DYNAMICS AND DISTURBANCE IN AN OLD-GROWTH FOREST REMNANT IN WESTERN OHIO

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DYNAMICS AND DISTURBANCE IN AN OLD-GROWTH FOREST REMNANT IN WESTERN OHIO

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ABSTRACT

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Forest communities are dynamic through time, reacting to shifts in disturbance and climate regimes. A widespread community shift has been witnessed in many forests of eastern North America wherein oak (*Quercus* spp.) populations are decreasing while maple (*Acer* spp.) populations are increasing. Altered fire regimes over the last century are thought to be the primary driver of oak-to-maple community shifts; however, the influence of other non-equilibrium processes on this community shift remains under-explored. Our study sought to determine the community structure and disturbance history of an old-growth forest remnant in an area of western Ohio where fires were historically uncommon. To determine community structure, abundance of woody species was measured within 32 plots at 4 canopy strata and dendrochronology was used to determine the relative age-structure of the forest. Dendroecological techniques were also used to determine the disturbance history of the site. We found that early- and mid-successional genera such as oaks and hickories (*Carya* spp.) decreased in abundance while maples increased in abundance. A shift in disturbance regime ca. 1890 was the primary reason for the observed change in community structure. A suite of ‘multiple-interacting drivers’ such as anthropogenic land use changes to the areas surrounding the site and alterations in herbivore population density were responsible for the dominance shift that has occurred in this old-growth forest remnant.

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INTRODUCTION

Forests are dynamic systems that are highly influenced by variations in climate conditions, biological interactions, and disturbance events (Sprugel 1991). These agents of influence are not mutually exclusive; for instance, fluctuations in climate patterns can trigger drought which can shift the competitive balance in forests and drive an increase in the frequency and intensity of fire (Sprugel 1991; Swetnam & Lynch 1993). Shifts in disturbance regimes can drive shifts in species composition, and these dynamics can occur across large spatial scales (Brown & Wu 2005; McEwan et al. 2011). Humans have altered forest processes for many millennia (Bowman et al. 2009), and it is often difficult to distinguish anthropogenic drivers of dominance shifts from natural ecological processes (Whitney 1994).

Oaks (*Quercus* spp.) have historically been one of the dominant genera in the Eastern Deciduous Forest (Abrams & Nowacki 1992; McShea & Healy 2002). Since the mid-twentieth century, ecologists have repeatedly noted a lack of oak regeneration in closed-canopy forests while more shade-tolerant species, like sugar maple (*Acer saccharum* Marsh.), are increasing in dominance (Braun 1950; Lorimer 1984; Nowacki et al. 1990; Cho & Boerner 1991; McEwan & Muller 2006). Most oak species are considered early- to mid-successional and require canopy-opening disturbance to achieve upper-canopy status, while maple species are considered late-successional and flourish in shaded, mesic environments (Canham 1988; Abrams 1992). Because oaks are relatively shade-intolerant, larger-scale and frequent disturbances that increase light availability are thought to benefit oak regeneration in eastern deciduous forests (Lorimer & White 2003). Changes in disturbance regimes are thought to be driving this oak-to-maple dominance shift throughout the eastern United States (Arthur et al. 1998; Nowacki & Abrams 2008).

Individual treefalls are the most frequent type of natural disturbance in old-growth forest ecosystems (Runkle 1982; Rentch 2002). Treefalls result in gaps in the canopy and allow for increased sunlight to reach the forest floor (Rentch 2002). Previous studies have shown that gap-scale disturbances result in increased sugar maple density (Cho & Boerner 1991; Goebel & Hix 1997). Larger scale natural disturbances, such as ice storms, tornadoes, and hurricanes, are less frequent, but also play a role in forest succession (Turner et al. 1997; Foster et al. 1998). Oaks tend to be less susceptible to ice storm damage than maples (Rebertus et al. 1997), but, according to previous studies, communities of understory trees growing in ice storm-created gaps do not differ from surrounding understory communities (Rebertus et al. 1997; Mou & Warrilow 2000). Dyer and Baird (1997) found that windstorms can promote maple's transition from the understory to midstory or canopy dominance.

Alterations in fire regimes have been proposed as the primary driver of oak-to-maple dominance shifts (Abrams 1992; Abrams & Nowacki 1992; Nowacki & Abrams 2008). Historically, Native Americans and European settlers used fire as a means of clearing land for agricultural purposes (Abrams & Nowacki 1992; Whitney 1994). In addition to fires started by lightning strikes, it is thought that historic anthropogenic forest burning has shaped the landscape of eastern deciduous forests for over 9,000 years (Abrams 1992). The hypothesis that fires have shaped oak populations across the eastern United States is widely accepted in the literature (Abrams 1992; Abrams & Nowacki 1992; Whitney 1994; McShea & Healy 2002; Nowacki & Abrams 2008), and prescribed fire has been utilized to inhibit oak-to-maple transitions (Hutchinson et al. 2005; Albrecht and McCarthy 2006; Green and Arthur 2010); however, Bowman et al. (2009) suggested that fire is not well understood as a natural process. It has been proposed that, while fires have played an important role in shaping the eastern deciduous forests, other drivers such as shifting climate patterns and the loss of keystone species have also influenced oak-maple dynamics in eastern United States (McEwan et al. 2011).

Reconstructions of forest disturbance history are often necessary to understand how succession has shaped forests through time, and can be accomplished using dendroecological techniques (Lorimer & Frehlich 1989; Rentch et al. 2002; Black et al. 2009; Hart et al. 2012). By looking at the annual growth rings of trees currently dwelling in the upper canopy of mature forests, inferences can be made about the history of the surrounding environment throughout the individual tree’s life (Black et al. 2009). Periods of increased growth, hereafter referred to as growth releases, are indicative of disturbances that altered the existing upper canopy stratum during that time (Black et al. 2009). The nature of disturbance can be inferred based on the scale and timing of growth releases (Lorimer & Frehlich 1989; Rentch 2002; Black et al. 2009).

A mesic, old-growth forest remnant in western Ohio provided the opportunity to study the role of disturbance in shaping community structure. The study site is characterized by poorly-drained soils (Boerner & Kooser 1991), and lies within a region where, historically, fires were rare (Nowacki & Abrams 2008). The specific objectives were to (1) characterize the community structure by surveying woody vegetation, (2) use dendrochronology to determine the successional state of the forest, (3) reconstruct disturbance history via dendroecological analysis to determine the scale and timing of disturbances, and (4) infer the role disturbance has played in driving dominance shifts within the study site.

MATERIALS AND METHODS

Study site

This study took place within Drew Woods State Nature Preserve (DWSNP, 40°15’N, 84°39’W), a 6 ha old-growth forest remnant located in west-central Ohio. The topography of DWSNP is relatively flat, and the soils have been previously characterized as Blount silt loam and Glynwood silt loam (Boerner & Kooser 1991). Climate at this site consists of warm, humid summers, cold winters, and no distinct dry season. The mean annual temperature is 10.2 °C and the mean annual precipitation is 95.5 cm (National Climatic Data Center 2012).

Vegetation sampling

Plots were established throughout DWSNP using a systematic sampling approach. Using data donated by the office of the Darke County Auditor, a digital grid with transects spaced 20 m apart was designed with ArcMap (version 9) software (Figure 1). Plot center stakes were established at alternating gridline intersections for a total of 32 plots (distance between stakes was ~40 m). Attempts were made to make plots equidistant; however, some gridpoint locations were avoided due to vernal and semi-permanent ponds. Nested, circular plots were established around each stake to measure the “upper-canopy” (314 m^2), the “shrub-layer” (10 m^2), and the “ground-layer” (1 m^2) in June and July of 2011. Within the upper-canopy plots, trees ≥ 2.54 cm diameter at breast height (DBH) were identified to species, measured for DBH, and classified further into 2 subcategories: overstory (stems ≥ 20 cm DBH) or midstory (stems ≥ 2.54 cm DBH, but < 20 cm DBH). Within shrub-layer plots, woody-stemmed individuals ≥ 50 cm in height, but < 2.54 cm DBH were identified to species and tallied. Within ground-layer plots, woody-stemmed individuals were identified, counted, and assigned a coverage class using a modified Domin scale (<1%, 1-4%, 5-10%, 11-25%, 26-35%, 36-50%, 51-75%, 76-90%, 91-100%; Dahl and Haduc 1941). These woody vegetation surveys were conducted in June and July of 2011. Vegetation data were used to calculate relative abundance, stem density (stems ha^{-1}), and relative basal area (m^2 ha^{-1}; upper-canopy plots only).

Dendrochronology

Dendrochronological sampling was conducted from August to December of 2011. Trees throughout the stand were selected based on appearance (Pederson 2010) and genus (only *Quercus*, *Fraxinus*, and *Carya* were sampled). Forty-seven total trees were sampled: 14 *Fraxinus* spp., 14 *Quercus* spp., and 19 *Carya* spp. Sampled trees were identified to species (when possible), measured for DBH, and the location was recorded using a handheld GPS unit. Tree core samples were then taken to the laboratory for sanding, counting, and measuring in accordance with standard dendrochronological techniques (Speer 2010). Ring-widths were measured using a Velmex® measuring system, and COFECHA software was used to ensure quality control at the 99% confidence level.

Data analysis

Vegetation data were subdivided into two groups: living trees and snags. For each plot, percent relative abundance and density (stems ha^{-1}) were calculated for all living individuals. Species dominance (m^2 ha^{-1}) was calculated for all living trees in the upper-canopy (overstory and midstory) except for minor species occurring in < 3 plots. Genera dominance (m^2 ha^{-1}) was calculated for all snags ≥ 2.5 cm DBH except for minor (occurring on < 3 plots) genera and unknowns. Shapiro-Wilk normality tests indicated data were not normally distributed; thus, Kruskal-Wallis one-way analyses of variance (nonparametric) were used to compare densities of living *Acer* spp., *Carya* spp., *Fraxinus* spp., and *Quercus* spp. within each forest stratum. Kruskal-Wallis was also used to test for differences in dominance of snags. When Kruskal-Wallis one-way analysis of variance tests yielded significant results ($P < 0.05$), post-hoc pair-wise comparisons were performed via Wilcoxon rank-sum tests (Bonferroni corrected). All statistical analyses were conducted using R software (version 4.12.2).

Canopy disturbance events were determined by comparing variations in ring-width measurements from increment core samples (Lorimer & Frelich 1989). All tree cores were analyzed for release events by comparing the annual growth averages as described by Lorimer and Frelich (1989). Using a rolling mean, when a 10-year growth average was ≥ 100% of the previous 10-year growth average, the tree was considered to have undergone a major release event. When a 10-year growth average was ≥ 50%, but < 100% of the previous 10-year growth average, the tree was considered to have undergone a minor release event (Lorimer and Frelich 1989). Release event data were then pooled by genera and decade of event.

The establishment and canopy accession strategy of each individual was determined by examining the innermost 40 annual rings of each sample and comparing the mean annual growth from years 1–20 to the mean growth from years 21–40 for each sample (Lorimer et al. 1988; McCarthy and Bailey 1996; Rentch et al. 2003). Trees with greater early growth were considered gap-originated, while trees with greater late growth were considered to be released from the understory (Rentch et al. 2003). Accession strategy classifications were then compared with the major release events previously calculated for each sample. Individuals were then classified as either of (1) gap-origin with no gap-release events, (2) gap-origin with gap-release events, (3) understory-origin with gap-release events, or (4) understory-origin with no gap-release events (Rentch et al. 2003; Hart et al. 2012). For the development of mean chronologies, increment cores were grouped by genus for analysis. Tree cores which had high inter-series correlation values (> 0.4) were selected to construct mean annual ring-width splines using SigmaPlot software (version 11). Included in this analysis were samples from *Carya* spp. (n = 8), *Fraxinus* spp. (n = 11), and *Quercus* spp. (n = 10) individuals.

RESULTS

Acer saccharum was the most abundant species in the overstory, midstory, and shrub-layers (Table 1), as well as the most dominant overstory and midstory species (Table 2). While *Quercus* and *Carya* species were abundant in the overstory, very few stems were found in the shrub and ground-layers (Figure 2). Kruskal-Wallis indicated significant differences in stem density between four genera of interest (*Acer* spp., *Quercus* spp., *Carya* spp., and *Fraxinus* spp.) in the overstory (H = 13.95, df = 3, P =0.003), midstory (H=77.49, df = 3, $P < 0.001$), shrub-layer (H = 49.10, df = 3, $P < 0.001$), and ground-layers (H = 39.94, df = 3, $P < 0.001$). Post-tests revealed that *Acer* spp. stem density was significantly greater than *Quercus* spp. and *Carya* spp. in the midstory, shrub-, and ground-layers (Figure 2, Table 3). Additionally, *Fraxinus* spp. density was significantly greater than *Quercus* spp. and *Carya* spp. at shrub- and ground-layers (Figure 2, Table 3).

Quercus was, by far, the most dominant snag genus in DWSNP (Figure 3). There was a significant difference in the snag dominance at DWSNP (U = 35.67, df = 5, $P < 0.00001$). Post-tests indicated that *Quercus* spp. snag basal area ($m^2\ ha^{-1}$) was significantly greater than *Acer* spp., *Carya* spp., *Fraxinus* spp., *Prunus* spp., and *Ulmus* spp. (Table 4).

Dendrochronological analysis indicated similar annual growth patterns between *Carya*, *Fraxinus*, and *Quercus* individuals (Figure 4). Dendroecological analysis revealed the average inner date of increment cores (*n* = 47) was 1881 (± 34.5 years). The largest tree sampled was a *Quercus bicolor* (Willd.) with a DBH of 112.0 cm. The largest *Carya* and *Fraxinus* individuals sampled were 59.4 and 95.7 cm DBH, respectively. The oldest increment core came from a *Carya* individual, and had an inner date of 1755 (Figure 5). The highest proportion (41.30% average, ± 10.53%) of releases to total samples occurred from 1820 through the 1870's. From 1870–1880, there were 8 (7 minor, 1 major) total releases from only 18 samples (Figure 6). In contrast, from 1880 through the 1930's, only 6.76% (± 6.34%) of total samples were subject to a release event. Over half (59.6%) of all samples were found to have originated in a gap, and were not subjected to a major release event (Table 5).

DISCUSSION

The results from this study indicated that DWSNP has undergone a dominance shift where oaks (*Quercus* spp.) and hickories (*Carya* spp.) have decreased in density, while maples (*Acer* spp.) have increased in density. This shift in dominance is similar to that seen in other studies conducted throughout the eastern United States (e.g. Abrams 1992; Rogers et al. 2008; McEwan et al. 2011). Forests at equilibrium generally have a similar species composition among canopy and sub-canopy layers (Turner et al. 1993; Runkle 2000; Fraver & White 2005), thus, the community structure of DWSNP indicated that the site was subjected to non-equilibrium processes in the past 160 years. In particular, it appears that DWSNP has been undergoing ‘mesophication’ as defined by Nowacki and Abrams (2008).

In addition to oaks being underrepresented in lower canopy strata, substantial oak decline has also occurred in DWSNP. Oaks comprised the vast majority of the standing dead biomass within DWSNP—a trend that is certainly puzzling. A previous study from 1991 noted a low density of snags within DWSNP and also noted that many of the large oaks appeared to be of the same cohort (Boerner & Kooser 1991). Our results indicated that many of these similarly-aged oaks are now dead. Understanding the cause of the pulse of oak mortality was not within the scope of this study, but oak decline has been documented in other studies (McCarthy et al. 2001; Shifley et al. 2006; Kabrick et al.

2008). Ascertaining the particular cause of mortality is complex (Franklin et al. 1987), and future studies are needed to determine the cause(s) of oak mortality at DWSNP.

We identified a change in the disturbance regime during the decade of the 1880's. Prior to the 1880's, disturbances occurred relatively frequently. These results suggest that most of the dominant oak, hickory, and ash individuals established during a period of time when disturbances were more frequent. A reduction in disturbances could have driven the proliferation of sugar maple, a species that thrives in closed-canopy environments (Canham 1988). While the accession strategy was also determined for all increment core samples, we found some individuals with a strategy (understory-origin, no gap release) not previously noted in the literature (Rentch et al. 2003; Hart et al. 2012). Theoretically, a shade-intolerant tree would need to either originate in a treefall gap, be released from the understory via disturbance, or both, but our results indicated that some individuals did not originate in a gap, and were not subjected to a growth release. The small size of DWSNP (~6 ha) likely makes it highly susceptible to edge effects due to the nature of the surrounding land parcels (3 agricultural fields and a road; Boerner & Kooser 1991). Additional light entering laterally into the stand may have aided some individuals of ostensibly shade-intolerant species in accessing the canopy without a canopy disturbance event.

Fire is a complex ecological process that plays a critical role in some ecosystems (Pyne 2007; Bowman et al. 2009). The relative absence of fire throughout much of the Eastern Deciduous Forest landscape over the last 90 years is considered to be the primary driver of oak to maple dominance shifts (Abrams 1992; Nowacki & Abrams 2008).

Although DWSNP has been undergoing ‘mesophication’ (Nowacki & Abrams 2008), it is unlikely that an altered fire regime has been the agent of community structure change. Un-drained forests within the glaciated region of west-central Ohio, where DWSNP is located, have been previously classified as oak-maple swamps (Anderson 1982; Boerner & Kooser 1991), a habitat that is unlikely to support frequent fires. Whitney (1982) investigated original land surveys from another glaciated region in Ohio and determined that fire disturbance was infrequent and unlikely to have been the primary driver of pre-settlement-era changes in community structure. Whitney (1982) also concluded that moisture availability and soil properties were more likely to have shaped the landscape of some pre-settlement forests in Ohio rather than a historic fire regime driven by Native American land use.

It is highly likely that the current community structure of DWSNP has been shaped by ‘multiple-interacting drivers’ (McEwan et al. 2011) of change over the last 200 years. These drivers likely included changes in climate, altered land-use in the adjacent landscape, and highly dynamic populations of important herbivores (especially white-tailed deer, *Odocoilus virginianus*; McEwan et al. 2011). For instance, changes in climate have been linked to dominance shifts in forests (Cook et al. 1987; Grissino-Mayer et al. 2004; Mueller et al. 2005). Droughts were more common in the 400 years prior to the 20th century (Cook et al. 2004), and a reduction in oak regeneration could be the result of wetter environments due to a changing climate (McEwan et al. 2011).

DWSNP has also been subjected to anthropogenic influences via the presence of agricultural fields on the east, west, and south sides of the preserve. Abiotic environments along edges in fragmented forests can vary compared to the interior of these forests (Murcia 1995), and, though we have not directly shown edge effects in this study, it is likely that alterations in land-use have impacted this system. Also, selective cutting and/or other major anthropogenic disturbances may have taken place within the site before 1855, as no verbal or historical record of DWSNP exists before that time (Boerner & Kooser 1991).

It is also possible that white-tailed deer (*Odocoileus virginianus*) herbivory has had a profound effect on the community structure of DWSNP. Over the last half-century, white-tailed deer populations have increased dramatically (Côté et al. 2004). Deer can significantly alter community structure by selectively browsing the understory of mature forests (Waller & Alverson 1997; Côté et al. 2004, Rooney 2009). White-tailed deer have been shown to prefer eating oak seedlings compared to maple seedlings (Strole & Anderson 1992), subsist on acorns during the fall (Healy 1997), and are known to invade corn fields (Wywialowski 1996). In a past study conducted in Ohio, it was shown that deer browsing had a greater impact on seedling populations than environmental gradients or climate changes (Boerner & Brinkman 1996). Alterations to the landscape of Ohio forests since European settlement have reduced the canopy cover of forests and have resulted in increased vegetation available for deer to eat at ground- and shrub-layers (Iverson & Iverson 1999). Additionally, historic predators of white-tailed deer, eastern timber wolves (*Canis lupus*) and mountain lions (*Puma concolor*), have disappeared from western Ohio's landscape since the settlement of Europeans (McCullough 1997; Paquet & Carbyn 2003; Côté et al. 2004). Given the literature that exists on white-tailed deer herbivory in the Eastern Deciduous Forest, it is highly likely that deer population dynamics have influenced long-term forest dynamics in this system.

Oncoming perturbations that will almost certainly impact DWSNP include the sudden loss of all individuals in the genus *Fraxinus* due to the emerald ash borer (*Agrilus planipennis*; Poland & McCullough 2006). If upper-canopy dwelling ash (*Fraxinus* spp.) are killed in the near future, the community structure of DWSNP will likely be altered again. Future vegetative surveys are needed to chronicle the changes within DWSNP after potential emerald ash borer infestations are realized. Global climate changes are also predicted to impact the vegetation of the eastern United States in the future (Iverson & Prasad 1998), and continued monitoring of DWSNP would allow for greater understanding of the non-equilibrium processes that influence Eastern Deciduous Forests. Continued monitoring and dendroecological analyses are needed to expand our knowledge of baseline forest dynamics in preserve sites such as DWSNP. Future studies investigating the multiple-interacting drivers of forest change are needed from this and other old-growth forests to further elucidate the specific factors that have shaped, and continue to shape, forest patterns and processes throughout eastern North America.

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APPENDIX

TABLES AND FIGURES

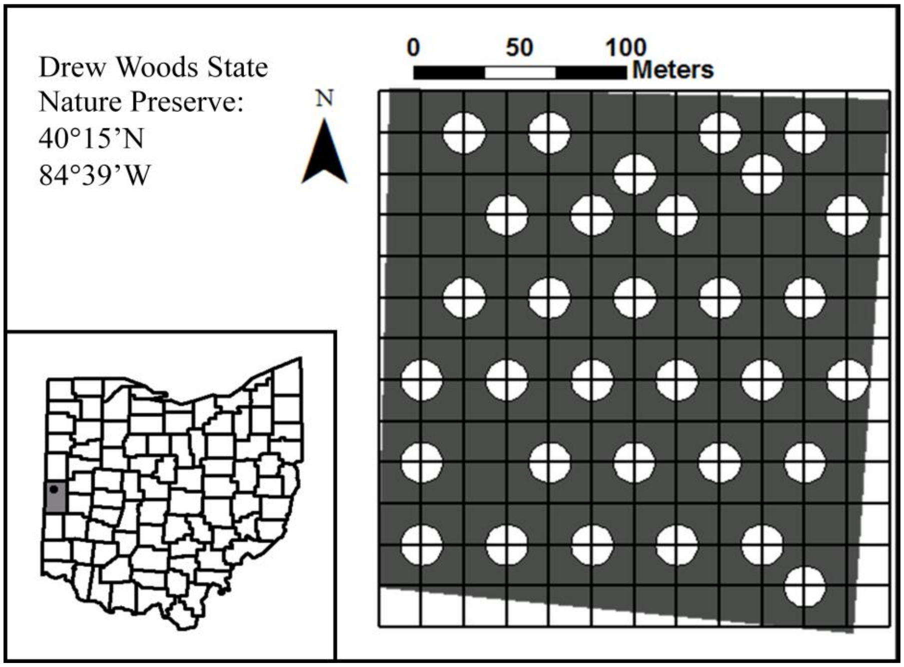

Figure 1. Map of Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio (shown in dark grey). White circles within the study area represent the overstory plot locations (314 m^2). Also shown is the digitally-created grid used for placement of the plots. Grid lines are spaced 20 m apart.

Table 1. Percent relative abundance of trees in the overstory at Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio. Woody vines not included.

	% Relative Abundance			
Species	**Overstory**	**Midstory**	**Shrub-layer**	**Ground-layer**
Acer saccharum	29.89	44.56	60.16	37.79
Carya ovata	21.26	1.44	0.49	-
Fraxinus spp.	6.90	1.92	15.12	42.44
Quercus alba	6.32	0.08	-	-
Quercus rubra	5.75	0.88	0.16	-
Carya laciniosa	4.60	0.24	-	-
Fagus grandifolia	3.45	-	-	-
Fraxinus quadrangulata	3.45	0.80	-	1.74
Aesculus glabra	2.87	7.44	2.11	-
Carya glabra	2.30	0.16	-	1.16
Ulmus rubra	2.30	14.00	13.01	9.30
Acer saccharinium	1.72	1.12	-	-
Aesculus flava	1.72	4.40	0.81	-
Quercus bicolor	1.72	-	-	-
Quercus macrocarpa	1.72	-	-	-
Carya tomentosa	1.15	0.56	0.16	-
Ulmus americana	1.15	3.12	0.49	0.58
Celtis occidentalis	0.58	2.40	1.63	1.16
Juglans nigra	0.58	-	0.16	-
Quercus stellata	0.58	-	-	-
Minor species[1]	-	16.88	5.70	4.64

[1] Minor species not included were: *Acer negundo, Carpinus caroliniana, Carya cordiformis, Cercis Canadensis, Cornus drummondii, Crataegus mollis, Crataegus punctata, Gymnocladus dioicus, Ostrya virginiana, Prunus serotina, Prunus virginiana, Quercus muehlenbergii,* and *Tilia americana.*

Table 2. Dominance of living trees within upper-canopy plots in Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio.

	Overstory Dominance		**Midstory Dominance**	
Species	**Mean Basal Area (m^2 ha^{-1})**	**Standard Deviation**	**Mean Basal Area (m^2 ha^{-1})**	**Standard Deviation**
Acer saccharum	9.43	10.84	37.04	30.42
Carya ovata	8.58	21.74	0.54	1.30
Fraxinus spp.	6.26	25.25	0.39	1.37
Quercus alba	4.20	12.16	0.03	0.18
Quercus rubra	4.10	11.91	0.21	0.92
Fraxinus quadrangulata	2.84	7.63	0.05	0.18
Quercus macrocarpa	1.47	6.50	-	-
Carya laciniosa	0.88	2.63	0.06	0.22
Fagus grandifolia	0.80	2.83	-	-
Aesculus glabra	0.45	1.27	1.56	3.28
Ulmus rubra	0.43	1.77	8.18	25.51
Carya tomentosa	0.14	0.56	0.07	0.18
Ulmus americana	0.14	0.58	0.35	0.60
Aesculus flava	0.11	0.34	1.21	3.75
Celtis occidentalis	0.07	0.37	0.20	0.89
Crataegus mollis	-	-	1.77	5.03
Carpinus caroliniana	-	-	1.43	4.10
Ostrya virginiana	-	-	0.58	1.67
Prunus serotina	-	-	0.41	0.94
Prunus virginiana	-	-	0.05	0.17
Minor species[1]	0.46	2.45	0.07	1.11

[1] Minor species not included were: *Acer negundo, Acer saccharinum, Amelanchier arborea, Carya cordiformis, Carya glabra, Cercis canadensis, Cornus drummondii, Crataegus punctata, Juglans nigra, Quercus bicolor, Quercus muehlenbergii, Quercus stellata,* and *Tilia americana.*

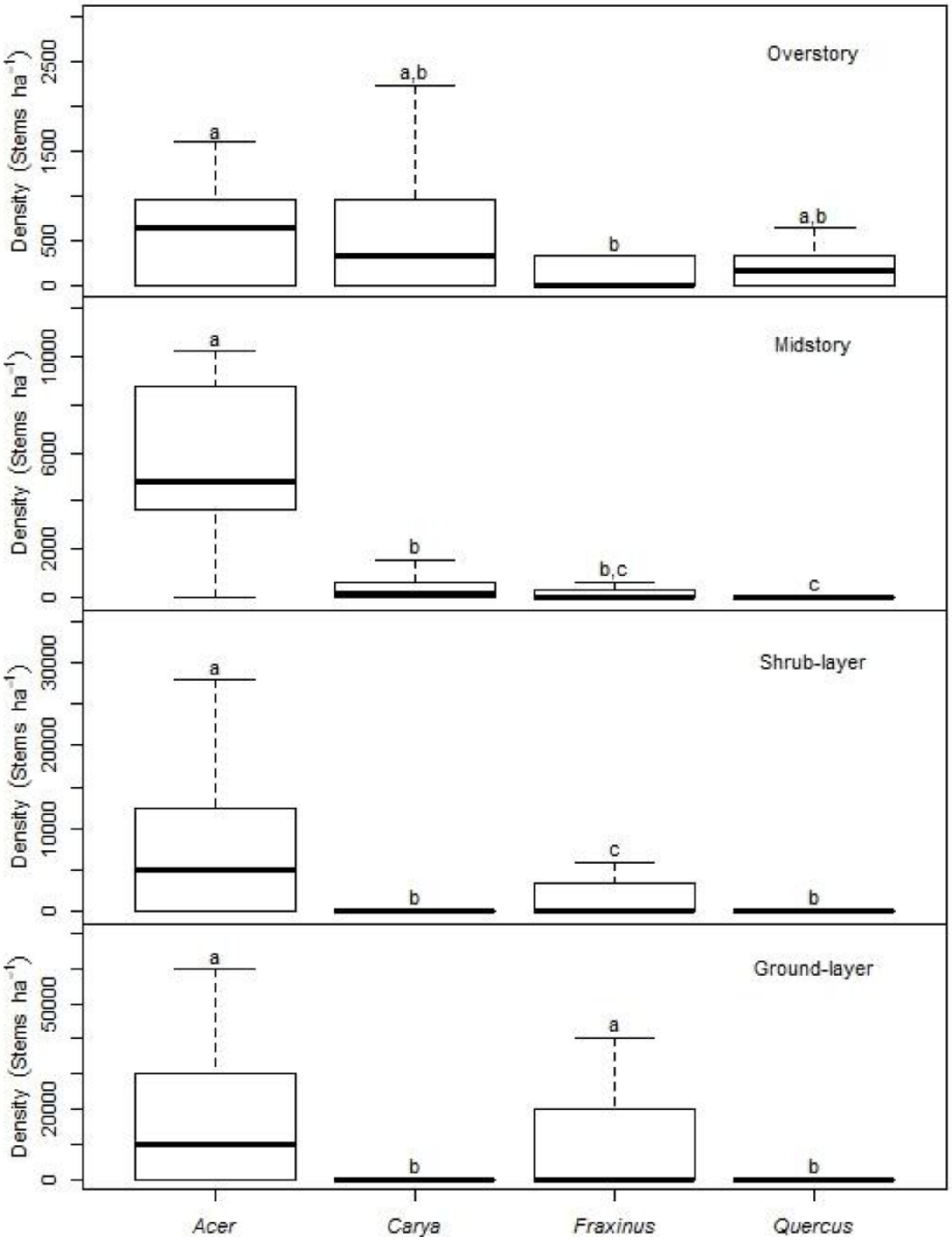

Figure 2. Comparison of mean density for four tree genera in each strata of Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio. Outliers are not shown. Note differences in y-axis scales.

Table 3. Pairwise comparisons using Wilcoxon Rank Sum tests to compare stem densities of four genera at four strata in Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio. *P*-values are given.

Pairwise Comparisons (Wilcoxon Rank Sum)

	Overstory		
	Acer	*Carya*	*Fraxinus*
Carya	1.0	-	-
Fraxinus	0.0045	0.0584	-
Quercus	0.1258	0.9754	0.8048

	Midstory		
	Acer	*Carya*	*Fraxinus*
Carya	<0.0001	-	-
Fraxinus	<0.0001	1.0	-
Quercus	<0.0001	0.029	0.203

	Shrub-layer		
	Acer	*Carya*	*Fraxinus*
Carya	<0.0001	-	-
Fraxinus	0.0275	0.0127	-
Quercus	<0.0001	1.0	0.0015

	Ground-layer		
	Acer	*Carya*	*Fraxinus*
Carya	<0.0001	-	-
Fraxinus	1.0	0.0068	-
Quercus	<0.0001	0.2521	<0.0001

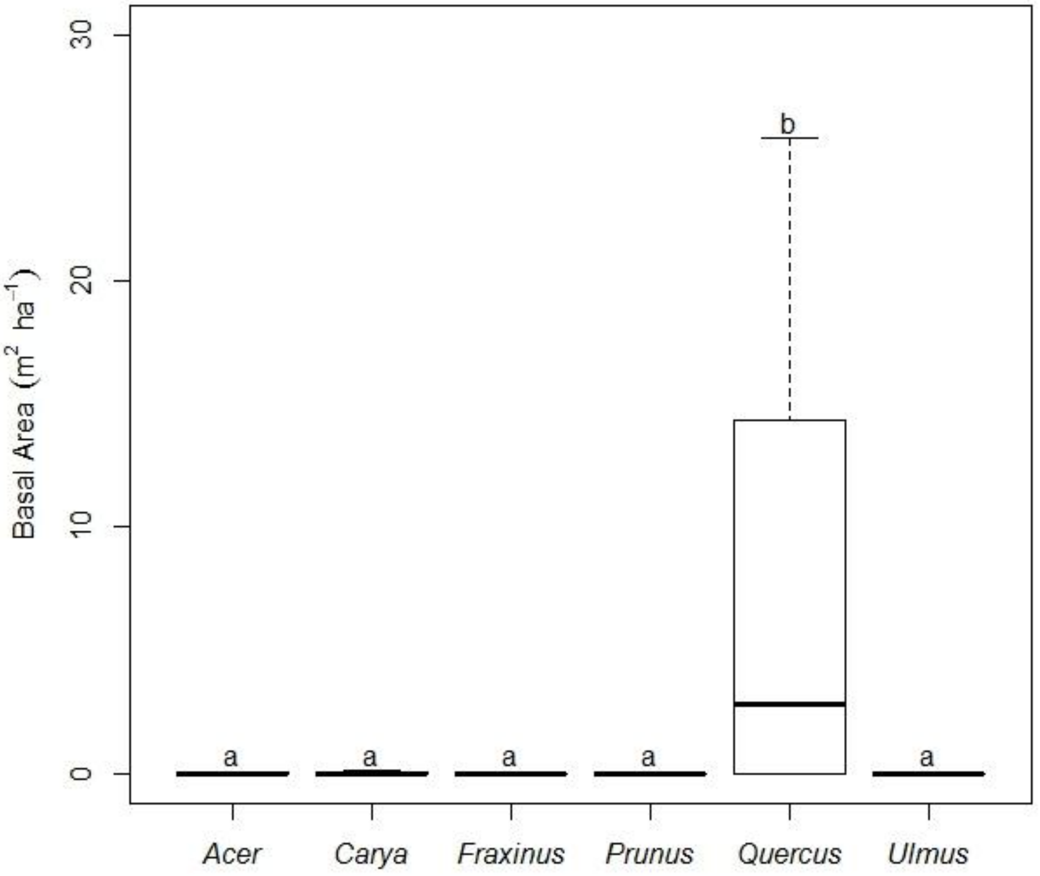

Figure 3. Basal area of snags within plots located in Drew Woods State Nature Preserve, an old-growth forest in western Ohio. *Quercus* snag basal area is significantly greater than all other genera ($P < 0.05$). Unknown and minor genera (*Crataegus*, *Ostrya*, and *Populus*) were not included.

Table 4. Pairwise comparisons using Wilcoxon Rank Sum tests to compare the basal area of snags in Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio. *P*-values are given.

Pairwise Comparisons of Snag Basal Area (Wilcoxon Rank Sum)

	Acer	*Carya*	*Fraxinus*	*Prunus*	*Quercus*
Carya	1.0	-	-	-	-
Fraxinus	1.0	1.0	-	-	-
Prunus	1.0	0.9245	1.0	-	-
Quercus	0.0099	0.0117	0.0006	0.0003	-
Ulmus	1.0	1.0	1.0	1.0	0.0027

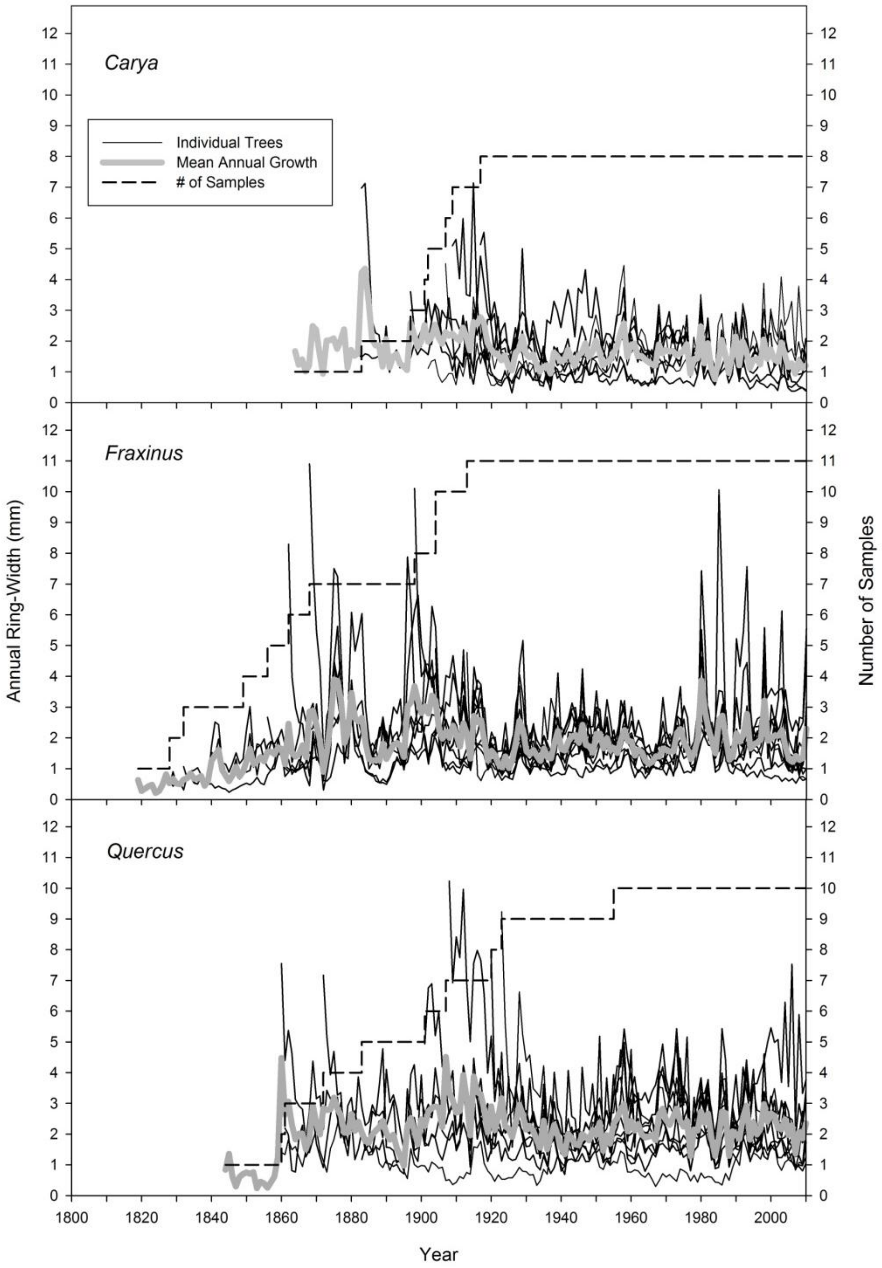

Figure 4. Individual and mean annual ring-widths of increment cores collected from Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio. Y-axis on the right shows the number of samples included.

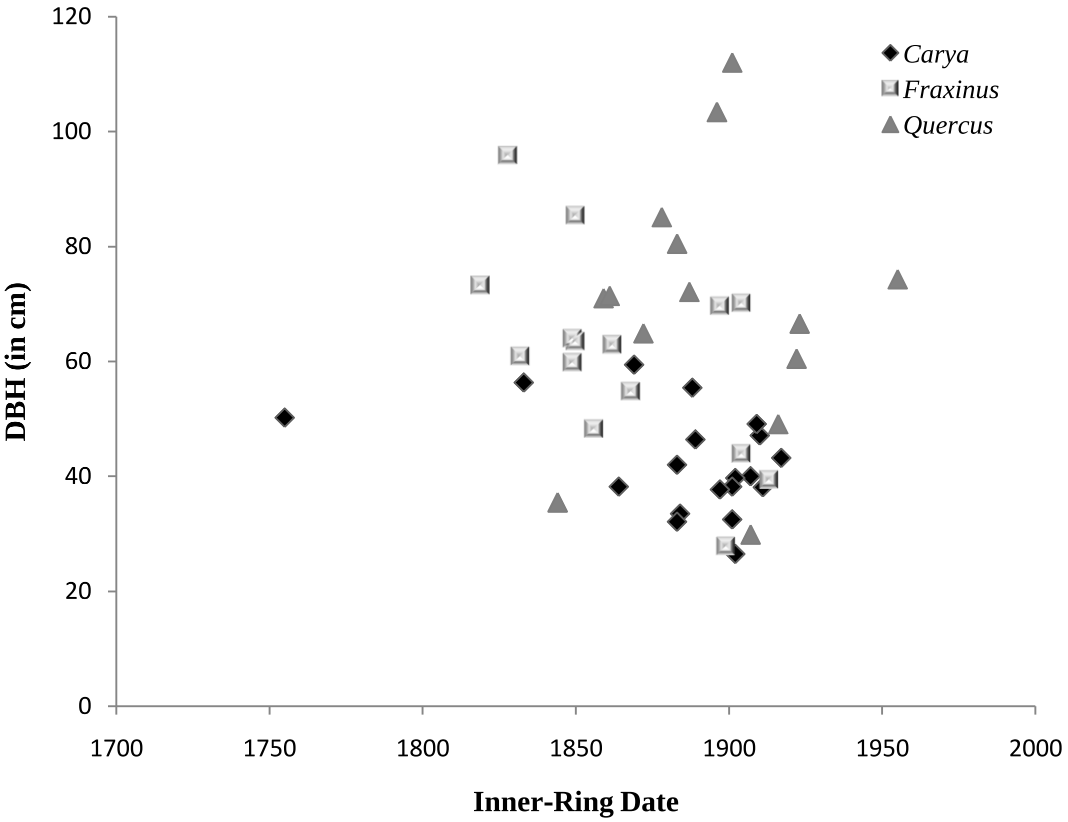

Figure 5. Diameters at breast height of sampled trees, and dates of inner-most ring from increment cores collected in Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio.

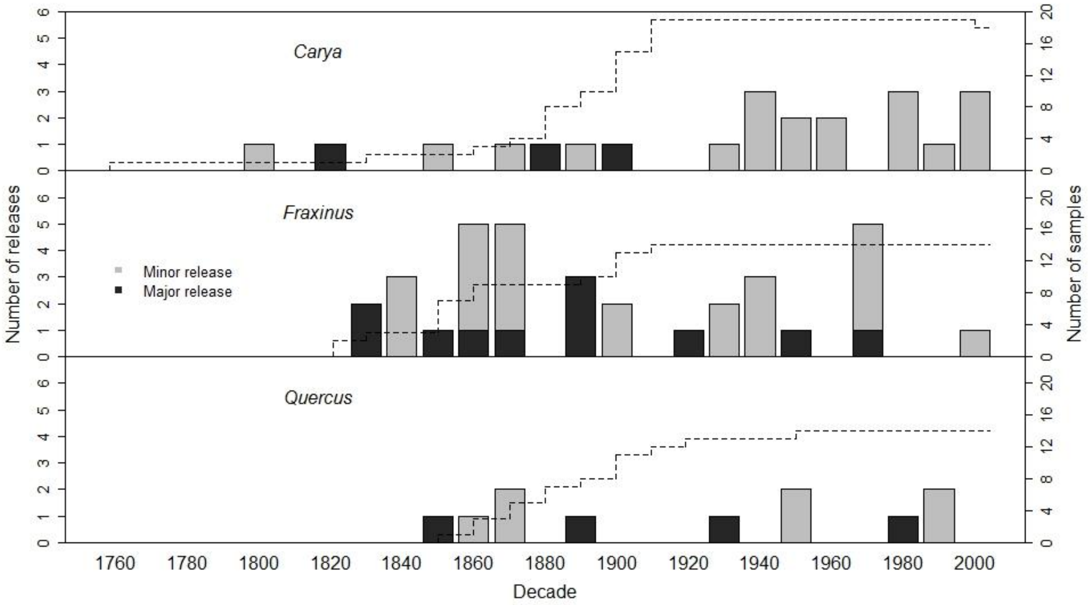

Figure 6. Release events by decade. Release events were determined by ring-width measurements from increment cores collected from Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio. Y-axis on the right shows the number of samples included.

Table 5. Accession strategies of sampled trees within Drew Woods State Nature Preserve, an old-growth forest remnant in western Ohio.

	Accession Strategy			
Genus	**Gap-origin, released**	**Gap-origin, no release**	**Understory-origin, released**	**Understory-origin, no release**
Carya	2	14	1	2
Fraxinus	3	4	5	2
Quercus	1	10	1	2