. R ²	P	VIF
<i>Quercus alba</i>				
1988: Square root (IV) = 2.568–0.0905(%SL) + 0.0353(K) – 0.5605(%OM) + 0.0837(%H)	4.36	0.269	0.002	1.619
2011: ln(IV) = 3.733 – 0.0127(%CC) – 52.914(N) – 0.0374(%SL)	15.12	0.440	< 0.001	1.886
<i>Quercus prinus</i>				
1988: IV = –38.972 + 0.742(%CC) – 5.928(AS) – 0.079(Mg) + 4.740(%C)	32.96	0.709	< 0.001	1.213
2011: Square root = 7.117 + 0.043(%CC) + 0.460(%C) – 1.700(pH) – 0.106(P)	26.18	0.660	< 0.001	1.285
<i>Quercus rubra</i>				
1988: Square root (IV) = 0.651–0.048(%SL) + 0.040(K) – 0.104(%Mg)	5.52	0.201	0.002	1.384
2011: Square root (IV) = –1.371 + 0.0177(K) – 0.196(CEC) + 0.0347(%Ca)	3.42	0.118	0.024	1.742
<i>Quercus velutina</i>				
1988: Square root (IV) = 6.016–0.0641(%SL) – 10.729(%N)	6.81	0.177	0.002	1.021
2011: Square root (IV) = 1.778 + 0.282(%C) – 0.0684(P) – 0.0126(%CC)	5.36	0.195	0.003	1.144
<i>Acer</i> spp.				
1988: IV = 0.117 + 0.00160(SP) + 0.0104(P) – 0.00150(%CC)	5.08	0.185	0.004	1.068
2011: IV = –13.504 + 0.233(%CC) + 4.187(%OM)	9.01	0.294	< 0.001	1.000
<i>Carya</i> spp.				
1988: Square root (IV) = 5.907 – 0.0556(K) – 0.0176(SP) + 0.0155(Mg) – 0.0173 (%CC)	7.13	0.254	< 0.001	1.547
2011: ln (IV) = 2.394–0.0352(%CC) + 0.0384(%H)	20.99	0.425	< 0.001	1.272
<i>Fagus grandifolia</i>				
1988: Square root (IV) = –0.918 + 0.0626(%SL) – 0.1.431(%C) + 244.089(MgN)	5.83	0.211	0.002	2.855
2011: Square root (IV) = 1.962 + 0.0129(SP) – 0.0929(P)	9.64	0.243	< 0.001	1.022
<i>Liriodendron tulipifera</i>				
1988: ln (IV) = 5.260–0.0122(Mg) – 0.110(%H)	12.13	0.292	< 0.001	1.588
Mixed-Effects Linear Regression: Species	<i>Rstand</i> STD	<i>Rstand</i> P	Marg. R ²	Cond. R ²
<i>Liriodendron tulipifera</i>				
2011: ln (IV) = 6.851 + 0.0389(Ca) – 0.0871 (%H) + REstand	0.3934	0.049	0.1898	0.316
<i>Populus grandidentata</i>				
1988: No model				
2011: ln (IV) = 0.0985 + 0.0193(K) – 0.279(CEC) + 0.0236(%CC) + REstand	0.3976	0.008	0.497	0.6117
<i>Prunus serotina</i>				
1988: No model				
2011: Square root (IV) = 3.0551–8.7673(C) + 0.5505(%OM) + REstand	1.0251	< 0.0001	0.157	0.597

related to more historically open canopies in post-harvest stands. Historic canopy cover was positively correlated with percent slope and negatively correlated with percent soil calcium saturation, which supports the intuitive conclusion that less steep areas with better soils were used for agriculture. However, of all the environmental variables we included in our analyses, historic canopy cover was most strongly correlated with the distribution of species across NMS axes and was a significant term in regressions of *Q. alba*, *Q. prinus*, *Q. velutina*, *Acer* spp., *Carya* spp., and *P. grandidentata* importance, suggesting that its relationship with species distributions extends beyond being a covariate with topo-edaphic variables.

4.2. Post-harvest shifts in composition

Results from this long-term study illustrate a dramatic shift in species composition 23 years after clearcutting on the HNF. Following overstory removal, all stands experienced decreased importance of *Quercus* and *Carya* species and increased importance of other species including *A. rubrum*, *L. tulipifera*, *P. grandidentata*, and *P. serotina*. This corresponds with other reports of poor competition by *Quercus* species following clearcut harvests in southern Indiana (Standiford and Fischer, 1980; George and Fischer, 1989; Jenkins and Parker, 1998) and elsewhere in the CHR (Sander and Graney, 1992; Lorimer, 1993; Campione et al., 2012).

Prior to harvest, *L. tulipifera* was a common canopy tree in those stands where it maintained or increased its importance 23 years after harvest. Prolific seed production, wide dispersal, seed-banking ability, and rapid growth allowed the successful establishment of this species following clearcut harvests and its longevity may allow it to dominate

these stands for many decades (Boring et al., 1981; Burns and Honkala, 1990; Lambers and Clark, 2003). Observed increases on higher quality sites where the species held less importance prior to harvest supports other observations in young clearcut stands in southern Indiana (George and Fischer, 1989; Jenkins and Parker, 1998; Morrissey et al., 2008). We observed some increase in *L. tulipifera* importance on dry-mesic sites, but it is questionable whether stems established post-harvest will persist under more xeric conditions. Studies have shown that the importance of *L. tulipifera* decreases through time following clearcut harvest on dry sites (Hilt, 1985; Jenkins and Parker, 1998), particularly after drought events. For example, Morrissey et al. (2008) speculated that an exceptional drought occurring from 1986 to 1988 reduced the density of *L. tulipifera* stems in their study of southern Indiana clearcut sites and we have seen similar declines on nearby sites after the 2012 drought (Meier and Saunders 2014). In the current study, *L. tulipifera* was well established in all post-harvest stands and persisted for 23 years, but these stands initiated after the 1986–1988 drought occurred, likely permitting *L. tulipifera* to remain highly competitive across most sites. Future drought events may reduce *L. tulipifera* importance and eventually allow less drought-sensitive, shade-tolerant species, such as *A. rubrum* or *A. saccharum*, to secure growing space. Further research is needed to understand the competitive ability of *L. tulipifera* as stands on dry and dry-mesic sites transition into later developmental stages.

The increased importance of *P. serotina* and ruderal *P. grandidentata* we observed after harvest illustrates how these species can outcompete *Quercus* and *Carya* species in young stands (Swaim et al., 2016). Largely absent in our stands prior to harvest, *P. grandidentata* grew rapidly on drier sites where it occupied growing space that might otherwise be

Table 4
Importance value of overstory trees (mean ± 1 SE) by species in pre-harvest (1988) and post-harvest (2011) stands on the Hoosier National Forest. Post-harvest data were collected 23 years after clearcutting. IV = (RD + RBA)/2, where RD = relative density and RBA = relative basal area. **Acer rubrum* and *A. saccharum* were not delineated in stands 4, 5, and 6 during the 1988 sampling and are combined as *Acer* spp. for these stands.

Species	Stand 1		Stand 2		Stand 3		Stand 4		Stand 5		Stand 6	
	1988	2011	1988	2011	1988	2011	1988	2011	1988	2011	1988	2011
<i>Acer rubrum</i>	5.4 ± 0.9	18.6 ± 3.8	3.6 ± 1.2	7.7 ± 2.0	6.0 ± 2.1	11.6 ± 2.9	–	15.0 ± 2.6	–	1.7 ± 1.0	–	7.9 ± 2.6
<i>A. saccharum</i>	9.6 ± 2.2	10.9 ± 3.3	18.7 ± 4.0	16.6 ± 4.0	21.3 ± 4.2	6.8 ± 1.7	–	3.4 ± 1.2	–	7.9 ± 3.0	–	24.8 ± 7.3
<i>Acer</i> spp.*	–	–	–	–	–	–	9.8 ± 3.0	–	–	–	24.5 ± 7.7	–
<i>Carpinus caroliniana</i>	0	0	0	0.2 ± 0.2	0	0.6 ± 0.3	0	0	0.7 ± 0.7	6.6 ± 1.6	0	0.3 ± 0.3
<i>Carya</i> spp.	5.9 ± 1.7	0.6 ± 0.3	4.3 ± 2.0	1.0 ± 0.3	14.4 ± 3.7	5.9 ± 2.4	21.4 ± 3.7	9.9 ± 3.0	7.3 ± 3.1	4.4 ± 1.5	14.0 ± 3.9	3.5 ± 1.2
<i>Cercis canadensis</i>	0	0	0	0.1 ± 0.1	0.4 ± 0.3	0.7 ± 0.2	0	2.6 ± 0.8	0.5 ± 0.5	1.2 ± 0.7	0.1 ± 0.1	1.2 ± 0.9
<i>Cornus florida</i>	14.5 ± 2.1	0.3 ± 0.1	3.7 ± 1.1	0.5 ± 0.2	5.6 ± 1.7	0.7 ± 0.3	9.7 ± 1.5	1.6 ± 0.4	9.8 ± 2.3	3.3 ± 0.9	9.6 ± 2.8	1.2 ± 0.5
<i>Fagus grandifolia</i>	8.5 ± 3.4	3.0 ± 0.7	3.2 ± 1.6	1.5 ± 0.9	5.6 ± 2.3	2.8 ± 0.7	0.9 ± 0.4	1.0 ± 0.4	10.0 ± 5.2	6.1 ± 2.7	5.8 ± 3.6	2.2 ± 1.0
<i>Fraxinus americana</i>	0.9 ± 0.4	2.5 ± 0.6	0.6 ± 0.4	7.6 ± 2.0	1.1 ± 0.4	3.5 ± 0.9	2.9 ± 1.3	5.3 ± 1.9	1.8 ± 1.1	5.8 ± 1.4	6.4 ± 2.7	3.5 ± 1.2
<i>Liriodendron tulipifera</i>	0	22.8 ± 5.8	0.2 ± 0.2	6.2 ± 4.1	10.1 ± 5.5	25.6 ± 6.4	4.9 ± 3.4	12.8 ± 3.1	13.7 ± 4.6	13.0 ± 1.8	10.9 ± 7.0	9.7 ± 2.9
<i>Nyssa sylvatica</i>	2.4 ± 0.7	0.7 ± 0.3	2.1 ± 1.3	1.4 ± 0.6	2.4 ± 0.9	3.6 ± 0.8	2.6 ± 1.1	1.9 ± 0.8	0.7 ± 0.6	0.6 ± 0.2	2.1 ± 1.4	1.8 ± 1.3
<i>Ostrya virginiana</i>	0	2.8 ± 1.1	0.5 ± 0.4	3.7 ± 0.9	0	6.3 ± 1.0	0.1 ± 0.1	1.4 ± 0.5	1.4 ± 0.8	7.8 ± 3.3	1.1 ± 0.4	4.0 ± 1.0
<i>Populus grandidentata</i>	0	9.5 ± 1.8	0	26.9 ± 3.1	0	3.2 ± 0.9	1.2 ± 0.6	3.6 ± 1.1	0	0.9 ± 0.4	0	3.8 ± 2.0
<i>Prunus serotina</i>	0	2.7 ± 0.8	0	13.1 ± 2.6	0.3 ± 0.3	17.0 ± 1.7	0.1 ± 0.1	5.4 ± 2.2	0	8.9 ± 1.9	1.1 ± 0.5	20.0 ± 2.5
<i>Quercus alba</i>	6.6 ± 1.4	0.2 ± 0.2	21.7 ± 3.5	0.8 ± 0.3	9.5 ± 3.0	3.8 ± 1.3	20.2 ± 5.3	10.8 ± 3.2	7.0 ± 3.8	2.1 ± 1.8	10.6 ± 6.3	1.1 ± 0.5
<i>Q. cocinea</i>	2.4 ± 0.9	1.6 ± 1.1	1.3 ± 0.7	1.7 ± 0.6	0.3 ± 0.3	1.6 ± 0.8	0.6 ± 0.6	6.5 ± 2.8	4.0 ± 4.0	4.6 ± 4.6	0	0.1 ± 0.1
<i>Q. muhlenbergii</i>	0	0	0	0	0	0.2 ± 0.1	0	0.1 ± 0.1	0.2 ± 0.2	0.5 ± 0.3	0	0
<i>Q. prinus</i>	34.3 ± 5.8	11.2 ± 3.2	27.9 ± 5.8	8.1 ± 3.1	0	0	0	0	0	0	0	0
<i>Q. rubus</i>	1.1 ± 0.5	0.8 ± 0.3	3.7 ± 2.0	1.3 ± 0.5	1.8 ± 0.7	1.0 ± 0.5	5.1 ± 2.4	0.2 ± 0.1	2.1 ± 1.3	2.3 ± 0.6	3.4 ± 1.8	0.9 ± 0.6
<i>Q. velutina</i>	4.9 ± 1.3	1.1 ± 0.5	4.3 ± 2.2	0.9 ± 0.5	9.3 ± 3.2	1.8 ± 0.6	15.5 ± 2.9	2.4 ± 0.6	10.5 ± 5.2	2.5 ± 1.4	6.4 ± 2.0	1.2 ± 0.4
<i>Sassafras albidum</i>	1.7 ± 0.6	8.5 ± 2.0	1.0 ± 0.6	0.1 ± 0.1	10.8 ± 3.4	1.2 ± 0.7	4.5 ± 1.8	14.4 ± 2.1	1.5 ± 1.0	11.5 ± 2.2	2.7 ± 2.1	1.6 ± 1.1
<i>Ulmus</i> spp.	0.1 ± 0.1	0.5 ± 0.4	0.0 ± 0.0	0.3 ± 0.2	0	0.8 ± 0.4	0.1 ± 0.1	0.3 ± 0.1	0.8 ± 0.8	5.3 ± 3.0	1.1 ± 0.7	3.6 ± 1.4
Other species	1.7 ± 1.0	1.5 ± 0.6	3.3 ± 1.2	0.3 ± 1.2	1.0 ± 0.5	1.5 ± 0.5	0.4 ± 0.2	1.4 ± 0.4	1.5 ± 0.7	2.8 ± 0.4	0.1 ± 0.1	7.4 ± 1.7

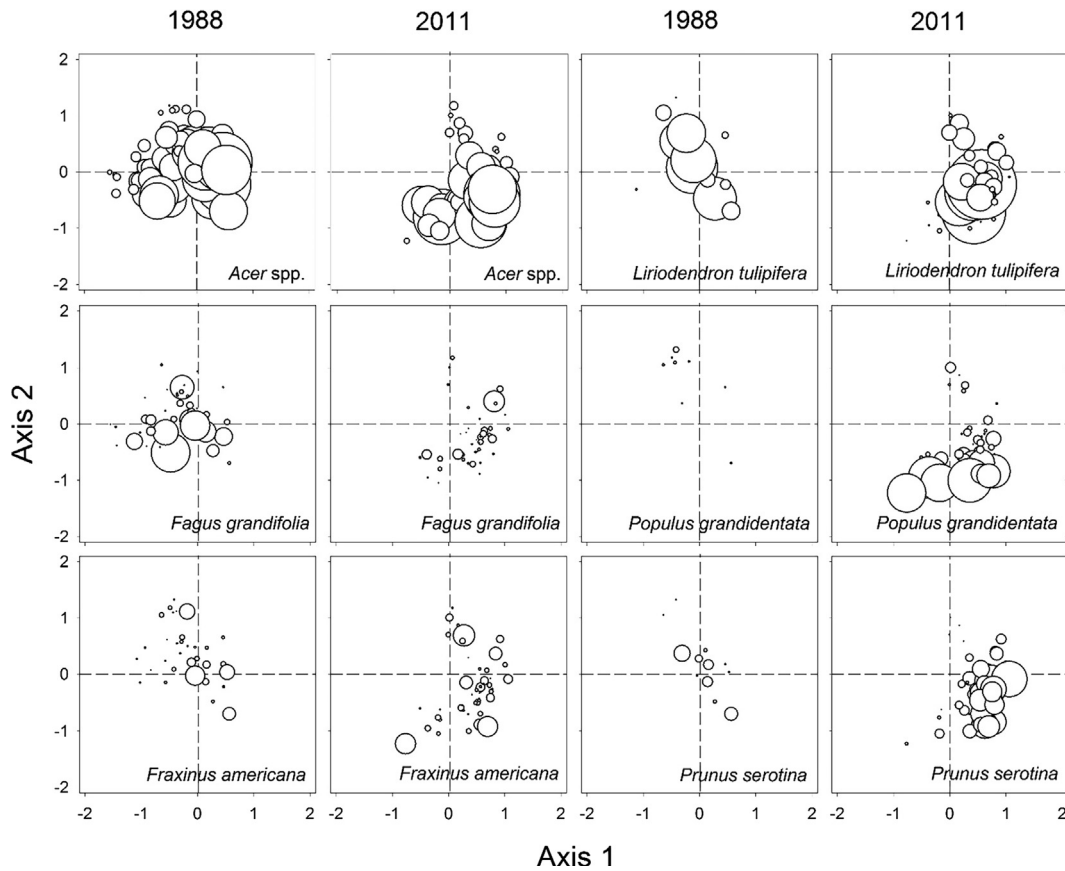


Fig. 3. Bubble plots of non-*Quercus* species importance overlain onto the NMS sample ordination of all six stands. Importance value of a species on a given plot is proportional to symbol size. (a) Pre-harvest (1988) species importance. (b) Species importance 23 years after harvest (2011).

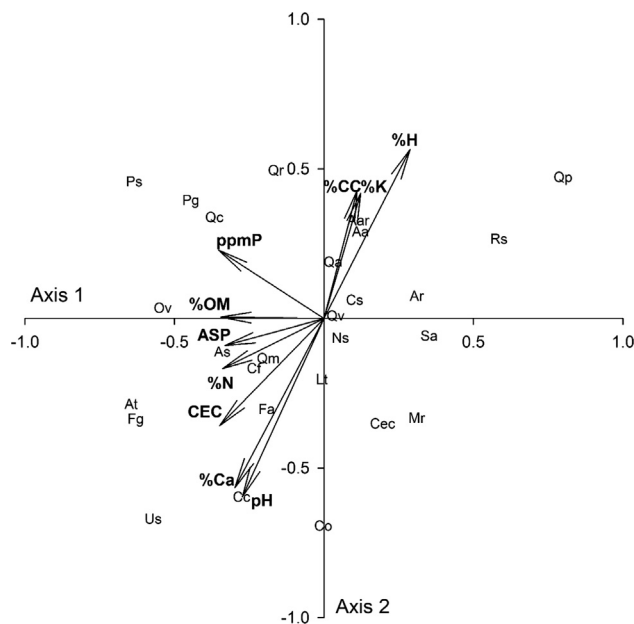


Fig. 4. NMS ordination of seedling species relative density across all six stands: Biplot of most important species in 2011 and dominant environmental variables ($r \geq 0.30$); ASP (transformed aspect), CEC (cation exchange capacity), %Ca (percent soil calcium saturation), %CC (percent historical canopy closure), %H (percent soil hydrogen), %K (percent potassium saturation), ppmP (soil phosphorus in ppm), pH (soil pH), %OM (percent organic matter), and %N (percent soil nitrogen) are shown as vectors. Explanations of species abbreviations are provided in Table 2.

utilized by dry-site hardwoods such as *Quercus* species (Kabrick et al., 2004). Barring future large canopy disturbances, the relatively short life span of *P. grandidentata* ensures it will eventually be replaced by other species, such as *A. rubrum*, that can establish under a closed canopy. In our 2011 survey, *A. rubrum* had the highest relative seedling density of any species in five of six study sites, highlighting the ability of this species to establish during stem exclusion.

On mesic and dry-mesic sites, *P. serotina* has filled a role similar to that of *P. grandidentata* on dry sites. Delayed germination, frequent seed crops, and wide dispersal by birds and mammals promote the establishment of *P. serotina* in many early-successional habitats without the presence of parent trees (Pairon et al., 2006; Vanhellefont et al., 2010). As an early-seral species, *P. serotina* replaced *Quercus* species on better sites in 23-year-old stands, and its ability to maintain a growth advantage over associated species for 60–80 years may safeguard against replacement on these more productive sites (Burns and Honkala, 1990).

Acer saccharum was an important species across all sites before treatment, and maintained similar importance 23 years after harvest. The high densities of small-diameter, advanced regeneration of *A. saccharum* forebode its dominance during stand development. Although a large proportion of these midstory *A. saccharum* stems were felled during harvest, smaller suppressed *A. saccharum* advance reproduction was released by the harvest. Also, since herbicides were not used on cut stems, dormant buds located on lower boles of cut *A. saccharum*s likely sprouted prolifically (Church and Godman, 1966), further perpetuating *A. saccharum* in developing stands. Traditionally, disturbance was thought to set succession back to an earlier stage. However, if the disturbance only affects canopy trees, accelerated succession may occur as suppressed stems are released (Abrams and Scott, 1989; Oliver and Larson, 1996). Although the 23-year-old stands in this study are

Table 5
Relative density (mean ± 1 SE) of woody seedlings (≤0.91 m height) by species in pre-harvest (1988) and post-harvest (2011) stands on the Hoosier National Forest. * *Acer rubrum* and *A. saccharum* were not delineated in stands 4, 5, and 6 during the 1988 sampling and are combined as *Acer* spp. for these stands.

Species	Stand 1		Stand 2		Stand 3		Stand 4		Stand 5		Stand 6	
	1988	2011	1988	2011	1988	2011	1988	2011	1988	2011	1988	2011
<i>Acer rubrum</i>	5.9 ± 2.2	38.9 ± 3.9	3.0 ± 1.1	22.0 ± 5.8	4.3 ± 1.5	46.5 ± 8.0	–	29.7 ± 5.1	–	21.7 ± 6.1	–	21.6 ± 5.7
<i>A. saccharum</i>	11.5 ± 3.1	1.8 ± 0.5	5.8 ± 1.6	1.4 ± 0.8	15.3 ± 3.0	2.1 ± 0.9	–	0.5 ± 0.2	–	2.5 ± 1.0	–	2.6 ± 0.7
<i>Acer</i> spp.*	–	–	–	–	–	–	9.2 ± 1.8	–	38.9 ± 5.4	–	36.0 ± 11.3	–
<i>Ailanthus altissima</i>	0	0	0	0	0	0	0	0	0	0	0	7.0 ± 2.3
<i>Asimina triloba</i>	0	0	0	0.2 ± 0.2	1.3 ± 1.3	0.6 ± 0.4	0	0	0.4 ± 0.4	0	0	0
<i>Carpinus caroliniana</i>	0	0	0	0.5 ± 0.3	0	0.7 ± 0.4	0	0.3 ± 0.3	0	18.8 ± 4.5	0.1 ± 0.1	0
<i>Carya</i> spp.	1.5 ± 0.5	0.9 ± 0.3	1.1 ± 0.3	4.4 ± 0.8	3.1 ± 0.6	2.0 ± 0.2	3.1 ± 0.6	7.4 ± 0.9	2.7 ± 0.5	3.3 ± 2.4	3.0 ± 0.8	2.0 ± 0.8
<i>Celtis occidentalis</i>	0.2 ± 0.2	0	0.7 ± 0.5	0	0.5 ± 0.3	0	0	0.6 ± 0.3	0	0	0	0.2 ± 0.1
<i>Cercis canadensis</i>	0.1 ± 0.1	0	0	0.4 ± 0.2	0.7 ± 0.5	3.4 ± 2.4	0.1 ± 0.1	16.7 ± 4.2	0	0.6 ± 0.3	0	2.3 ± 1.8
<i>Cornus florida</i>	31.8 ± 6.6	0.1 ± 0.1	4.5 ± 1.6	0	15.9 ± 7.2	0.1 ± 0.1	11.0 ± 1.6	0.7 ± 0.6	11.2 ± 1.7	0	12.6 ± 7.5	2.8 ± 1.2
<i>Fagus grandifolia</i>	3.3 ± 1.0	0.1 ± 0.1	1.1 ± 0.8	0.6 ± 0.4	2.8 ± 0.7	0.6 ± 0.5	0.6 ± 0.3	0.2 ± 0.1	4.1 ± 1.4	0.1 ± 0.1	2.4 ± 0.7	0.3 ± 0.2
<i>Fraxinus americana</i>	1.1 ± 0.4	6.4 ± 1.5	6.7 ± 1.5	3.4 ± 1.2	6.9 ± 2.9	7.5 ± 1.9	5.5 ± 2.0	10.5 ± 3.6	11.0 ± 4.1	10.4 ± 1.7	9.3 ± 2.9	9.4 ± 3.0
<i>Liriodendron tulipifera</i>	0.2 ± 0.1	4.3 ± 1.7	0.3 ± 0.2	2.1 ± 1.4	0.1 ± 0.1	3.5 ± 0.8	1.7 ± 0.7	4.5 ± 1.6	0.5 ± 0.3	4.7 ± 1.4	0.2 ± 0.2	4.4 ± 1.3
<i>Nyssa sylvatica</i>	1.1 ± 0.5	0.2 ± 0.1	1.4 ± 0.8	0.9 ± 0.4	0.2 ± 0.2	0.5 ± 0.2	3.0 ± 1.3	0.9 ± 0.3	0.6 ± 0.4	2.4 ± 0.6	1.4 ± 0.6	0.9 ± 0.6
<i>Ostrya virginiana</i>	0	7.2 ± 5.9	0.7 ± 0.7	13.1 ± 3.3	0	8.3 ± 1.6	3.2 ± 1.3	2.0 ± 0.7	14.6 ± 6.3	11.7 ± 3.4	4.0 ± 1.0	12.7 ± 4.5
<i>Populus grandidentata</i>	0	1.3 ± 0.9	0	4.5 ± 3.0	0	0.1 ± 0.1	3.2 ± 1.4	0.7 ± 0.3	0.7 ± 0.4	0.6 ± 0.2	0.7 ± 0.6	0.2 ± 0.1
<i>Prunus serotina</i>	0.3 ± 0.2	1.8 ± 0.4	2.3 ± 0.8	26.9 ± 7.3	2.2 ± 0.6	10.7 ± 3.5	1.8 ± 0.9	2.1 ± 1.0	1.0 ± 0.4	1.0 ± 0.6	2.8 ± 0.9	12.6 ± 4.4
<i>Quercus alba</i>	0.9 ± 0.3	0.2 ± 0.2	1.2 ± 0.8	3.6 ± 1.7	1.9 ± 0.6	0.5 ± 0.3	5.2 ± 2.2	2.1 ± 0.7	0.3 ± 0.3	1.1 ± 1.0	1.0 ± 0.5	0
<i>Q. coccinea</i>	0.1 ± 0.1	0	0	0.7 ± 0.4	0	0	0.1 ± 0.1	0.1 ± 0.1	0	0.2 ± 0.2	0	0
<i>Q. muhlenbergii</i>	0	0	0	0	0.2 ± 0.2	0.1 ± 0.1	0	0	0	0	0	0
<i>Q. prinus</i>	3.2 ± 2.2	8.5 ± 3.9	6.8 ± 2.3	1.3 ± 0.7	0.1 ± 0.1	0	0	0	0	0	0	0
<i>Q. rubra</i>	0.7 ± 0.3	0.2 ± 0.1	2.2 ± 1.1	0.5 ± 0.3	0	0.1 ± 0.1	1.1 ± 0.7	0.1 ± 0.1	0	0.1 ± 0.1	2.4 ± 0.8	0
<i>Q. velutina</i>	2.4 ± 0.7	0. ± 0.2	3.9 ± 1.5	0.9 ± 0.4	0.8 ± 0.8	0.5 ± 0.3	9.0 ± 2.5	1.5 ± 0.3	4.8 ± 3.9	0.5 ± 0.3	2.4 ± 1.5	1.1 ± 0.6
<i>Rhus</i> spp.	0	2.7 ± 1.4	0	0.2 ± 0.2	0	0.9 ± 0.4	0	0.1 ± 0.1	0	0	0	0
<i>Sassafras albidum</i>	15.1 ± 5.9	13.8 ± 3.0	11.8 ± 2.9	4.1 ± 1.2	10.3 ± 3.3	2.4 ± 0.7	29.6 ± 4.4	16.1 ± 2.8	3.2 ± 1.8	5.0 ± 1.8	7.0 ± 3.0	3.9 ± 2.0
<i>Ulmus</i> spp.	0	2.8 ± 1.9	0	0.5 ± 0.3	0.5 ± 0.3	7.8 ± 4.9	0.8 ± 0.3	0.9 ± 0.4	0.5 ± 0.3	7.0 ± 3.2	8.8 ± 7.3	15.1 ± 7.2
<i>Viburnum acerifolium</i>	18.2 ± 6.1	1.4 ± 1.1	34.8 ± 6.6	5.9 ± 3.4	21.1 ± 7.5	0.5 ± 0.4	10.8 ± 5.1	1.4 ± 0.7	1.6 ± 1.0	1.4 ± 0.8	3.5 ± 2.5	0
Other species	0.6 ± 0.3	6.5 ± 3.3	11.7 ± 2.7	2.0 ± 0.6	11.8 ± 3.0	0.7 ± 0.3	0.9 ± 0.3	0.7 ± 0.3	3.6 ± 2.0	3.6 ± 2.3	2.5 ± 1.7	1.0 ± 0.5

Table 6
Relative density (mean ± 1 SE) of woody saplings (> 0.91 m height; < 5.1 cm dbh) by species in pre-harvest (1988) and post-harvest (2011) stands on the Hoosier National Forest. *Acer rubrum* and *A. saccharum* were not delineated in stands 4, 5, and 6 during the 1988 sampling and are combined as *Acer* spp. for these stands.

Species	Stand 1		Stand 2		Stand 3		Stand 4		Stand 5		Stand 6	
	1988	2011	1988	2011	1988	2011	1988	2011	1988	2011	1988	2011
<i>Acer rubrum</i>	8.5 ± 4.2	15.4 ± 5.8	6.1 ± 2.3	12.1 ± 4.0	1.4 ± 0.9	2.7 ± 2.4	–	17.3 ± 5.4	–	0.7 ± 0.6	–	5.1 ± 2.1
<i>A. saccharum</i>	19.0 ± 7.8	17.0 ± 8.1	30.2 ± 9.7	34.4 ± 10.3	21.1 ± 5.8	24.4 ± 8.1	–	11.1 ± 6.9	–	32.3 ± 6.8	–	42.0 ± 12.1
<i>Acer</i> spp.	–	–	–	–	–	–	22.7 ± 7.1	–	49.2 ± 5.2	–	59.0 ± 15.7	–
<i>Atlantus altissima</i>	0	0	0	0	0	0	0	0	0	0	0	0.8 ± 0.7
<i>Amelanchier arborea</i>	0	1.2 ± 1.2	0	0	0	0	0.7 ± 0.7	0	0.4 ± 0.4	0	0	0
<i>Asimina triloba</i>	0	0	0	0	6.0 ± 5.4	4.2 ± 4.0	0	1.4 ± 1.3	3.3 ± 3.3	2.2 ± 0.9	0	0
<i>Carpinus caroliniana</i>	0	0	0	0	0	1.3 ± 1.2	0	1.4 ± 1.3	0	12.4 ± 3.3	0	0
<i>Carya</i> spp.	0	0	0	3.8 ± 1.5	1.6 ± 1.1	4.6 ± 1.6	0	1.1 ± 1.0	1.1 ± 0.6	2.6 ± 1.5	1.2 ± 1.2	0
<i>Cercis canadensis</i>	0	0	0	0	0	0	0	1.1 ± 1.0	0	1.9 ± 1.7	0	2.3 ± 2.1
<i>Cornus florida</i>	34.2 ± 8.0	0	7.6 ± 2.1	1.0 ± 0.7	24.4 ± 7.7	3.3 ± 2.1	24.3 ± 4.4	2.2 ± 2.1	14.8 ± 2.5	2.5 ± 1.4	21.1 ± 8.0	0
<i>Fagus grandifolia</i>	8.0 ± 2.8	20.4 ± 4.7	2.4 ± 1.5	6.6 ± 3.8	7.5 ± 2.5	5.5 ± 2.8	2.9 ± 1.5	3.1 ± 3.2	11.1 ± 4.0	17.6 ± 4.5	5.3 ± 2.7	6.3 ± 3.6
<i>Fraxinus americana</i>	0.7 ± 0.6	3.3 ± 2.1	8.6 ± 3.8	9.1 ± 3.3	1.4 ± 0.7	5.8 ± 2.2	1.9 ± 1.0	7.4 ± 5.1	6.7 ± 2.1	3.0 ± 1.4	0.6 ± 0.6	13.3 ± 4.7
<i>Liriodendron tulipifera</i>	0	3.1 ± 1.9	0.2 ± 0.2	1.8 ± 1.4	0.6 ± 0.6	1.4 ± 1.4	2.2 ± 2.2	3.7 ± 2.4	0	3.7 ± 2.3	0.9 ± 0.9	7.4 ± 6.0
<i>Nyssa sylvatica</i>	1.0 ± 0.6	0	1.2 ± 0.6	0	0	6.7 ± 5.4	5.3 ± 2.9	7.8 ± 4.1	0	1.3 ± 1.2	1.8 ± 1.8	2.0 ± 1.8
<i>Ostrya virginiana</i>	0.5 ± 0.5	20.6 ± 9.0	1.0 ± 1.0	15.1 ± 6.7	0	21.1 ± 5.1	2.2 ± 1.2	5.9 ± 3.8	3.9 ± 1.4	4.7 ± 2.8	3.3 ± 3.3	2.6 ± 1.6
<i>Populus grandidentata</i>	0	0	0	0.5 ± 0.5	0	0.8 ± 0.8	3.7 ± 2.2	0	0.6 ± 0.6	0	0.7 ± 0.7	0
<i>Prunus serotina</i>	0	6.3 ± 6.0	1.5 ± 0.6	2.9 ± 1.9	0	1.7 ± 1.1	4.4 ± 2.9	0	0.2 ± 0.2	0	0.6 ± 0.6	2.6 ± 1.6
<i>Quercus alba</i>	0	0	0.6 ± 0.4	2.9 ± 1.8	1.8 ± 0.7	6.7 ± 3.4	1.2 ± 0.9	7.3 ± 4.4	0.9 ± 0.7	2.0 ± 1.8	0	0
<i>Q. cocinea</i>	0	0	0	2.7 ± 1.8	0	0	0	4.4 ± 2.3	0	0	0	0
<i>Q. prinus</i>	1.8 ± 1.5	2.1 ± 1.4	2.9 ± 0.9	6.7 ± 5.4	0	0	0	0	0.3 ± 0.3	0	0	0
<i>Q. rubra</i>	0	3.7 ± 3.5	0.9 ± 0.6	0.4 ± 0.4	0	0	0	0	0.2 ± 0.2	0.9 ± 0.8	0.7 ± 0.7	0
<i>Q. velutina</i>	1.1 ± 0.6	0	1.1 ± 0.6	0.9 ± 0.6	0	2.5 ± 2.4	6.3 ± 4.4	2.8 ± 2.1	0.3 ± 0.3	0.6 ± 0.5	0	7.2 ± 3.4
<i>Rhus</i> spp.	0	0.4 ± 0.4	0	0	0	0	0	0	0	1.3 ± 1.2	0	0
<i>Sassafras albidum</i>	6.3 ± 3.0	5.3 ± 3.4	4.3 ± 2.8	0	8.8 ± 3.9	0	15.5 ± 4.6	21.9 ± 8.7	0.2 ± 0.2	6.8 ± 3.5	0.6 ± 0.6	4.3 ± 4.0
<i>Ulmus</i> spp.	0	0	0	1.1 ± 1.1	0.9 ± 0.9	0	0.6 ± 0.6	0	0	0.7 ± 0.7	1.3 ± 1.3	4.1 ± 2.4
<i>Viburnum acerifolium</i>	13.9 ± 6.3	0	20.8 ± 5.9	0.7 ± 0.7	13.2 ± 5.9	0.2 ± 0.2	2.2 ± 2.2	0	0.2 ± 0.2	0	2.0 ± 2.0	0
Other species	4.9 ± 1.7	1.2 ± 1.2	10.7 ± 3.0	0	11.5 ± 7.7	7.1 ± 6.8	3.7 ± 2.2	0	6.7 ± 3.2	2.6 ± 1.7	0.9 ± 0.9	0

currently dominated by early-seral species, sapling layers are largely dominated by *A. saccharum*, suggesting a likely future shift towards dominance by late-seral, self-replacing species. In the seedling layer, limited *Quercus* species reproduction is largely occurring on poor sites with low soil pH and limited nutrient availability.

4.3. Management implications

Maintaining *Quercus* in post-harvest stands located on more productive sites often depends on adequate densities of large advance reproduction at time of harvest (Sander and Clark, 1971). In some cases, large numbers of smaller *Quercus* seedlings are present, but these stems cannot compete with fast growing early-succession species (e.g., *P. serotina* and *S. albidum*) and the dense cover of ruderal herbaceous species (e.g., *Rubus* spp.). In the current study, *Quercus* importance drastically decreased following clearcut harvests, likely due to a lack of large advance reproduction that would have competed better in the post-harvest environment. The exception occurred on dry sites with historically closed canopies, where species like *Q. prinus* successfully established from stump sprouts originating from harvested trees (Swain, 2013), largely due to their higher propensity to sprout from sawlog-sized parents (Weigel and Peng, 2002). In a decade-long study of clearcut harvests on the HNF, Weigel and Peng (2002) found *Q. prinus* was the only species to maintain competitive success probabilities above 0.90 in year 1, year 5, and year 10. Although *Q. prinus* importance was relatively low 23 years after harvest, the high proportion of sprout origin trees may allow it to increase in relative importance as the stand matures and shorter-lived species such as *P. grandidentata* and *S. albidum* begin to die out. Other studies have also observed greater importance of *Quercus* species relative to mesophytic competitors following clearcutting on xeric sites (Hilt, 1985; Jenkins and Parker, 1998), and a prevalence of stump sprouts in post-harvest stands (Arthur et al., 1997; Morrissey et al., 2008).

Management strategies and practices following clearcutting may have produced more desirable species composition in our post-harvest stands. Pre-commercial crop tree thinnings that release desirable *Quercus* species during stem exclusion often improve *Quercus* stocking and dominance (Ward, 2009; Dey et al., 2010). This technique not only helps control undesirable overstory species, but helps reduce highly competitive midstory species such as *O. virginiana* and *S. albidum*, which were abundant in our post-harvest stands.

Periodic burning favors the establishment of *Quercus* species by increasing light levels on the forest floor and reducing competition (Brose et al., 2013; Iverson et al., 2017). Under this regime, high root:shoot ratio and the ability to resprout makes *Quercus* a strong competitor compared to mesophytic competitors that invest resources in aboveground growth. However, this trait makes *Quercus* a poor competitor in large canopy openings in the absence of fire where slower rates of shoot growth create a competitive disadvantage. Prior to overstory treatment, prescribed burning may be used as a site preparation tool to increase the relative abundance of *Quercus* seedlings by capitalizing on their superior ability to resprout after repeated burning compared to many mesophytic competitors (Brose et al. 2013).

Post-harvest burning is most effective during the earlier stages of stem exclusion (Brose and Van Lear, 1998). As stems reach larger diameters (> 10–13 cm) during later stages, and hence greater bark thicknesses, low intensity fire is less likely to top-kill mesophytic competitors (Brose et al., 2013; Schafer et al., 2015). As an alternative to clearcutting, two- or three-stage shelterwood treatments would also have offered a more viable option for regenerating *Quercus* in these stands. These methods provide adequate light to foster root development of shade-intolerant reproduction prior to final release while limiting establishment of faster growing species such as *P. serotina* and *L. tulipifera* (Loftis, 1990; Iverson et al., 2017). When combined with prescribed burning and herbicide treatments that control competitors and allow the well-established root systems of *Quercus* species to

resprout and establish as large advance reproduction, these techniques have proven successful and may offer the best hope for regenerating *Quercus* across much of the CHR (Dey et al., 2010). Once established, thinning should be used to release these crop trees before they lose vigor (Dey, 2014).

5. Conclusions

Clearcutting upland hardwoods on the HNF without additional control of competing vegetation has created a considerable shift in overstory species importance 23 years after harvest. Our results confirm that clearcutting alone is not an adequate disturbance for regenerating or maintaining historically *Quercus*-dominated forests in southern Indiana (George, 1988; Jenkins and Parker, 1998; Morrissey et al., 2008). However, on dry sites with historically closed canopies, *Q. prinus* persisted in the canopy of post-harvest stands, although a much reduced importance. The composition of pre-harvest stands was largely determined by more intense anthropogenic disturbances that often accompanied historic land use practices; and forest succession varied along edaphic and topographic gradients. The canopy dominance of *Quercus* in pre-harvest stands suggests that *Quercus* benefited from a historic regime that was dominated by anthropogenic disturbance (i.e., fire, grazing and heavy cutting) that allowed the genus to become dominant across environmental gradients. Without management to limit competitors, *Quercus* species will continue to disappear from all but the poorest sites, while species such as *A. rubrum* and *L. tulipifera* will continue to dominate across much of the environmental gradient. If clearcut harvesting continued throughout the CHR, then it is likely that *Quercus* would continue to decrease in importance, and with each forest rotation there would be fewer and fewer *Quercus* stems until the genus is lost or relegated to the status of a minor associate in the new forest types. As the number of seed-bearing *Quercus* trees decrease in the overstory from one rotation to the next, the likelihood of abundant oak advance reproduction decreases. Therefore, relying on *Quercus* stump sprouts to perpetuate *Quercus* in new stands is a losing strategy in the long-term because not all large, older overstory *Quercus* are vigorous sprouters (Weigel and Peng 2002). If maintaining *Quercus* species is a primary goal, alternatives to clearcutting should be considered, such as shelterwood prescriptions that include prescribed burning or herbicide control of competing vegetation to promote *Quercus* regeneration. Intermediate stand treatments, such as precommercial crop tree release, offer other viable options for sustaining desired levels of *Quercus* stocking in new stands.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.06.028>.

References

- Abrams, M.D., 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiol.* 7, 227–238.
- Abrams, M.D., Scott, M.L., 1989. Disturbance-mediated accelerated succession in two Michigan forest types. *For. Sci.* 35, 42–49.

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Limp, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
- Arthur, M.A., Muller, R.N., Costello, S., 1997. Species composition in a central hardwood forest in Kentucky 11 years after clearcutting. *Am. Midland Naturalist* 137, 274–281.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* 67, 1–48.
- Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. *J. For.* 64, 691–692.
- Boring, L.R., Monk, C.D., Swank, W.T., 1981. Early regeneration of a clearcut southern Appalachian forest. *Ecology* 62, 1244–1253.
- Brose, P.H., Van Lear, D.H., 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Can. J. For. Res.* 28, 331–339.
- Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2013. A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in eastern North America? *For. Sci.* 59, 322–334.
- Burns, R.M., Honkala, B.H., 1990. *Silvics of North America: Volume 2. Hardwoods*. United States Department of Agriculture, Forest Service.
- Campione, M.A., Nagel, L.M., Webster, C.R., 2012. Herbaceous-layer community dynamics along a harvest-intensity gradient after 50 Years of consistent management. *Open J. For.* 2, 97–109.
- Church, T.W., Godman, R.M., 1966. The formation and development of dormant buds in sugar maple. *For. Sci.* 12, 301–306.
- Clark, F.B., Watt, R.F., 1971. Silvicultural methods for regenerating oaks. In: White, D.E., Roach, B.A. (Eds.), *The Silviculture of Oaks and Associated Species*. USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA, pp. 37–43.
- Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Demchik, M., Sharpe, W.E., 2000. The effect of soil nutrition, soil acidity, and drought on northern red oak (*Quercus rubra* L.) growth and nutrition on Pennsylvania sites with high and low red oak mortality. *For. Ecol. Manage.* 136, 199–207.
- Dey, D.C., 2002. The Ecological Basis for Oak Silviculture in Eastern North America. In: McShea, W.J., Healy, W.M. (Eds.), *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Johns Hopkins University Press, Baltimore, MD, pp. 60–79.
- Dey, D.C., Royo, A.A., Brose, P.H., Hutchinson, T.F., Spetich, M.A., Stoleson, S.H., 2010. An ecologically based approach to oak silviculture: A synthesis of 50 years of oak ecosystem research in North America. *Revista Colombia Forestal* 13, 201–222.
- Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *Forest Sci.* 60, 926–942.
- Ellison, A.M., Banks, M.S., Clinton, B.D., Colburn, E.A., Elliot, K., Ford, C.R., Foster, D.R., Kloepfel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Houe, B.V., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3, 479–486.
- Fei, S., Kong, N., Steiner, K.C., Moser, W.K., Steiner, E.B., 2011. Change in oak abundance in the eastern United States from 1980 to 2008. *For. Ecol. Manage.* 262, 1370–1377.
- Futuyma, D.J., Gould, F., 1979. Associations of plants and insects in a deciduous forest. *Ecol. Monogr.* 49, 33–50.
- George, D.W., 1988. *Tree regeneration response to clearcut harvesting on the Hoosier National Forest*. MS Thesis, Purdue University, West Lafayette, IN.
- George, D.W., Fischer, B.C., 1989. The effects of site and age in tree reproduction in young upland hardwood clearcuts. In: Rink, G., Budelsky, C.A. (Eds.), *Proceedings of the Seventh Central Hardwood Conference*. NC-132. U.S. Department of Agriculture, Forest Service, Carbondale, IL, pp. 40–47.
- Guyette, R.P., Dey, D.C., Stambaugh, M.C., 2003. Fire and human history of a barren-forest mosaic in southern Indiana. *Am. Midl. Nat.* 149, 21–34.
- Guyette, R.P., Dey, D.C., Stambaugh, M.C., Muzika, R.-M., 2005. Fire scars reveal variability and dynamics of eastern fire regimes. In: *Fire in Eastern Oak Forests: Delivering Science to Land Managers*, Proceedings of a Conference. USDA Forest Service, Ohio State University, Columbus, Ohio, pp. 20–39.
- Hilt, D.E., 1985. Species composition of young central hardwood stands that developed after clearcutting. In: Dawson, J.O., Majerus, K.A. (Eds.), *Proceedings of the 5th Central Hardwood Forest Conference*, 15–17 April 1985. Department of Forestry, University of Illinois Urbana, Champaign, Ill, Champaign, Illinois, pp. 11–14.
- Homoya, M.A., Abrell, D.B., Aldrich, J.R., Post, T.W., 1985. The natural regions of Indiana. *Proc. Indiana Acad. Sci.* 94, 245–268.
- Iverson, L.R., Hutchinson, T.F., Peters, M.P., Yaussy, D.A., 2017. Long-term response of oak-hickory regeneration to partial harvest and repeated fires: influence of light and moisture. *Ecosphere* 8:e01642. [10.1002/ecs2.1642](https://doi.org/10.1002/ecs2.1642).
- Jenkins, M.A., 2013. The history of human disturbance in forest ecosystems of southern Indiana. In: Swihart, R.K., Saunders, M.R., Kalb, R.A., Haulton, G.S., Michler, C.H. (Eds.), *The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management*. U.S. Department of Agriculture, Forest Service, Northern Forest Experiment Station Gen. Tech. Rep. NRS-P-108, Newtown Square, PA, USA, pp. 2–11.
- Jenkins, M.A., Pallardy, S.G., 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Can. J. For. Res.* 25, 1119–1127.
- Jenkins, M.A., Parker, G.R., 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. *For. Ecol. Manage.* 109, 57–74.
- Johnson, P., Shifley, S., Rogers, R., 2009. *The Ecology and Silviculture of Oaks*. CABI Publishing, New York.
- Kabrick, J.M., Shifley, S.R., Jensen, R.G., Larsen, D.R., Grabner, J.K., 2004. Oak forest composition, site quality, and dynamics in relation to site factors in the southeastern Missouri Ozarks. In: Spetich, M.A. (Ed.), *Upland oak ecology symposium: history, current conditions, and sustainability*. Gen. Tech. Rep. SRS-73. USDA Forest Service, Southern Research Station, Asheville, NC, pp. 311.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: tests in linear mixed effects models. *J. Stat. Soft.* 82, 1–26.
- Lambers, J.H.R., Clark, J.S., 2003. Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. *Can. J. For. Res.* 33, 783–795.
- Latham, R.E., Ricklefs, R.E., 1993. Continental comparisons of temperate-zone tree species diversity. In: Ricklefs, R.E., Schluter, D. (Eds.), *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 294–314.
- Levanič, T., Čater, M., McDowell, N.G., 2011. Associations between growth, wood anatomy, C isotope discrimination and mortality in a *Quercus robur* forest. *Tree Physiol.* 31, 298–308.
- Loftis, D.L., 1990. A shelterwood method for regenerating red oak in the southern Appalachians. *For. Sci.* 36, 917–929.
- Lorimer, C.G., 1993. Causes of the oak regeneration problem. In: *Oak Regeneration: Serious Problems, Practical Recommendations*, USDA Forest Service General Technical Report SE-84. Southeastern Forest Experiment Station, Asheville, North Carolina, pp. 14–39.
- McCune, B., Grace, J.B., Urban, D.L., 2002. *Analysis of Ecological Communities*. MjM Software Design Glenden Beach, Oregon, USA.
- McCune, B., Mefford, M.J., 2011. *PC-ORD: Multivariate Analysis of Ecological Data*. MjM Software Design, Glenden Beach, Oregon, USA.
- McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34, 244–256.
- McGee, C.E., 1987. Clearcutting in upland hardwoods: panacea or anathema? In: Hay, R.L., Woods, F.W., DeSelm, H. (Eds.), *Proceedings of the 6th Central Hardwood Forest Conference*. University of Tennessee, Knoxville, pp. 21–29.
- Meier, A.R., Saunders, M.R., 2014. Initial observations on tree mortality following a severe drought in 2012 in two Indiana state forests and implications for long-term compositional dynamics. In: Groninger, J.W., Holzmueller, E.J., Nielsen, C.K., Dey, D.C. (Eds.), *Proceedings of the 19th Central Hardwood Forest Conference*. Gen. Tech. Rep. NRS-P-142. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 347–350.
- Morrissey, R.C., Jacobs, D.F., Seifert, J.R., Fischer, B.C., Kershaw, J.A., 2008. Competitive success of natural oak regeneration in clearcuts during the stem exclusion stage. *Can. J. For. Res.* 38, 1419–1430.
- Nelson, T.C., 1955. Chestnut replacement in the southern highlands. *Ecology* 36, 352–353.
- Neter, J., Kutner, M.H., Nachtsheim, C.J., Wasserman, W., 1996. *Applied linear regression models*. Irwin, Chicago.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58, 123–138.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*, Update edition. John Wiley & Sons Inc.
- Opler, P.A., 1974. Oaks as evolutionary islands for leaf-mining insects. *Am. Sci.* 62, 67–73.
- Pairon, M., Chaberrie, O., Casado, C.M., Jacquemart, A.-L., 2006. Sexual regeneration traits link to black cherry (*Prunus serotina* Ehrh.) invasiveness. *Acta Oecol.* 30, 238–247.
- Pallardy, S.G., Rhoads, J.L., 1993. Morphological adaptations to drought in seedlings of deciduous angiosperms. *Can. J. For. Res.* 23, 1766–1774.
- Parker, W.C., Dey, D.C., 2008. Influence of overstory density on ecophysiology of red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*) seedlings in central Ontario shelterwoods. *Tree Physiol.* 28, 797–804.
- Plieninger, T., Rolo, V., Moreno, G., 2010. Large-scale patterns of *Quercus ilex*, *Quercus suber*, and *Quercus pyrenaica* regeneration in central-western Spain. *Ecosystems* 13, 644–660.
- Ponder Jr, F., 2004. Ecological regions and soil conditions in the Hoosier-Shawnee ecological assessment area. The Hoosier-Shawnee Ecological Assessment. Gen. Tech. Rep. NC244. St. Paul, MN: US Department of Agriculture, Forest Service, North Central Research Station, pp. 9–22.
- R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Last accessed on May 24, 2018.
- Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* 95, 85–94.
- Roach, B.A., Gingrich, S.F., 1968. Even-aged silviculture for upland central hardwoods. Forest Service, USDA Forest Service, Agricultural Handbook, 39p.
- Sander, I.L., Clark, F.B., 1971. Reproduction of upland hardwood forests in the Central States. Agriculture Handbook No. 405. U.S. Department of Agriculture, Forest Service.
- Sander, I.L., Graney, D.L., 1992. Regenerating oaks in the central states. In: *Oak Regeneration: Serious Problems Practical Recommendations*. USDA Forest Service GTR SE-84, pp. 174–183.
- Schafer, J.L., Breslow, B.P., Hohmann, M.G., Hoffmann, W.A., 2015. Relative bark thickness is correlated with tree species distributions along a fire frequency gradient. *Fire Ecol.* 11, 74–87.
- Shrestha, B.B., 2003. *Quercus semecarpifolia* Sm. in the Himalayan region: Ecology, exploitation and threats. *J. Himalayan Sci.* 1, 126–128.
- Sieber, E., Munson, C.A., 1992. *Looking at History: Indiana's Hoosier National Forest Region, 1600 to 1950*. US Dept. of Agriculture, Forest Service.
- Soil Survey Staff, Natural Resources Conservation Service, USDA, 2017. *Web Soil Survey*

- <http://websoilsurvey.nrcs.usda.gov/>. Accessed October 10, 2017.
- Southwood, T.R.E., 1961. The number of species of insect associated with various trees. *J. Anim. Ecol.* 30, 1–8.
- Standiford, R.B., Fischer, B.C., 1980. Fifteen year results of three harvesting methods on composition and development of regeneration in southern Indiana upland hardwoods. In: Garrett, H.E., Cox, G.S. (Eds.), *Proceedings of the 3rd Central Hardwood Forest Conference*, 16–17 September 1980, Columbia, Missouri. University of Missouri Press, Columbia, Missouri, pp. 408–419.
- Swaim, J.T., 2013. Stand development and the competitive ability of oak (*Quercus* spp.) following silvicultural clearcutting on the Hoosier National Forest. M.S. Thesis. Purdue University, West Lafayette, IN, 106 p.
- Swaim, J.T., Dey, D.C., Saunders, M.R., Weigel, D.R., Thornton, C.D., Kabrick, J.M., Jenkins, M.A., 2016. Predicting the height growth of oak species (*Quercus*) re-production over a 23-year period following clearcutting. *For. Ecol. Manage.* 364, 101–112.
- Trimble, G.R., Hart, G., 1961. An appraisal of early reproduction after cutting in northern Appalachian hardwood stands. Northeastern Forest Experiment Station, Forest Service, US Department of Agriculture.
- Van Kley, J., Parker, G., Franzmeier, D., Randolph, J., 1995. Field guide: ecological classification of the Hoosier National Forest and surrounding areas of Indiana. USDA Forest Service, Hoosier National Forest.
- Vanhellemont, M., Wauters, L., Baeten, L., Bijlsma, R.-J., De Frenne, P., Hermy, M., Verheyen, K., 2010. *Prunus serotina* unleashed: invader dominance after 70 years of forest development. *Biol. Invasions* 12, 1113–1124.
- Vodka, S., Konvicka, M., Cizek, L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *J. Insect Conserv.* 13, 553–562.
- Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. *J. Ecol.* 98, 725–736.
- Ward, J.S., 2009. Intensity of precommercial crop tree release increases diameter growth and survival of upland oaks. *Can. J. For. Res.* 39, 118–130.
- Weigel, D.R., Peng, C.-Y.J., 2002. Predicting stump sprouting and competitive success of five oak species in southern Indiana. *Can. J. For. Res.* 32, 703–712.
- Woods, F.W., Shanks, R.E., 1959. Natural re- placement of chestnut by other species in the Great Smoky Mountains National Park. *Ecology* 40, 349–361.
- Zavaleta, E.S., Hulvey, K.B., Fulfrost, B., 2007. Regional patterns of recruitment success and failure in two endemic California oaks. *Divers. Distributions* 13, 735–745.