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Short-term, spatial regeneration patterns following expanding group shelterwood harvests and prescribed fire in the Central Hardwood Region

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ABSTRACT

Throughout eastern North America, oaks (*Quercus*) are a foundational tree species, but are regenerating poorly, particularly on mesic sites. This regeneration failure has spurred development of new management practices that create heterogeneous regeneration conditions that better match oak's response to disturbances such as surface fire and windthrow. Expanding group shelterwood systems are designed to produce diverse regeneration conditions and have a high edge-to-forest interior ratio, where intermediate light levels may be beneficial for oak regeneration. We present data on early regeneration patterns from a large-scale experiment designed to assess the combined effects of these silvicultural systems and prescribed fire on oak regeneration, ecosystem resilience, and spatial and compositional heterogeneity in the Central Hardwood Region. Using transect-based surveys, we investigated the spatial patterns of woody regeneration within and outside of burned and unburned 2- or 3-stage group shelterwoods in factorial replicates at two different sites. Two years following the initial harvest, the south-facing site had substantial competitive oak regeneration just outside of the harvested groups on the northern, eastern, and western sides, but the east-facing site did not. On a stand level, tulip poplar (*Liriodendron tulipifera*) and sassafras (*Sassafras albidum*) regeneration increased in both sites, oak increased in the south-facing site, hickory (*Carya*) increased in the east-facing site, and maple (*Acer*) was relatively unaffected by the treatments. Competitive oak regeneration in the forest matrix just outside of the harvested groups in the south-facing site holds promise to regenerate a stand with a substantial oak component and high overall diversity, given the shelterwood groups will be expanded outward in successive entries and burned repeatedly over time.

1. Introduction

The current structure and composition of many North American forests reflects decades of fire suppression and production-focused management practices that homogenized stands to meet rigid compositional and structural targets, resulting in stands with diminished resilience and ecological memory (Drever et al., 2006; Guyette et al., 2002; Long, 2009; Puettmann et al., 2009; Webster et al., 2018). Faced with future climatic uncertainties and disease outbreaks, restoring forest diversity and resiliency while still meeting production objectives is of high concern (Mori et al., 2013; Puettmann, 2011). Managers and ecologists increasingly recognize that restoring resilience requires reassessing traditional harvesting methods to better align with an ecosystem's natural disturbance regime (Drever et al., 2006; Puettmann and Ammer, 2007). While natural disturbance-based approaches are theoretically promising (Franklin et al., 2007, Long, 2009), large-scale research on these approaches is sparse and attempts to apply these systems are not always successful (Fahey et al., 2018; Kern et al., 2017; Palik et al., 2002).

In eastern North America, many hardwood forests are dominated by mature oak (*Quercus*) and hickory (*Carya*) overstory, but have very little oak regeneration (Abrams, 2003, Aldrich et al., 2005). Loss of oak as a dominant canopy species will cause substantial changes in resource availability and cascading trophic effects throughout deciduous forests of eastern North America (McShea et al., 2007; Smith, 2006). Factors implicated in oak regeneration failure include: fire suppression; reduction of small canopy gaps; invasive species; and increased herbivory (Guyette et al., 2002; Nowacki and Abrams, 2008). Regardless of the contributing factors, ultimately, contemporary management practices frequently do not match oak's adaptations to disturbance and, therefore, fail to provide conditions necessary for adequate regeneration (Arthur et al., 2012; Dey, 2002; Jenkins and Parker, 1998).

Many eastern oak species are considered intermediately shade tolerant and fire-adapted (e.g., resprouting ability, thick bark at maturity,

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and hypogeal germination); however, traditional management often does not align with these traits (Arthur et al., 2012; Dey, 2002; Johnson et al., 2009). In unharvested or lightly harvested stands (e.g., single-tree selection), more mesic, shade tolerant species such as maple (*Acer*) and beech (*Fagus*) typically dominate the regeneration layer, whereas complete or heavy overstory removal (e.g., clearcuts or large group selection openings) shifts composition to faster growing, early successional species such as tulip poplar (*Liriodendron tulipifera*) and sassafras (*Sassafras albidum*; Dey, 2002; Swaim et al., 2016). Furthermore, after decades of fire suppression, and corresponding increase in understory density, single prescribed fires do little to modify regeneration patterns (Brose et al., 2013; Alexander et al., 2008; Dey and Fan, 2009; Hutchinson et al., 2012). Generally, oak regeneration is most successful when silvicultural methods emulating partial or patchy stand mortality are used in concert with prescribed fire (Brose et al., 1999; Hutchinson et al., 2012; Kern et al., 2017).

There is some evidence that oaks may regenerate well on the edge of and just outside of gaps where light levels are intermediate; however, most studies solely focus on regeneration within harvest gaps (Lhotka and Stringer, 2013; Schmidt and Klumpp, 2005; Schulte et al., 2011). Expanding group shelterwoods (patterned after a Bavarian or Bayerischer Femelschlag; Puettmann et al., 2009), remove small percentages of a stand in a series of expanding, small- to medium-sized canopy openings similar to those caused by wind or tree senescence, and create stands with high structural, age class, and species diversity (Seymour, 2005). While this silvicultural regeneration system has been used in North American coniferous and mixedwood systems (Arseneault et al., 2011; Raymond et al., 2009), it remains largely untested in hardwood systems. Expanding group shelterwoods maintain a high edge-to-forest interior ratio that might promote advanced oak regeneration in the forest matrix directly outside of harvest groups in the area slated for subsequent harvests (Arseneault et al., 2011; Lhotka and Stringer, 2013).

While altered regeneration along “high-contrast” ecological edges (e.g., roads, paths, pasture boundary) is well documented; there is little empirical information describing “lower-contrast” edges, such as intra-stand harvested gaps altering regeneration in the surrounding forest matrix (Arseneault et al., 2011; Lhotka and Stringer, 2013; Matlack, 1993; Schmidt and Klumpp, 2005). The forest understory is typically a light-limited system, and harvest boundaries dramatically alter this resource along a spatial gradient extending from within the harvest opening into the adjacent forest matrix (Lhotka and Stringer, 2013; Voicu and Comeau, 2006). The light that filters through a harvest gap into the adjacent forest matrix is affected by gap size, percent of overstory removed within the gap, and edge orientation (N, E, S, W; Matlack, 1993).

Beginning in 2014, a landscape-scale, temporally replicated expanding group shelterwood and prescribed fire experiment was initiated in southern Indiana to promote oak regeneration and increase stand-level heterogeneity. Past research and oak autecology suggest that shelterwood groups will produce areas with intermediate light levels required for oak regeneration and the concurrent use of prescribed fire should further reduce shade-tolerant, but fire-sensitive competitors; however, these two treatments have never been tested together in an expanding group shelterwood system (Brose et al., 1999; Hutchinson et al., 2012; Loftis, 1990). We present results from an exploratory study designed to assess early spatial regeneration patterns in the first two replicates of this study, each of which contained four factorial treatments: 2- and 3-stage expanding group shelterwoods, with and without prescribed fire. Specifically, we investigated how oak, hickory, maple, sassafras, and tulip poplar regeneration patterns were affected by group shelterwood and prescribed fire treatments and orientation (N, E, S, W) within and outside of initial shelterwood gaps. Additionally, we assessed how competitive oak regeneration was affected by the presence of specific non-oak seedlings, basal area, and canopy cover. We concentrated our analyses on the presence of established seedlings, rather than overall abundance, to better predict future composition and available advanced regeneration for subsequent gap expansions (Iverson et al., 2008).

2. Methods

2.1. Study site

This research was conducted at Naval Support Activity (NSA) Crane in Martin County, Indiana. Most of the 210 km^2 of forested land on NSA Crane is secondary growth originating from the 1850s–1930s; has a similar history to many forests in the Central Hardwood Region; is managed predominantly for oak and hickory; and is relatively unaffected by base operations. Currently, harvests at NSA Crane total approximately 525–600 ha per year (3 MMBF per year), which accounts for about 40% of annual growth on the base (T. Osmon, NSA Crane Forester, pers. commun.).

NSA Crane lies in the Crawford Upland physiographic province, a rugged sandstone plateau broken up by well-defined stream valleys with well-drained acid silt loam soils (Franzmeier et al., 2004; Homoya et al., 1984). The forest matrix is predominantly mixed oak-hickory and dominated by white oak (*Q. alba*), northern red oak (*Q. rubra*), black oak (*Q. velutina*), shagbark hickory (*C. ovata*), and pignut hickory (*C. glabra*). These forests have been managed using various silvicultural techniques, most recently focusing on uneven-aged management using single-tree and group selection harvests (T. Osmon, pers. commun.).

2.2. Experimental design

This experiment was designed to assess the combined, long-term effects of expanding group shelterwoods and prescribed fire on oak regeneration, ecosystem resilience, and structural variability in the Central Hardwood Region. Two replicates were installed each of which contained five ~10 ha treatments: (1) 2-stage (i.e., two entries to completely remove midstory and overstory); (2) 3-stage; (3) 2-stage with prescribed fire; (4) 3-stage with prescribed fire; and (5) unharvested and unburned control. Replicate one was installed in 2014 and replicate two was installed in 2015. Each treatment will be expanded outward on a 10-year cycle to form a mosaic of irregularly-aged regeneration.

In the first cutting cycle, shelterwood groups (hereafter referred to as ‘gaps’) were created with diameters approximately 2–2.2 times the canopy height (~0.4 ha), and a permanent system of skid trails was established. In subsequent cuttings, the gaps will be expanded outward so that the total area harvested from each treatment is approximately 20% of the stand area, after which the stand will not be harvested for 50 years. The 2-stage shelterwood treatments receive midstory removal followed by a complete overstory removal cut 10 years later. The 3-stage shelterwood treatments receive midstory removal followed by a 50% basal area reduction establishment cut and a final complete overstory removal cut 10 and 20 years after the initial midstory removal, respectively. In all gaps, midstory removal extends beyond the gap boundary to form a ‘midstory buffer strip’ around the gap, roughly equal to the area of the next planned harvest (20% of stand area; Fig. 1). In the first harvest cycle, the midstory removal and first overstory cut (complete or 50%) occurred simultaneously. Prescribed fires, implemented across the entire treatment stands in the late fall, are planned to be repeated on a 5-year cycle and are executed to produce a variable fire severity mosaic to promote regeneration heterogeneity.

2.3. Treatment implementation

Marking was done by the NSA Crane Staff following existing NEPA-approved management plans for NSA Crane. For the 3-stage shelterwood harvests, white oaks were retained in gaps when possible, although other oaks were left as needed to meet basal area targets. Prior

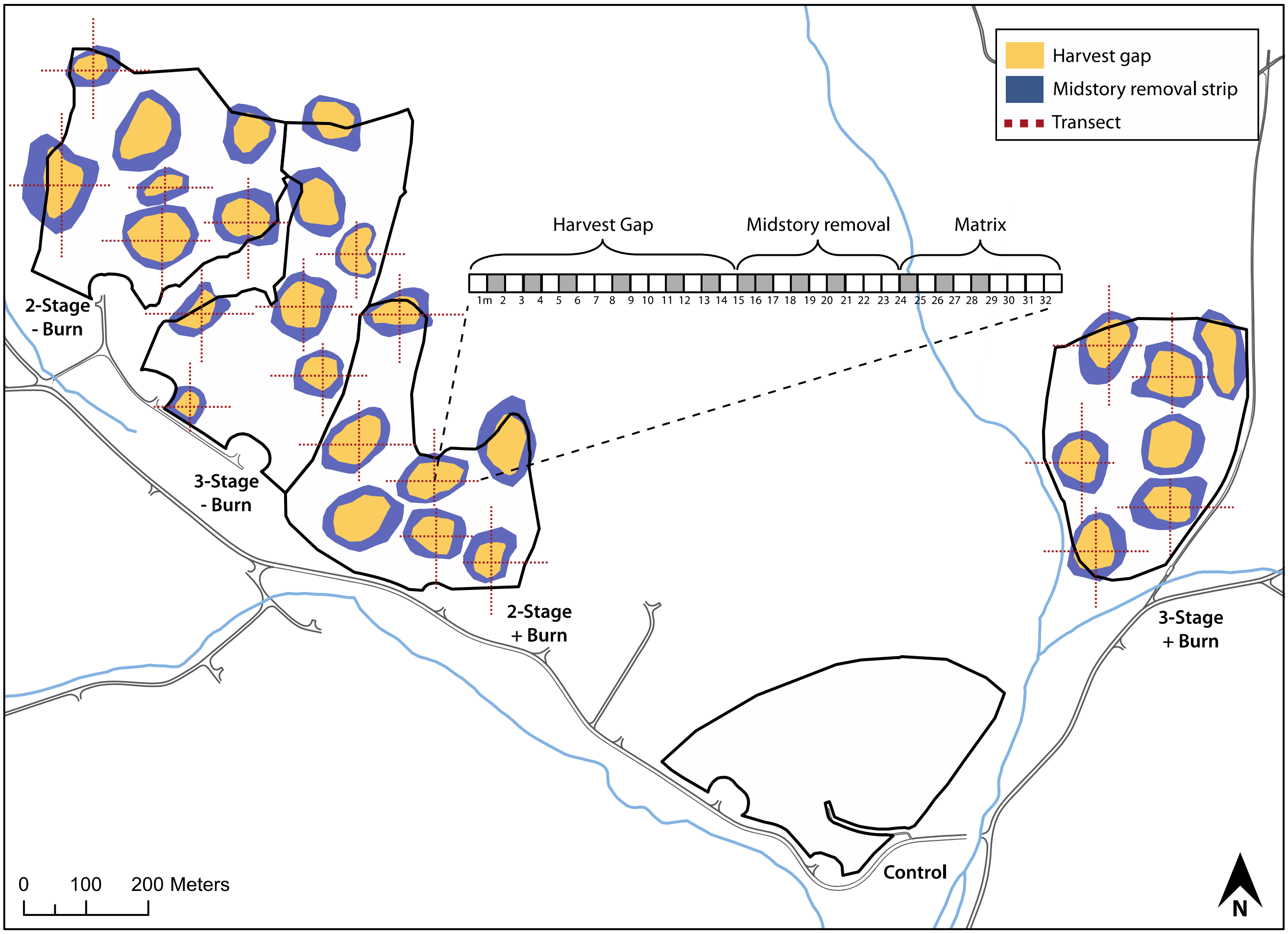

Fig. 1. Map depicting replicate one including treatment stands, harvest gaps, and transect locations. The transect inset depicts the sampling scheme along a hypothetical transect with grey boxes indicating quadrat locations. Replicate two followed a similar design.

to harvest, all subcanopy trees < 20 cm diameter at breast height (dbh) were removed in marked harvest gaps and midstory removal buffer areas using mechanical clearing saws and chainsaws. An herbicide mix of 15% triclopyr (Garlin 4 Ultra®; DowAgroSciences), 3% imazypyr (Stalker®; Cyanimad), and 82% bark oil (Ax-It®; Townsend Chemical) was sprayed on stumps of aggressively sprouting species (e.g., tulip poplar) and invasives such as Callery pear (*Pyrus calleryana*) and tree-of-heaven (*Ailanthus altissima*). Burns followed on November 3rd, 2014 for replicate one and November 5th, 2015 for replicate two. Harvests were conducted in mid-winter, on firm albeit not frozen ground, as merchantable timber harvests using a private contractor. Trees were felled by chainsaws, trimmed at merchantable height and skidded, a standard system for the region. Treetops were trimmed or broken into short lengths, dispersed and left on site; therefore, skid trails and ghost trails (i.e., 1-pass) were throughout gaps. Overall 2.9% of quadrats had > 50% coarse woody debris cover, and 2.1% of the total quadrats fell on skid trails.

While the silvicultural treatments applied to replicate one and two were kept as similar as possible, these sites differed in several key ways. Both replicates had similar stand basal areas and overstory compositions, except for a slightly higher tulip poplar, American beech (*Fagus grandifolia*), and white ash (*Fraxinus americana*), and lower hickory component in replicate two (Table 1). Replicate one generally has a south to southwest aspect and has an average slope of 33%; while replicate two generally has an east to southeast aspect and has an average slope of 38%. Harvests for replicate one coincided with a good acorn mast year with 21.1 ± 36.2 (mean ± SD) acorns recorded per m^2 of oak crown area over the entire fall at the nearby Hardwood Ecosystem

Table 1
Mean pre-treatment basal area (± SE) (m^2 ha^{-1}) of focal overstory tree species in each replicate. Data were collected summer 2014 and 2015 for replicates one and two, respectively using a variable radius plot (basal area factor = 2.296 m^2 ha^{-1}).

	Replicate One	*Replicate Two*
Oak spp.	8.9 ± 0.7	8.3 ± 0.8
Hickory spp.	5.9 ± 0.6	1.6 ± 0.2
Maple spp.	3.2 ± 0.4	3.4 ± 0.4
Tulip poplar	2.1 ± 0.4	4.7 ± 0.5
Sassafras	0.2 ± 0.1	0.4 ± 0.2
Other	1.9 ± 0.3	3.8 ± 0.4
Total	22.2 ± 0.6	22.3 ± 0.6

Experiment (HEE). However, harvests for replicate two occurred following a poor mast year with 5.3 ± 9.7 acorns recorded per m^2 of oak crown area. Over the last decade, mast crops ranged from 0 to 25 acorns per m^2 of oak canopy at the HEE (Kellner et al., 2014, unpublished data). The prescribed fire for replicate one burned with a higher intensity and was hotter (218.0 ± 81.7 °C) than for replicate two (162.7 ± 89.3 °C; see also Supplementary Material Fig. A).

2.4. Data collection

Before any treatment in late summer 2014 (replicate one) or late summer 2015 (replicate two), 20 randomly selected plots were established and surveyed in each treatment stand to quantify advanced regeneration (~1 plot per ha). At each plot, woody regeneration was surveyed in four 1.2 m diameter circular quadrats (1.13 m^2). Quadrats were centered 6.67 m away from plot center at 45°, 135°, 225°, and 315° azimuths. At each quadrat, all woody regeneration was recorded by species in the following height classes: 1 = less than 30 cm total height; 2 = 30–60 cm total height; 3 = 60 cm to breast height (1.37 m); 4 = greater than breast height, but less than 1.5 cm dbh. For replicate one, these points were resurveyed in the summer of 2016 two years post-harvest, hereafter referred to as the 'post-treatment stand-level' survey.

Fine-scale regeneration surveys were conducted two growing seasons after the initial harvests in the late summer of 2016 (replicate one) and 2017 (replicate two) to quantify initial woody regeneration in and around harvest gaps (hereafter 'post-treatment gap-focused' survey). Five gaps were randomly selected per replicate in each of the following treatments: 2-stage; 3-stage; 2-stage with prescribed fire; and 3-stage with prescribed fire. In each gap, transects were run from the center of the gap, as determined in ArcGIS, in each cardinal direction through the midstory removal buffer and into the unharvested matrix. Along each transect all woody regeneration less than 1.5 cm dbh was surveyed in 1 m × 1 m quadrats.

Quadrat placement along the transect was determined by gap and midstory buffer strip size so that the gap, midstory buffer strip, and matrix were all surveyed adequately. Quadrats were positioned 1, 3, and 5 m (1–2, 3–4, and 5–6 m) from the gap centroid; halfway between the gap centroid and gap edge; −5, −3, and −1 m from the gap edge ("gap" quadrats); 0, 2, 5, 9, 15, 27, and 33 m from the gap edge into the midstory buffer strip ("midstory" quadrats); and 0, 2, 5, 9, 15, and 21 m from the edge of the midstory removal buffer into the unharvested matrix ("matrix" quadrats). When the midstory buffer strip was narrower than 33 m (most were), midstory removal quadrats were not taken past the boundary with the forest matrix, and the forest matrix quadrats began at the boundary. We stopped sampling forest matrix quadrats at the midpoint between gaps, which was frequently less than 21 m (Fig. 1). This sampling focused on the transition areas between treatments where differences in regeneration were predicted to be most notable. Transects ranged from 20 to 98 m with an average length of 54.7 m.

At each quadrat, woody regeneration in each height class was recorded by species using the same methods as the initial, pre-harvest surveys. The height and species of the tallest seedling and tallest oak seedling in each quadrat were recorded. At each quadrat, a variable radius point sample with a BAF 2.296 $m^2\ ha^{-1}$ prism was taken to estimate basal area and a spherical densiometer reading was taken to estimate percent canopy closure.

2.5. Analysis

We analyzed woody regeneration spatial patterns for oak, hickory, maple, tulip poplar, and sassafras seedlings by calculating the proportion of quadrats that contained at least one individual of the genus/species that was > 30 cm tall, hereafter referred to as established seedlings. These five groups accounted for 96% of the total individuals surveyed. We analyzed presence of an established seedling, rather than total abundance, because as the regeneration layer ages, seedlings will outcompete each other and eventually quadrats will likely be stocked with a single individual. All analyses used program R version 3.3.2 (R Core Team, 2016), and were conducted separately for the two replicates because year, acorn mast crop, average fire temperature, and aspect differed between the sites. We set the Type-1 error rate at $\alpha = 0.05$, but results with p-values under 0.1 are also noted. For full model results, see supplementary material.

For replicate one, we used logistic regression to analyze the proportion of quadrats stocked with at least one established individual of each focal species in pre-treatment, post-treatment stand-level, and post-treatment gap-focused surveys. This analysis was not conducted for replicate two because post-treatment stand-level data was not taken. To account for different-sized quadrats in the gap-focused and stand-level surveys, we used the binomial distribution with a complementary log-log link function and an offset term for quadrat area. For all other logistic regressions, the logit link function was used.

For both replicates, we used a mixed-effects logistic regression model to analyze how position within a stand (gap interior, midstory buffer strip, forest matrix), treatment (burned 3-stage shelterwood, unburned 3-stage shelterwood, burned 2-stage shelterwood, unburned 2-stage shelterwood), transect direction (N, E, S, W), and the interaction between position and direction affected the probability of a quadrat being stocked with at least one established seedling for each focal group. All mixed-effects logistic regression models included transect ID as random effect. Models were fit with the lme4 package (Bates et al., 2009). For all mixed-effects logistic regression models, we also calculated marginal and conditional R^2 values, on the logit link scale, to assess the amount of variation accounted for by fixed effects and the whole model including random effects, respectively, using the piecewiseSEM package (Lefcheck, 2016; Nakagawa and Schielzeth, 2013).

To better assess spatial patterns of oak regeneration, we analyzed the proportion of quadrats stocked with a competitive oak seedling, defined as being 90% as tall as the tallest seedling in the quadrat, using the same model structure described above. Numerous studies have established that future oak dominance probability is closely related to the height of nearby woody species, and defining competitive oak regeneration based on a height threshold compared to nearby woody competitors is a valuable predictive tool, even for young reproduction (Brose et al., 2008; Dey and Fan, 2009; Swaim et al., 2016). Given the young age of the reproduction in this study, we chose a threshold of 90%, which is close to, but slightly higher than the threshold frequently used for older reproduction (Morrissey et al., 2010; Spetich et al., 2002).

We also examined how the probability of a competitive oak seedling was affected by the presence of specific, established non-oak seedlings (> 30 cm); basal area; and canopy cover in three separate mixed-effects logistic regression models for each replicate. Separate models were run for each of these analyses given correlations between the explanatory variables. These models were included to explore factors influencing competitive oak regeneration generalizable to other silvicultural studies, but were not compared with a formal model selection procedure because this study was implemented to explore effects of specific silvicultural treatments. The model assessing the effect of established non-oak seedlings included the presence/absence of an established hickory, maple, tulip poplar, and sassafras seedling. The models assessing the effect of basal area or percent canopy cover estimates included: standardized basal area or percent canopy cover, burn treatment, direction, and the interaction between direction and basal area or canopy cover.

3. Results

3.1. Replicate one

The proportion of quadrats stocked with an established oak, sassafras, and tulip poplar seedling increased two years following burn and shelterwood harvests in both the stand-level and gap-focused surveys (Fig. 2). The proportion of established hickory and maple seedlings did not change from the pre-treatment survey to either of the post-treatment surveys (Fig. 2).

Established oak regeneration > 30 cm tall displayed a significant interaction between position within the stand and direction, which was driven by low stocking of established regeneration in the forest matrix and midstory buffer strip on the south side of the harvested canopy gaps, whereas there was no effect of cardinal direction in the gap centers (Fig. 3). There was higher stocking in the gap centers compared to the forest matrix ($z = 3.66$, $p < 0.01$), and no effect of different burn or shelterwood treatments. Overall the model accounted for 24%

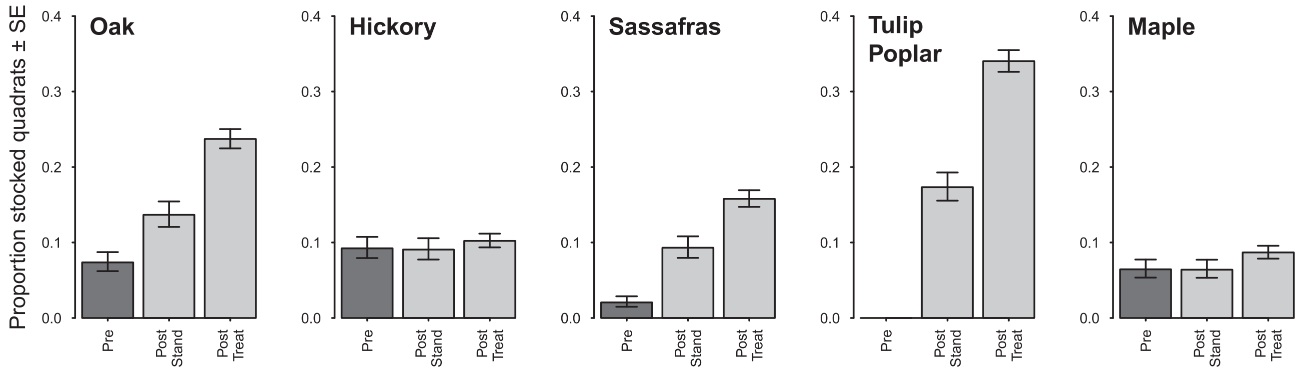

Fig. 2. Predicted (± SE) proportion of quadrats stocked with an established (> 30 cm) seedling from replicate one averaged across treatment stands for the five focal groups. Surveys occurred: pre-treatment at permanent monitoring points 'Pre'; 2 years post-treatment at permanent monitoring points 'Post Stand'; and 2 years post-treatment on gap-focused transects 'Post Treat'. Model predicted proportions account for different quadrat sizes in pre- and post-stand level surveys (1.13 m^2) and post-treatment gap-focused surveys (1 m^2). Pre-treatment surveys occurred summer 2014 and both post-treatment surveys occurred following two growing seasons in summer 2016 at NSA Crane in southern Indiana.

of the variation in oak regeneration (i.e. conditional $R^2 = 0.24$), 12% of which was accounted for by the fixed effects (i.e. conditional $R^2 = 0.12$; Fig. 3, Table 2).

The odds of established hickory regeneration were 54% and 60% lower in the burned 2-stage ($z = -2.15$, $p = 0.03$) and 3-stage ($z = -2.46$, $p = 0.01$) shelterwood than the unburned 2-stage shelterwood. Fixed effects accounted for 10% and whole model accounted for 20% of the hickory regeneration variation. The odds of established sassafras regeneration were 3.5 times higher in the 3-stage burned shelterwood than the 2-stage unburned shelterwood ($z = 3.02$, $p < 0.01$). The interaction between position within the stand and direction was significant, driven by a high proportion of regeneration in the matrix on the north side of the gaps compared to the other directions (marginal $R^2 = 0.18$, conditional $R^2 = 0.36$). The odds of established tulip poplar regeneration were 61.2 times higher in the gap ($z = 5.43$, $p < 0.01$) and 11.6 times higher ($z = 3.11$, $p < 0.01$) in the midstory removal buffer than in the forest matrix. Tulip poplar regeneration was also significantly higher in the 2-stage shelterwood harvests than 3-stage harvests (marginal $R^2 = 0.41$, conditional $R^2 = 0.47$). Maple regeneration was reduced in the burn treatments, but was otherwise unaffected by the treatments (marginal $R^2 = 0.23$, conditional $R^2 = 0.36$; Fig. 3, Table 2).

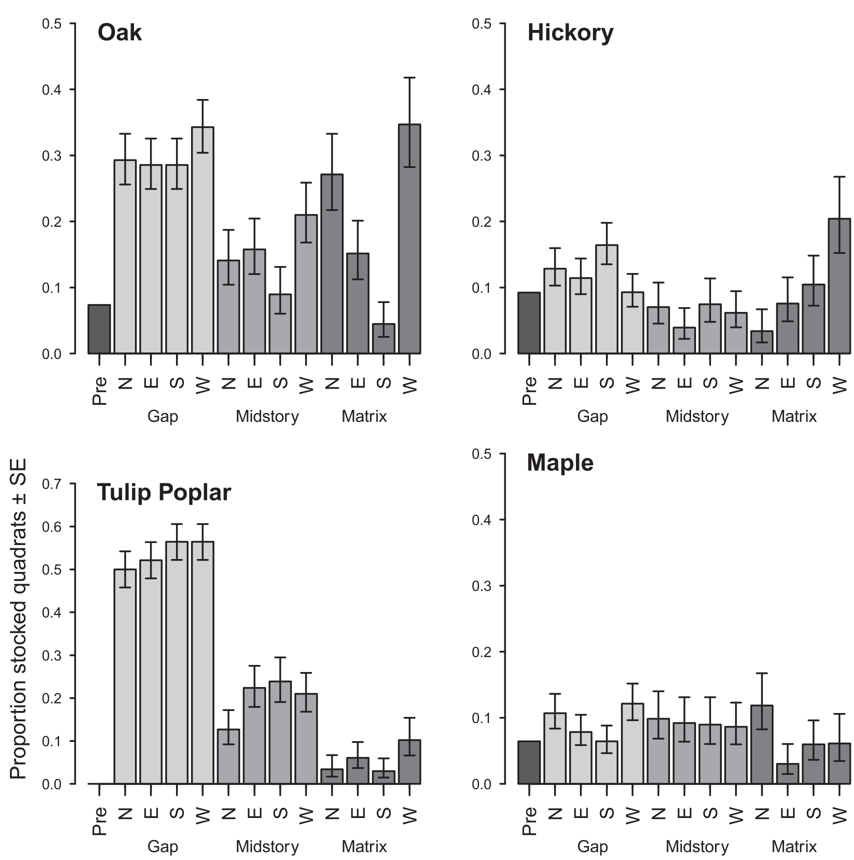

Fig. 3. Average (± SE) proportion of quadrats stocked with an established (> 30 cm) seedling from replicate one averaged across silvicultural and burn treatments for the five focal groups. Pre-treatment levels are displayed for visual comparison on the leftmost side of the graph. Treatments were installed fall and winter 2014 at NSA Crane in southern Indiana and regeneration surveys occurred late summer 2016. Note different y-axis scale for tulip poplar.

Table 2
Significant factors and effect directions (positive: +, negative: −) for the probability of quadrats stocked with an established (> 30 cm tall) oak, hickory, tulip poplar, sassafras, or maple seedling and competitive oak seedling (> 90% as tall as tallest non-oak seedling in the quadrat) at different positions within a stand, silvicultural treatments, direction relative to harvest groups, and position × direction interaction in replicates one and two, which were installed fall/winter 2014 and 2015 at NSA Crane in southern Indiana. Regeneration surveys occurred late summer 2016 and 2017, respectively. For full model results, see supplementary material Tables A-C. *** $p \leq 0.01$, ** ≤ 0.05, * ≤ 0.1.

Independent variable	Replicate One						Replicate Two					
	Oak (> 30 cm)	Oak (comp.)	Hickory	Sassafras	Tulip Poplar	Maple	Oak (> 30 cm)	Oak (comp.)	Hickory	Sassafras	Tulip Poplar	Maple
(Intercept)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)	*** (−)
Gap	*** (+)			* (+)	*** (+)		** (−)	*** (−)			*** (+)	
Midstory removal					*** (+)						*** (+)	
2-stg. shelterwood w/ burn			** (−)			*** (−)		* (−)		*** (+)	*** (+)	
3-stg. shelterwood w/ burn			** (−)	*** (+)	*** (−)	*** (−)				** (+)	*** (−)	* (−)
3-stg. shelterwood w/o burn					*** (−)		* (−)		*** (−)	** (+)	** (−)	
East	* (+)	*** (+)										
North	*** (+)	** (+)		* (+)								
West	*** (+)	*** (+)			* (+)							
Gap × East	* (−)	*** (−)					** (+)		** (−)			
Midstory removal × East		*** (−)										
Gap × North	*** (−)	** (−)		* (−)								
Midstory removal × North	* (−)			** (−)								
Gap × West	*** (−)	** (−)	* (−)	* (+)			** (+)			* (−)		
Midstory removal × West	* (−)	** (−)			* (−)							
Marginal R^2	0.12	0.05	0.10	0.18	0.41	0.23	0.16	0.10	0.17	0.16	0.38	0.07
Conditional R^2	0.24	0.15	0.20	0.36	0.47	0.36	0.26	0.14	0.34	0.43	0.44	0.29

Note: Reference is matrix, 2-stage shelterwood, un-burned, and south.

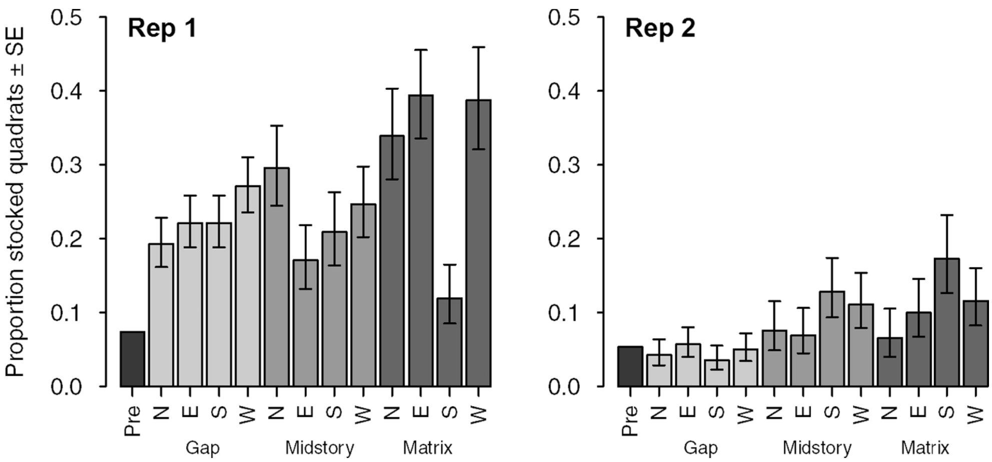

Fig. 4. Average (± SE) proportion of quadrats stocked with a competitive oak seedling (> 90% as tall as tallest non-oak seedling in the quadrat) from replicate one and two averaged across silvicultural and burn treatments. Pre-treatment levels are displayed for visual comparison on the left-most side of the graph. Treatments were installed fall and winter 2014/2015 and surveyed for regeneration late summer 2016/2017 at NSA Crane in southern Indiana.

Table 3
Significant factors and effect directions (positive: +, negative: −) for the probability of a quadrat containing a competitive oak (> 90% as tall as tallest non-oak seedling in the quadrat) given then presence of an established (> 30 cm tall) hickory, sassafras, tulip poplar, or maple seedling for replicate one and two installed fall/winter 2014 and 2015 and surveyed late summer 2016 and 2017 at NSA Crane in southern Indiana. For full model results, see supplementary material Table D. *** $p \le 0.01$, ** ≤ 0.05, * ≤ 0.1.

Independent variable	*Replicate One*		*Replicate Two*	
(Intercept)	***	(−)	***	(−)
Hickory presence				
Sassafras presence	***	(−)	**	(−)
Tulip poplar presence	***	(−)	***	(−)
Maple presence	*	(−)		
Marginal R^2	0.08		0.31	
Conditional R^2	0.19		0.34	

The overall number of quadrats stocked with a competitive oak seedling (height within 90% of the tallest seedling) was not substantially different than the number of quadrats stocked with an established oak seedling > 30 cm; however, the two metrics displayed different patterns. The interaction between position within the stand and direction was still significant and driven by low regeneration in the southern matrix, and a very high proportion of competitive regeneration in other three matrix directions. Gap positions were no longer significantly higher from matrix positions ($z = 1.48$, $p = 0.14$). This model did have a lower marginal R^2, 0.05, than the model for established seedlings > 30 cm (Fig. 4, Table 2).

The odds of a quadrat being stocked with a competitive oak seedling was 61% and 50%, lower if there was a tulip poplar ($z = -4.97$, $p < 0.01$) or sassafras ($z = -2.73$, $p < 0.01$) seedling > 30 cm tall in the quadrat as well. The presence of other established seedlings explained slightly more variation than the model that included treatment effects and position within the stand (marginal $R^2 = 0.08$, conditional $R^2 = 0.19$; Table 3). Basal area and canopy cover also had low predictive ability for the presence of competitive oak with marginal $R^2 = 0.04$ and 0.04 and conditional $R^2 = 0.13$ and 0.15, respectively. The only significant factor in either of these models was the interaction between basal area and transect direction, which demonstrated that as basal area increased, competitive oak regeneration increased more on the western side of gaps than on the southern side ($z = 2.3$, $p = 0.02$; Table 4).

3.2. Replicate two

In general replicate two had lower oak, sassafras, hickory, and maple regeneration than replicate one and had higher tulip poplar regeneration. Established oak regeneration still displayed an interaction between position within the stand and direction, but it was driven by higher regeneration in the southern matrix. Additionally, oak regeneration was lower in gaps than forest matrix ($z = -2.39$, $p = 0.02$; marginal $R^2 = 0.16$, conditional $R^2 = 0.26$). Overall there were 5.4 times fewer quadrats stocked with an established oak seedling than

Table 4
Significant factors and effect directions (positive: +, negative: −) for the probability of a quadrat containing a competitive oak seedling (> 90% as tall as tallest non-oak seedling in the quadrat) given the basal area (BA) or canopy cover above the quadrat, burn treatment, and basal area or canopy cover × direction interaction in replicate one and two. Treatments were installed fall/winter 2014 and 2015 at NSA Crane in southern Indiana and surveyed late summer 2016 and 2017, respectively. For full model results, see supplementary material Table D. *** $p \le 0.01$, ** ≤ 0.05, * ≤ 0.1.

Independent variable	*Replicate One*				*Replicate Two*			
	BA		Canopy Cover		BA		Canopy Cover	
(Intercept)	***	(−)	***	(−)	***	(−)	***	(−)
BA/ Canopy cover							**	(+)
Burn	*	(−)	*	(−)				
East								
North								
West	*	(+)						
BA/Canopy cover × East								
BA/Canopy cover × North							**	(−)
BA/Canopy cover × West	**	(+)						
Marginal R^2	0.04		0.04		0.04		0.09	
Conditional R^2	0.13		0.15		0.12		0.16	

Note: Reference is un-burned and south.

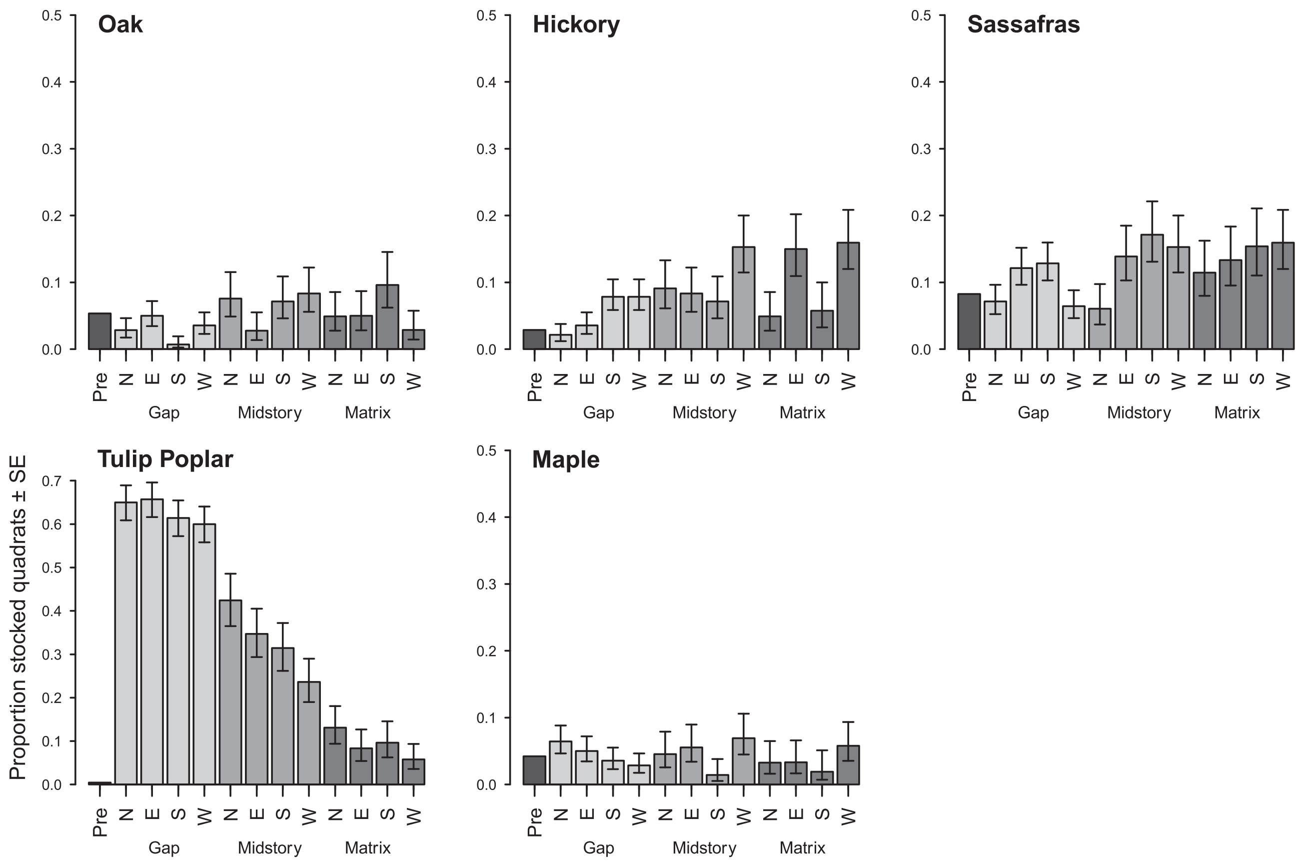

Fig. 5. Average (± SE) proportion of quadrats stocked with an established seedling (> 30 cm) from replicate two averaged across silvicultural and burn treatments for the five focal groups. Pre-treatment levels are displayed for visual comparison on the leftmost side of the graph. Treatments were installed fall and winter 2015 at NSA Crane in southern Indiana and regeneration surveys occurred late summer 2017. Note different y-axis scale for tulip poplar.

replicate one (Fig. 5, Table 2).

Hickory regeneration was lower in the 3-stage unburned shelterwood than the 2-stage unburned shelterwood ($z = -2.78$, $p = 0.01$). There was a significant interaction between position within the stand and direction driven by low amounts of regeneration on the north and south sides of the gaps compared to the east and west sides (marginal $R^2 = 0.17$, conditional $R^2 = 0.34$). Sassafras regeneration was lower in the 2-stage unburned shelterwood than the 2-stage burned ($z = 3.81$, $p < 0.01$), 3-stage unburned ($z = 2.07$, $p = 0.04$), and 3-stage burned shelterwoods ($z = 2.21$, $p < 0.01$; marginal $R^2 = 0.16$, conditional $R^2 = 0.43$). Similar to replicate one, tulip poplar regeneration was higher in the gap ($z = 5.90$, $p = 0.03$) and midstory removal buffer ($z = 3.14$, $p < 0.01$) than in the forest matrix. Tulip poplar regeneration was also lower in the 3-stage unburned ($z = -2.13$, $p = 0.03$) and 3-stage burned ($z = -3.12$, $p < 0.01$) than the 2-stage unburned shelterwood, and higher in the 2-stage burned shelterwood than the 2-stage unburned shelterwood ($z = 2.69$, $p = 0.01$; marginal $R^2 = 0.38$, conditional $R^2 = 0.44$). Maple did not display any significant trends (marginal $R^2 = 0.07$ conditional $R^2 = 0.29$; Fig. 5, Table 2).

The odds of a quadrat being stocked with a competitive oak were 83% less likely in the gap ($z = -2.96$, $p < 0.01$) than the forest matrix. No other factors in the model that included position within a stand, treatment, transect direction, and interaction between position and direction were significant (marginal $R^2 = 0.10$, conditional $R^2 = 0.14$; Fig. 4, Table 2). In the model that included the presence of specific, established non-oak species, the odds of a quadrat being stocked with a competitive oak seedling were 90% and 73% lower if there was an established (> 30 cm) tulip poplar ($z = -5.49$, $p < 0.01$) or sassafras ($z = -2.13$, $p = 0.03$) seedling in the quadrat. The presence of competitors explained substantially more variation than the model that included treatment effects and position within the stand (marginal $R^2 = 0.31$, conditional $R^2 = 0.34$; Table 3). The interaction between direction and percent canopy cover was significant, driven by larger increases in competitive oak regeneration with increasing canopy cover in the southern matrix than northern matrix ($z = -2.20$, $p = 0.03$). However as canopy cover increased competitive oak regeneration generally also increased ($z = 2.03$, $p = 0.04$). Both the basal area and canopy cover models displayed low marginal R^2 (0.04, 0.09) and conditional R^2 (0.12, 0.16; Table 4).

4. Discussion

Natural regeneration patterns can be difficult to quantify and predict following ecological-based silvicultural treatments because these treatments are designed to regenerate compositionally and structurally diverse stands (Dey, 2014; Kern et al., 2017; Webster et al., 2018). In these systems regeneration patterns are influenced by a suite of interacting factors including resource, seed tree, and germination substrate availability; competition with advanced regeneration; herbivory; and seed dispersal, which can lead to complex regeneration patterns, such as those observed in this study (Caspersen and Saprunoff, 2005; Kellner and Swihart, 2017; Webster et al., 2018). The first replicate of this study had significant competitive oak regeneration (i.e., > 90% as tall as the tallest seedling in the quadrat) just outside of the harvest gaps on the northern, eastern, and western sides, likely due to the intermediate light levels in these gap positions (Figs. 3 and 4). This pattern has been discussed anecdotally for many years, but, to our knowledge, very few formal studies have quantified this observation (Arseneault et al., 2011; Lhotka and Stringer, 2013; Schmidt and Klumpp, 2005). Given the southern tilt of the sun in the northern hemisphere, the matrix on the north side of the gaps receives the most light, the south side receives the least light, and the west and east sides receive more morning and evening light, respectively (Marquis, 1965). While this pattern was evident for established oak seedlings > 30 cm, it was much more pronounced when we accounted for the height of competing seedlings. This was driven, in part, by robust tulip poplar regeneration in the gap interiors that overtopped oaks seedlings, which are slower growing in high-light environments (Fig. 2). The importance of the interaction between position within a stand and direction was further corroborated by the low ability of canopy cover or basal area to predict competitive oak regeneration (Table 4).

Competitive oak regeneration was substantially lower in replicate two and displayed somewhat different patterns than replicate one (Fig. 4, Table 2). Replicate two had a higher proportion of quadrats stocked with a competitive oak in the forest matrix compared to the gap centers, but did not display an interaction between position within a stand and cardinal direction (Table 2). There are several possible drivers for these trends including lower acorn production concurrent with the harvest, lower prescribed burn temperature (Supplementary Fig. A), and the eastern site aspect with more mesic, cool, and damp site conditions (Johnson et al., 2009). In replicate two, the abundance of established oak seedlings on the southern side of gaps was unexpected. An east-facing slope should somewhat exacerbate the southern tilt of the sun making the southern sides of the gaps even shadier than the southern side of gaps on a south-facing slope (Marquis, 1965). It is possible that this regeneration was driven by light filtering through the northern side of nearby gaps or the ridge top since the site was somewhat steeper then replicate one.

Across both sites, managers successfully increased both structural and compositional diversity through increases in the sassafras and tulip poplar regeneration component in both replicates, and oak regeneration in replicate one (Figs. 2 and 5). The ratio of the marginal R^2 (proportion of variation explained by fixed effects) and conditional R^2 (proportion of variation explained by the entire model including the random effect, transect) for individual species gives an idea of the relative importance of factors related to treatments versus individual transect characteristics such as seed tree availability (Nakagawa and Schielzeth, 2013). For tulip poplar, fixed effects in the model, including position within a stand and silvicultural treatment, were more important than the variation between transects, whereas random transect-level factors explained more of the variation in hickory and sassafras regeneration. On the more xeric site, replicate one, transect variation was more important for xeric oak species, and treatment variation was more important for mesic maple species. This relationship was flipped in the more mesic replicate two, where treatment effects explained more of the variation in oak regeneration and transect-level variation explained more of the maple variation (Table 2). This suggests the diverse regeneration patterns observed in this study were likely driven by both structure modification (for tulip poplar, maple in replicate one, oak in replicate two), and seed tree retention or other local ecological factors (for hickory, sassafras, oak in replicate one, maple in replicate two).

Over the last few decades there has been substantial mechanistic work on the specific factors effecting oak growth and development; however, few large-scale studies have assessed silvicultural systems that recreate these conditions on a broad scale across local resource gradients (Brose et al., 2008; Dey and Fan, 2009; Loftis and Mcgee, 1993; McEwan et al., 2011). The divergent regeneration patterns between these two replicates highlight the need for large scale studies that assess the efficacy of altering current forester-applied harvesting methods to incorporate knowledge from carefully controlled, mechanistic studies (Franklin et al., 2007; Kern et al., 2017; Saunders et al., 2014; Webster et al., 2018). Like many large-scale experiments, this study was limited by confounding factors; however, moving forward it should be relatively easy to identify factors of interest and design small-scale, mechanistic experiments to investigate these factors in isolation (Saunders and Swihart, 2013). For instance, in replicate one, maples and hickories were negatively affected by the burn treatments, whereas in replicate two burns did not significantly affect either of these species. It is not clear if this was driven by the more mesic character of replicate two, or by the lower burn temperatures on this site, but it would be relatively easy to separate these factors experimentally (Alexander et al., 2008; Johnson et al., 2009).

These results represent an early attempt to characterize regeneration patterns and inform future research directions and management; however, these dynamics will likely continue to shift (Pretzsch and Zenner, 2017; Zenner et al., 2012). The regeneration patterns presented here are still affected by stochastic processes including seed availability, herbivory patterns, burn heterogeneity, and inter-annual climate variation (Abrams and Johnson, 2013; Abrams and Steiner, 2013). Considering this limitation, we chose to combine common genera with more than one species (oaks, hickories, and maples) to explore regeneration patterns at the site more generally, but this certainly constrained our analyses. For instance, the two most common oak species on our site, northern red oak and white oak, were shown to respond differently to intermediate light levels with white oak favoring > 40% sunlight, while 15–40% sunlight promotes northern red oak (Brose and Rebbeck, 2017). As regeneration patterns stabilize at these sites, future research will be able to ask more focused questions about the processes driving spatial patterns of community organization.

While we assessed the effect of prescribed burns, it is generally accepted that it takes multiple burns to substantially increase oak regeneration, which potentially explains the minimal effect of prescribed fire in our results (Arthur et al., 2012; Hutchinson et al., 2012). Only after multiple burns will the possible benefits of implementing prescribed fire in concert with expanding group shelterwoods be clear. Initial prescribed fires in this study damaged small oak seedlings, in addition to killing more fire sensitive species; however many of these damaged oak seedlings resprouted vigorously, which is consistent with results from previous studies (Barnes and Van Lear, 1998; Brose et al., 2013). Additionally, these initial fires should reduce the litter and duff layers promoting acorn germination and oak establishment in areas slated for future harvests (Arthur et al., 2012; Johnson et al., 2009; Royse et al., 2010). Given the adaptive nature of this silvicultural system, fire frequencies and fire-free intervals can be adjusted based on observed regeneration patterns.

This study demonstrates the benefits of critically considering a system's disturbance ecology and the autecology of target species to adapt silvicultural methods used in superficially dissimilar systems, which are actually driven by similar underlying ecological processes. We showed very high levels of competitive oak regeneration in the forest matrix outside of small shelterwood gaps on the northern, eastern, and western edges at our more xeric site. Given the shelterwoods used in this experiment will be expanded outward in successive entries, the higher proportion of competitive oak regeneration in these areas holds promise to regenerate a stand with a substantial oak component and high overall diversity.

5. Declarations of interests

None

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.10.043.

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