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# Harvested opening size affects cohort development and failures in a second-growth northern hardwood forest

Samuel P. Knapp[a,*], Christel C. Kern[b], Christopher R. Webster[a]

[a] College of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA
[b] USDA Forest Service, Northern Research Station, 5985 Highway K, Rhinelander, WI 54501, USA

## ABSTRACT

Group selection is one potential tool in contemporary, uneven-aged silviculture for mitigating increased dominance by shade-tolerant species while continuing to meet stocking goals and harvest quotas. However, recent experimental group-selection openings in northern hardwood forests on some sites in the Upper Great Lakes region have failed to meet management goals of increased tree diversity and timely natural regeneration. Few observational studies have documented the long-term stand development of nascent cohorts following group-selection prescriptions. This study revisits a long-term group-selection experiment which previously found that opening size had little effect on regeneration diversity and found that large areas devoid of saplings and dominated by understory vegetation were common more than a decade following harvest. Our goals were to reassess the state of stand development and diversity within harvested openings, as well as look for early post-harvest indicators of regeneration success or failure after 23 years. At 23 years post-harvest, we found that opening size had little effect on regeneration diversity but rather influenced patterns of cohort development. Smaller openings (6–20 m diameter) showed signs of self-thinning, while larger openings (30–46 m diameter) showed divergent developmental patterns including both self-thinning and ongoing sapling recruitment. Most areas of regeneration failures persisted through 23 years, and the largest openings (46 m diameter) were most likely to display regeneration failure, with 42% of subplots devoid of saplings but containing dense understory vegetation. The density of understory vegetation at 2 years post-harvest had no effect on year-23 sapling density. Instead, only seedling/sapling density in year 2 correlated with regeneration success after 23 years. These results suggest that in northern hardwood forests in the upper Great Lakes region, opening creation alone may not produce the desired effects of increased canopy diversity and sustained timber yields. Canopy openings >30 m diameter appear more likely to result in partial, multi-decade regeneration failures compared to smaller openings; however, our results highlight the importance of advance regeneration for preventing these failures. Thus, simultaneously achieving management goals of increased tree diversity and adequate regenerative stocking with group selection likely requires additional inputs (e.g. herbivore protection, planting, scarification, herbicides, repeated thinning, etc.) beyond the current status quo.

## 1. Introduction

Contemporary northern hardwood forest management in North America operates on a paradigm of sustained yields via uneven-aged, partial cutting at short, regular time intervals (Webster et al. 2018). However, the predominant uneven-aged management system—single-tree selection—tends to favor regeneration of shade-tolerant species by emulating single-tree mortality and sustaining low understory light levels (Nyland 1998). Routine implementation of single-tree selection throughout the upper Great Lakes has increasingly homogenized hardwood forests in favor of maple species (*Acer* spp.; Schulte et al. 2007), reduced functional-trait diversity (Sabatini et al. 2014), and increased the overall risk of resource losses due to climate change and/or novel diseases and pests (Millar et al. 2007).

Group selection is an alternative and/or supplemental uneven-aged silvicultural system that may diversify composition and structure of managed northern hardwoods (Woods 2000, Kern et al. 2014). Group selection is designed to emulate intermediate-scale disturbances with multiple-tree openings ranging from 400–2,000 $m^2$ and create recruitment opportunities for disturbance-adapted and light-demanding species (Denslow 1980, Wisconsin Deparment of Natural Resources 2013a). Group selection has been successfully implemented in hardwoods across eastern North America (Leak 1999, Leak 2003, Webster and Lorimer 2005, Falk et al. 2010, Prevost et al. 2010, Gauthier et al. 2016), but regional and site-specific factors have sometimes hindered achieving management goals related to both cohort development and increased diversity (Kern et al. 2017). Problems with both stand development and regeneration diversity have been particularly common with group-selection harvests in the upper Great Lakes region of North America (Kern et al. 2017).

Naturally regenerating cohorts in several group-selection experiments in the upper Great Lakes region have displayed patterns of delayed sapling recruitment—i.e. stand initiation (Oliver and Larson 1996)—within openings (Metzger and Tubbs 1971, Matonis et al. 2011,

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* Corresponding author.
*E-mail address:* samuel.knapp@fulbrightmail.org (S.P. Knapp).

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Kern et al. 2013, Knapp et al. 2019a). In some cases, aggressive layers of herbaceous and/or shrubby vegetation, especially *Rubus* spp., have been responsible for regeneration delays persisting for multiple decades (Metzger and Tubbs 1971, Widen et al. 2018). These examples contrast with suggestions that tree seedlings should grow through and overtop aggressive ruderal vegetation within a decade following harvest (Donoso and Nyland 2006, Engelman and Nyland 2006). Furthermore, limited availability of seeds or suitable microsite conditions (Willis et al. 2016) as well as ungulate herbivory (Horsley et al. 2003, Matonis et al. 2011) have also been shown to delay and/or reduce propagule colonization in harvested openings. Prolonged sapling recruitment and inadequate stocking both have potential consequences for tree form (e.g., poor self-pruning), forest certification, and harvest scheduling. However, delaying the onset of self-thinning—i.e. stem exclusion (Oliver and Larson 1996)—may harbor unexpected benefits such as longer establishment windows for new colonists (Franklin et al. 2002) and producing multiple age and/or size classes within openings. Few studies have documented cohort development in group-selection openings beyond 15 years post-harvest, so the full extant and consequences of delayed stand development in these and similar openings remains relatively unknown.

In addition to instances of delayed stand development, group selection has sometimes failed to meet goals of increased tree diversity in uneven-aged managed stands in the Upper Great Lakes region. In these stands, group-selection openings sometimes fail to regenerate diverse cohorts with mixed shade tolerance (Arseneault et al. 2011, Bolton and D'Amato 2011). The legacies of exploitive harvesting in the late 19th and early 20th centuries and decades of single-tree selection may have altered compositional diversity across the Great Lakes region and, thus, be a factor limiting resultant diversity following group selection and other medium-scale disturbances (Whitney 1987, Neuendorff et al. 2007, Schulte et al. 2007). Overabundant herbivores, especially white-tailed deer (*Odocoileus virginianus*), have also had profound impacts on regeneration composition and development in the region by altering local species assemblages and suppressing growth (Matonis et al. 2011, Kern et al. 2012, Sabo et al. 2019). Understanding how these and other factors combine to affect both cohort development and diversity is vital to understanding if group selection is a viable silvicultural tool for increasing forest diversity in the region. Monitoring is also important for documenting ongoing effects of climate change on forest dynamics in northern hardwoods (Swanston et al. 2018).

In this study, we revisited a long-term silvicultural experiment (Kern et al. 2013) with goals of reassessing the compositional patterns of regeneration and the state of cohort development within harvested openings from 13 to 23 years following harvest, as well as using early-post-harvest data (year 2) to predict long-term regeneration patterns (year 23). We paid special attention to our tallest height class of saplings (>2.13 m height) as the most relevant to management goals at 23 years post-harvest. In year 13, experimental openings were dominated by three species—sugar maple (*Acer saccharum* Marsh.), ironwood [*Ostrya virginiana* (Mill.) K. Koch], and white ash (*Fraxinus americana* L.)—while smaller openings had the highest diversity metrics for trees >0.61 m height (Kern et al. 2013). [H1] We hypothesized that these general compositional patterns and diversity differences among opening-size treatments in trees >0.61 m height would be present in trees >2.13 m in year 23. However, we expected to find different patterns of stand development between small and large openings. In year 13, openings 6–20 m diameter were often fully stocked but with evident self-thinning. [H2] In these smaller openings, we expected declines in overall stem density and diversity metrics as crowns closed laterally and attrition progressed in favor of shade-tolerant species between years 13 and 23. In contrast, larger openings 30–46 m diameter were often poorly stocked in year 13, and some openings had large areas with hindered and prolonged sapling recruitment due to competitive understory vegetation and possibly herbivory. For large openings, we present competing hypotheses regarding the status of stand development in year 23. [H3a] If advancement beyond sapling recruitment was only temporarily delayed in the larger openings, we expected to find increased sapling stem density and declining diversity metrics due to height increases by mostly shade-tolerant species. [H3b] If there were continued delays in sapling recruitment, we expected to find stem density and diversity metrics static in larger openings between years 13 and 23. In year 13, regeneration failures—areas that were poorly stocked and dominated by understory herbs and shrubs—were common in larger openings. [H4] We predicted that areas of regeneration failure observed in year 13 would persist to year 23 and be most prevalent in larger openings. [H5] Lastly, we hypothesized that high densities of herbaceous plants and shrubs at 2 years post-harvest would negatively correlate with tree stem density after 23 years.

## 2. Methods

### 2.1. Study site

The site is 136 ha of second-growth northern hardwoods located in the Chequamegon-Nicolet National Forest (N45°56′, W88°59′) in Forest County of northeastern Wisconsin, USA. Landscape features are of glacial origin and are characterized by rolling kame hills and kettle basins with frequent pits and mounds from past blowdown events. The primary soil type is Padus sandy loam (a coarse-loamy, mixed, superactive, frigid Alfic Haplorthod) in occasional complexes with Pence sandy loam (a sandy, isotic, frigid, Typic Haplorthod; Soil Survey Staff 2017). Vegetation is typical of the ATD (*Acer saccharum-Tsuga canadensis/Dryopteris spinulosa*) habitat type in the habitat classification system created by Kotar et al. (2002). Common understory plants included spinulose shield fern (*Dryopteris spinulosa* [Vill.] H.P. Fuchs), wild lily-of-the-valley (*Maianthemum canadense* Desf.), and Jack-in-the-pulpit (*Arisaemea triphyllum* [L.] Schott). Sugar maple comprised the majority of canopy trees (85.4%) with occasional inclusions of American basswood (*Tilia americana* L.) (4.3%), yellow birch (*Betula alleghaniensis* Britt.) (3.2%), and white ash (*Fraxinus americana* L.) (2.4%), with rare occurrences of eight other species including ironwood (*Ostrya virginiana* [Mill.] K. Koch), black cherry (*Prunus serotina* Ehrh.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), eastern white pine (*Pinus strobus* L.), and white birch (*Betula papyrifera* Marsh.) (Knapp et al. 2019b). The site was extensively harvested for white pine in the 1870–1890s (Rhemtulla et al. 2009), commercially clearcut for hardwoods in the 1930s, and afterwards left unmanaged until study initiation in 1994 (Kern et al. 2013). Prior to study initiation, the stand was estimated to be 60 year-old second-growth with density ranging from 89 to 285 stems $ha^{-1}$ and basal area ranging from 20–39 $m^2$ $ha^{-1}$ for stems over 4 cm dbh (diameter at breast height, 1.37 cm; Kern et al. 2013).

### 2.2. Study design

The Divide Canopy Gap Study—named for nearby Divide Road—was established in 1994 and consists of a randomized complete block experimental design. Prior to study initiation, the site was surveyed and delineated into seven uniform blocks, four of which were randomly selected for study. The experimental blocks were delineated into 0.4 ha squares, and each treatment level was randomly assigned to three squares per block. The study treatment was harvest-created gap size (cut in winters of 1994 and 1995) with six levels (based upon gap diameter): 0 m (reference), 6 m, 10 m, 20 m, 30 m, and 46 m. The treatment levels reflected the range of possible gap sizes for conversion to uneven-aged management (Wisconsin Deparment of Natural Resources 2013b). Thus, across the study area, there were 12 unharvested reference plots and 60 canopy openings (12 per treatment).

The forest matrices of the four experimental blocks (excluding 0.4 ha reference sites) were thinned following the guidelines of Erdmann (1986) for converting even-aged, second-growth northern hardwood stands to uneven-aged conditions. This "improvement cut" was a commercial harvest intended to remove damaged/diseased stems expected to accrue minimal economic value and stems anticipated to die from self-thinning. The gaps were created with commercial harvests done alongside the improvement cut, removing all trees >11.4 cm dbh within the prescribed gap radii in the winters of 1994 and 1995. Additionally, the gaps were cleaned of all submerchantable saplings (>2.5 cm dbh) to provide growing space for young seedlings and facilitate quality, vigorous regeneration.

Woody stems and understory vegetation were surveyed in five subplots located on four transects along the cardinal directions radiating from the center of each canopy opening/reference plot (Fig. 1). Tree stems <0.61 m height were measured within 1 m squares, while stems >0.61 m height were measured within a 1.83 m radius of each subplot center. Distances between subplots varied by treatment: 3.7–7.4 m for 6 m, 10 m, and 20 m openings, and 11 m for reference plots, 30 m openings, and 46 m openings (Fig. 1).

### 2.3. Field sampling

Data collection of woody and herbaceous vegetation occurred pre-harvest (1994–1995) and at 2, 6, 13, and 23 years post-harvest (1997, 2001, 2008, and 2018 respectively). Percent cover of herbaceous vegetation and woody shrubs was visually estimated within 1 $m^2$ permanent quadrats centered on subplots, recorded into eight coverage classes (0%, 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, and ≥ 75%), and grouped as forbs, ferns, graminoids, or shrubs. In the year 2 survey, stem density of shrubs within quadrats was also tallied by species. Tree stems under 0.61 m height (unstretched) were counted by species within 1 $m^2$ permanent quadrats centered on subplots into two height classes: <0.15 m and 0.15–0.61 m. Within 1.83 m radii of each subplot center, tree stems 0.61–2.13 m and >2.13 m height were tallied by species, and the tallest individual for each species was measured for height and dbh (if applicable). Species nomenclature followed the USDA Plants Database (USDA 2019).

### 2.4. Data analyses

Regeneration was divided into three height classes relevant to development at 23 years post-harvest: seedlings (<0.61 m), small saplings (0.61–2.13 m), and large saplings (>2.13 m). Analyses used only subplots within the prescribed treatment opening dripline ($n = 5$ per opening/reference), except in 6 m openings and reference plots where the five inner-most subplots were used (Fig. 1). Shade tolerance, although not formally analyzed, was classified for tree species using the tables of Niinemets and Valladares (2006). All means are presented plus or minus standard error of the mean.

Linear mixed-effects models (LMM) were used to test many of our hypotheses and were created using *R* version 3.5.3 (R Core Team 2019) and the *nlme* package v. 3.1–137 (Pinheiro et al. 2019). Models were estimated with restricted maximum likelihoods (Zuur et al. 2009), and post-hoc comparisons, when applicable, were made using estimated-marginal means in the *emmeans* package v. 1.3.3 (Lenth 2019). Unless otherwise stated, models used subplot-level data and had random effects of plots (i.e. individual canopy gaps or reference plots) nested within experimental blocks. The Benjamini-Hochberg procedure was used to correct for multiple comparisons, when applicable, within sets of results (Benjamini and Hochberg 1995). A false-discovery rate—the chance of accepting a false-positive result as significant—of 0.25 was used to adjust our standard significance threshold of α = 0.05.

To test for changes in species density and relative abundance within

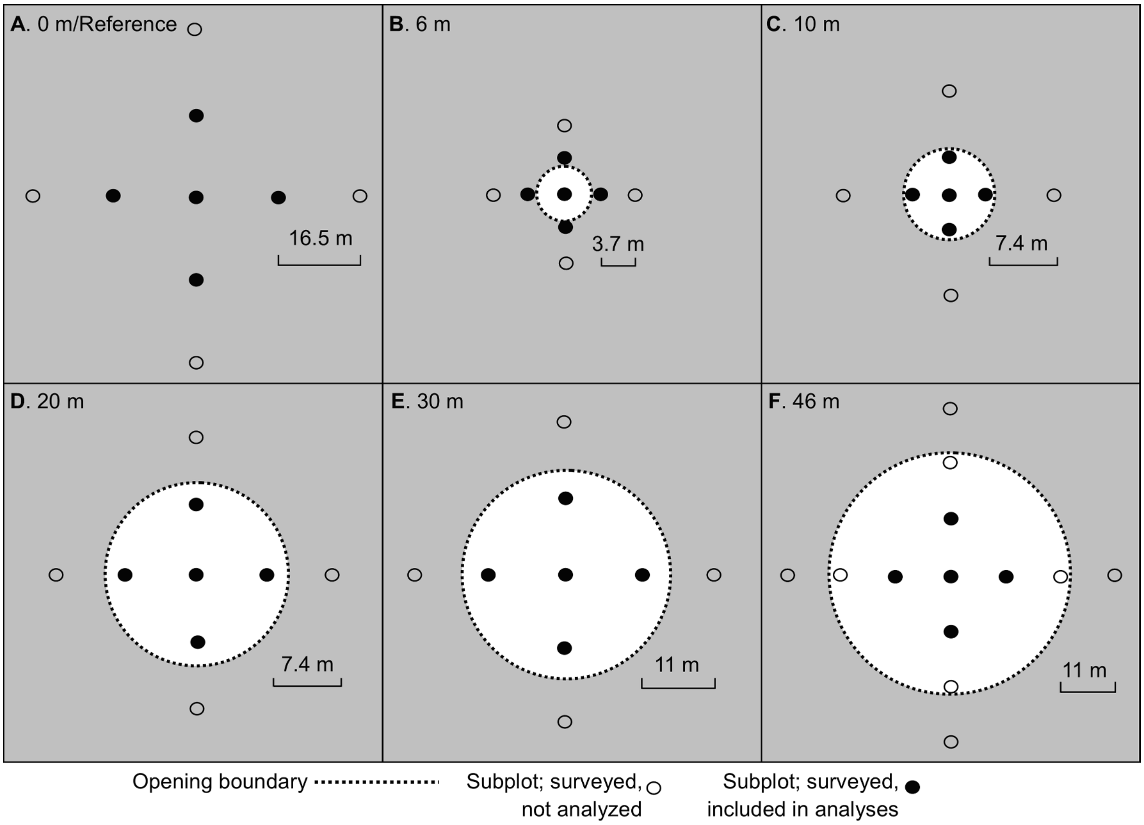

**Fig. 1.** Layout of our six experimental group-selection opening treatments in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Grey areas represent the forest matrix, while white areas within dotted lines represent canopy openings commercially harvested in the winters of 1994–95, with all stems >2.5 cm dbh removed following harvests. Small circles represent subplots, and closed (black) subplots were those included in analyses. Scale bars also represent distances between subplots for each treatment. Each treatment had three replicates per each of four experimental blocks, for 12 total replicates per treatment.

openings over time, we made LMMs of large saplings (>2.13 m height) in canopy openings (no reference plots) between years 13 and 23. Density and relative abundance (modeled separately) were predicted by study year, and we only tested for changes in the three primary species: sugar maple, ironwood, and white ash. Density and relative abundance data were untransformed, and model assumptions were checked visually.

Species compositional differences among treatments were determined using multiple response permutation procedures (MRPP). MRPP is a non-parametric procedure that can quantify the extent to which species assemblages within groups (i.e. treatments) differ from one another. The test statistic is similar to Student's *t* and is a standardized difference between the weighted-mean within-group distance $\delta$ from observed and expected values. The *p*-value describes the likelihood that observed differences between groups are due to chance. The effect size is represented by the chance-corrected within-group agreement *A*, which describes the homogeneity within groups: if $A = 1$, all observations within a group are equal; if $A = 0$, heterogeneity within groups is random, and if $A < 0$, heterogeneity within groups is greater than what is expected by chance (McCune and Grace 2002). We used *R* version 3.5.3 (R Core Team 2019) and the *vegan* package v. 2.5–4 (Oksanen et al. 2019) to perform MRPPs on the tree regeneration within treatments. Primary matrices contained species relative abundance in openings/references for combinations of study years and height classes, and Sørenson (Bray-Curtis) distances and 999 iterations were used for calculating $\delta$. Groups were defined by opening-size treatments within each study year and height class, and pairwise group comparisons were used for determining individual treatment differences when the overall MRPP was significant. The Benjamini-Hochberg procedure was used to correct for multiple comparisons when pairwise treatment comparisons were necessary for a given study year and height class combination with a false-discovery rate of 0.25 (Benjamini and Hochberg 1995).

To analyze patterns of year-23 stem density, species richness, and evenness (Shannon's), LMMs were used to test for differences among treatments. We also re-analyzed data from the year 13 dataset—see Kern et al. (2013) for which height classes for tree regeneration were <0.15 m, 0.15–0.61 m, and >0.61 m—using our updated height classes: <0.61 m, 0.61–2.13 m, and >2.13 m, and we created separate models for each combination of metric (density, richness, or evenness), height class, and study year. For our models predicting species richness or evenness (analyzed separately), plot-level data were used with treatments (opening size) as fixed effects and experimental blocks as random effects. Density, richness, and evenness data were untransformed, and assumptions for each model were checked visually. Post-hoc comparisons were made among treatments for each model.

To find differences between study years 13 and 23, LMMs of large sapling stem density, species richness, and evenness (Shannon's; analyzed separately) predicted by study year were created for the individual treatments. For these models, a variance structure that allowed for different variances between strata (i.e. study year) was chosen over an undefined variance structure or data transformations on the basis of AIC (Zuur et al. 2009). After seeing initial results, we added a separate analysis to better address our hypotheses about cohort development in areas with delayed regeneration (H3a–b). We defined regeneration failure within subplots as: (1) no tree stems over dbh height (>1.37 m) within a 1.83 m radius and (2) >50% combined coverage of herbaceous vegetation and shrubs in 1 $m^2$ quadrats. We created a new set LMMs using a subset of the data including only subplots meeting our definition of regeneration failure in year 13 and with the same effects and variance structure as models before. Density, richness, and evenness data were untransformed, and model assumptions were all checked visually.

For year 23, differences in the prevalence of regeneration failures among treatments were analyzed with LMMs. The number of subplots meeting our definition of regeneration failure (defined above) were summed for each opening/reference in year 13 and 23. Models predicted the frequency of regeneration failure in year 23 with treatment as the fixed effect and experimental block as the random effect. Model assumptions were checked visually, and post-hoc comparisons were made among treatments. We also tested for changes in the frequency of regeneration failures over time. A LMM of regeneration failure frequency predicted by study year (i.e. years 13 and 23) was made with the same random effects structure.

To understand the predictability of year 23 regeneration patterns, LMMs were used to assess the efficacy of forecasting long-term regeneration success with markers available at 2 years post-harvest. The response variable in models was density of large saplings (>2.13 m height) in year 23, and predictor variables were percent coverage of forbs, ferns, graminoids, or shrubs and overall tree stem density in year 2, all assessed at the subplot level. Models were constructed separately for each predictor variable, and all variables were $\log_{10}$ transformed to linearize relationships and meet model assumptions of homoscedasticity. *P*-values of individual predictors were used to assess model fits.

## 3. Results

After 23 years, large saplings (>2.13 m height) in openings were primarily composed of sugar maple (50 ± 5%), ironwood (26 ± 4%), and white ash (21 ± 3%), while sugar maple dominated the seedling (<0.6 m height, 88 ± 2%) and small sapling classes (0.61–2.13 m height, 68 ± 5%) (Fig. 2, Table A.1). Between 13 and 23 years post-harvest, the densities of both large sugar maple and white ash saplings in openings declined—respectively from 1,990 ± 280 $ha^{-1}$ to 1,470 ± 180 $ha^{-1}$ (LMM, $p = 0.005$) and from 1,470 ± 370 $ha^{-1}$ to 550 ± 100 $ha^{-1}$ (LMM, $p < 0.001$)—while the density of large ironwood saplings in openings remained relatively unchanged (450 ± 80 $ha^{-1}$ to 500 ± 70 $ha^{-1}$; Fig. 2, Tables A.2 and A.3). During that time, only the relative abundance of large white ash saplings within openings decreased slightly from 23 ± 3% to 21 ± 3% (LMM, $p = 0.061$), while the relative abundance of large sugar maple and ironwood saplings in openings remained relatively unchanged (LMMs, $p \geq 0.360$, Tables A.1 and A.3).

Analyzing year 13 data with updated height classes, we found that the species composition of large saplings (>2.13 m height) did not differ among opening sizes in year 13 (MRPP, $p \geq 0.401$, Table A.5). We also did not find differences in the richness or evenness of large saplings among treatments at 13 years post-harvest (LMMs, $p \geq 0.121$, Table A.4). Instead, compositional differences among treatments were only found within small saplings (0.61–2.13 m height) in year 13 (MRPP, $p = 0.006$), as well as differences in richness (LMM, $p < 0.001$) and evenness (LMM, $p = 0.002$).

At 23 years post-harvest, compositional differences were not observed among any opening-size treatments for either seedlings (<0.61 m height) or large saplings (>2.13 m height) (MRPP, $p \geq 0.143$), and only between 10 m and 20 m openings for small saplings (0.61–2.13 m height) (MRPP, $p = 0.018$; Table 1, Table A.5). Likewise, neither species richness nor evenness differed with opening size for seedlings or large saplings (LMM, $p \geq 0.178$, Table A.4). Only small saplings (0.61–2.13 m height) exhibited differences in species richness between 20 m gaps (2.1 ± 0.4 species) and 46 m gaps (0.7 ± 0.2 species) (LMM, $p = 0.007$; Fig. 3, Table A.4).

Between years 13 and 23, large sapling stem density decreased in smaller (6 m, 10 m, and 20 m diameter) and large (46 m diameter) openings (LMM, $p \leq 0.013$) and remained unchanged in 30 m openings and reference plots (LMM, $p \geq 0.47$; Fig. 2, Table A.6). Furthermore, neither the species richness nor evenness for large saplings changed between years 13 and 23 in any opening size (LMM, $p \geq 0.126$) (Fig. 3, Table A.6). When data were subset to include only subplots that met our definition of regeneration failure in year 13, we found that sapling density did not significantly change between years 13 and 23 (LMM, $p = 0.09$; Table A.6)

At 23 years post-harvest, large gaps (46 m) were most likely to have areas of regeneration failure (42 ± 11% of subplots), while reference plots, 6 m gaps, and 20 m gaps had the fewest subplots meeting our

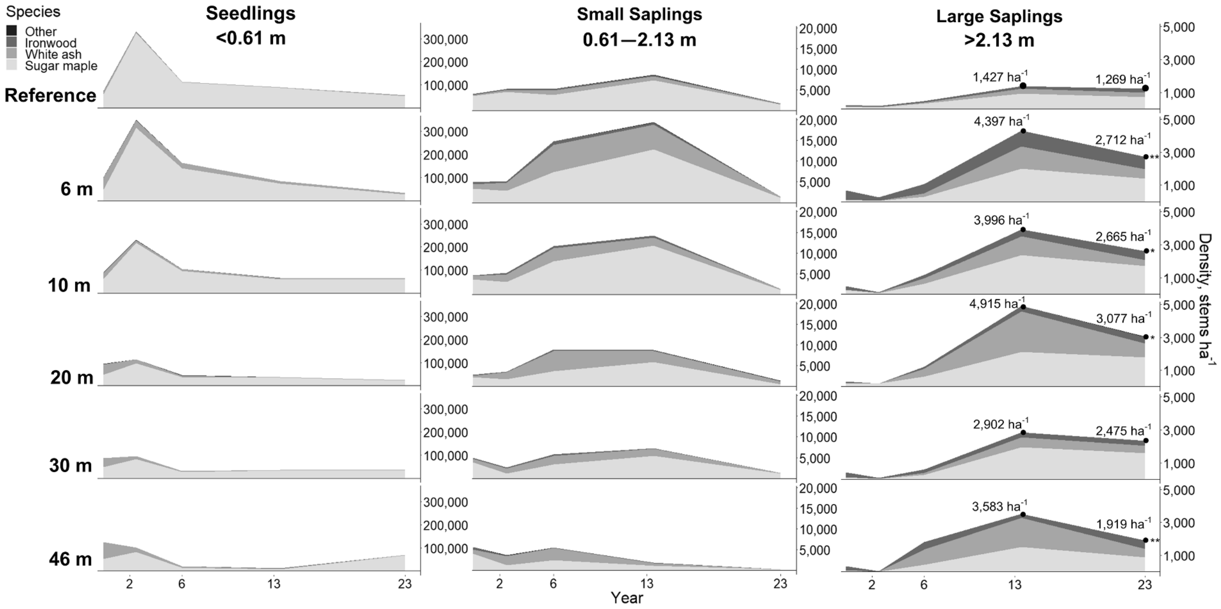

**Fig. 2.** Regeneration composition and density over time within experimental group-selection openings in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Graphs are grouped in columns by height class (labeled along the top) and in rows by opening-size treatment (labeled along the far left; $n = 12$ for each treatment). Note differences in density scales between height classes. Colors denote each species' contribution to total density. Asterisks next to year 23 total densities for large saplings denote significant differences from year 13 total densities found with LMMs:$^{*}p \leq 0.05$, $^{**}\ p \leq 0.01$.

**Table 1**
Compositional groupings of seedlings and saplings in experimental group-selection openings in the Chequamegon-Nicolet National Forest, USA, determined by pairwise Multiple Response Permutation Procedures (MRPP). Significance at α = 0.05 was adjusted for multiple comparisons using the Benjamini-Hochberg procedure and a false-discovery rate of 0.25.

| Year | Year 2 (1997) | | | Year 13 (2008) | | | Year 23 (2018) | | |
|---|---|---|---|---|---|---|---|---|---|
| Height Class | <0.61 *m* | 0.61–2.13 *m* | >2.13 *m* | <0.61 *m* | 0.61–2.13 *m* | >2.13 *m* | <0.61 *m* | 0.61–2.13 *m* | >2.13 *m* |
| *Opening Size* | | | | | | | | | |
| 0 *m* | **a** | **a** | **ab** | **a** | **ab** | **a** | **a** | **ab** | **a** |
| 6 *m* | **b** | **ab** | **ab** | **ab** | **ab** | **a** | **a** | **ab** | **a** |
| 10 *m* | **b** | **ab** | **ab** | **d** | **a** | **a** | **a** | **a** | **a** |
| 20 *m* | **b** | **ab** | **a** | **bc** | **b** | **a** | **a** | **b** | **a** |
| 30 *m* | **b** | **ab** | **ab** | **abc** | **ab** | **a** | **a** | **ab** | **a** |
| 46 *m* | **b** | **b** | **b** | **c** | **c** | **a** | **a** | **ab** | **a** |

definition of regeneration failure (3 ± 2%, 7 ± 7%, and 12 ± 4% of subplots, respectively; LMM, Fig. 4, Table A.7). The prevalence of subplots that met our criteria for regeneration failure between 13 and 23 years post-harvest did not vary significantly over time (LMM, $p = 0.399$; Fig. 4). Of subplots with failed regeneration in year 13, only 11 of 75 (15%) contained any saplings >2.13 m by year 23. Mean stem density did not differ among opening sizes for any height class after 23 years (LMM, $p \geq 0.079$; Fig. 2, Table A.4).

Of the variables tested, overall tree-stem density at 2 years post-harvest was the only significant predictor of the stem density of large saplings (>2.1 m height) at 23 years post-harvest in linear mixed-effects models ($p < 0.0001$). The coverage of herbaceous plants (forbs, graminoids, and ferns) and woody shrub density at 2 years post-harvest were not indicative of large-sapling density after 23 years (Table 2).

## 4. Discussion

After 23 years of monitoring at the Divide Canopy Gap Study, opening size continued to have little effect on regeneration composition within harvested openings, and sugar maple, ironwood, and white ash continued to dominate regeneration layers. Compositional differences among opening sizes found for saplings 0.61–2.13 m height in year 13 were not found in taller height classes by year 23. In smaller openings (6–20 m diameter), cohort development was characteristic of self-thinning in year 23, with declining sapling density and static diversity metrics over the last decade. Larger openings had more complex regeneration dynamics with divergent developmental patterns that often co-occurred within individual openings. While most of the land area in large openings was adequately stocked, regeneration failures—areas dominated by understory vegetation devoid of saplings—were common in the largest openings, and we found that most regeneration failures observed in year 13 persisted to year 23. The abundance of understory vegetation at 2 years post-harvest did not correlate to regeneration success in year 23; instead, only stocking in year 2 adequately predicted stocking in year 23. Thus, our results may highlight the importance of advance regeneration in preventing long-term regeneration delays and the potential for detecting such delays when timely stocking is a primary goal.

### 4.1. Regeneration compositional patterns

When reanalyzing year 13 data with our updated height classes (<0.61 m, 0.61–2.13 m, and >2.13 m), we expected to find the same compositional differences among opening sizes as found by Kern et al.

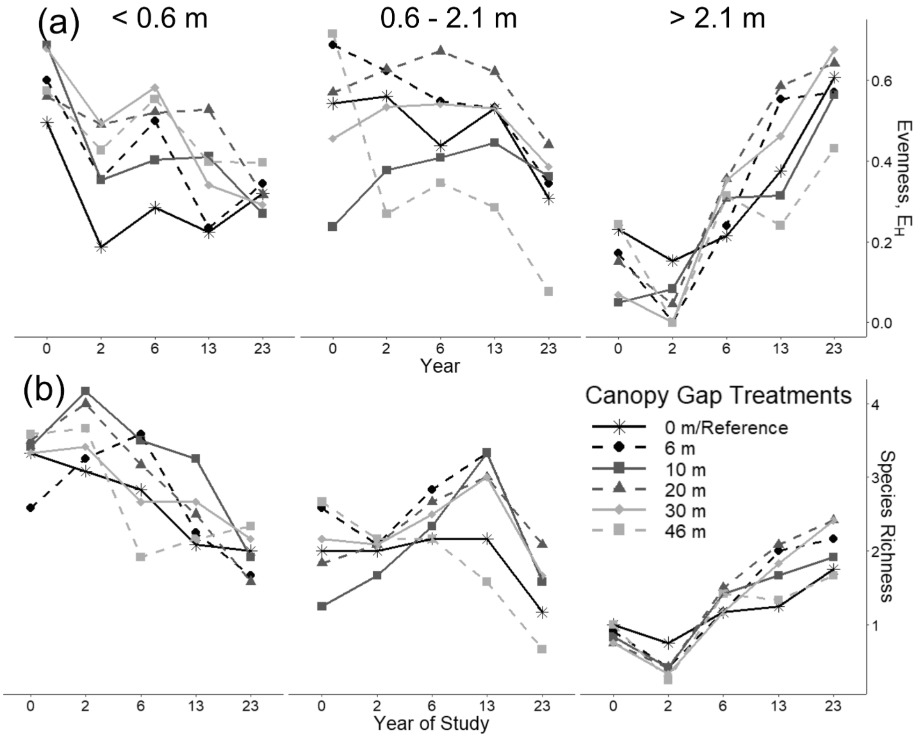

**Fig. 3.** Evenness (Shannon's; a) and species richness (b) of woody stems over time within experimental group-selection openings in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Opening-size treatments are represented as different lines ($n = 12$ for each treatment).

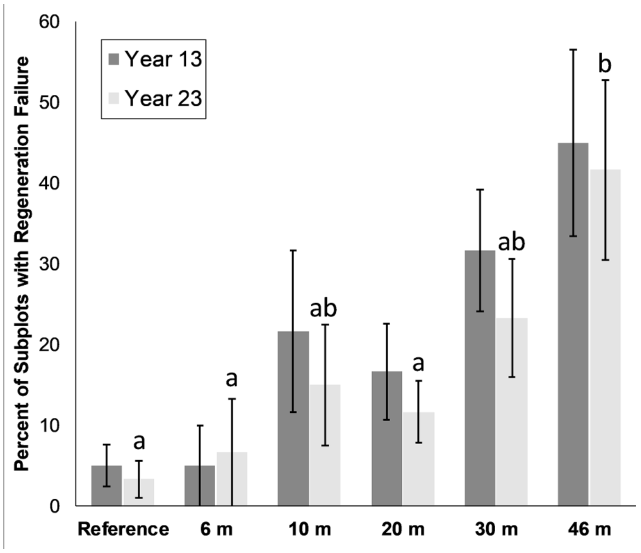

**Fig. 4.** The percentage of subplots within opening-size treatments meeting our definition of regeneration failure in year 13 and year 23 within experimental group-selection openings in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Regeneration failures were defined as subplots without tree stems taller than dbh height (1.37 m) and containing ≥50% cumulative aerial cover of herbaceous plants and shrubs. Lowercase letters denote groupings from post-hoc comparisons of estimated marginal (least-squares) means of the percentage of subplots with regeneration failures in year 23 and were derived from LMMs. [1-column fitting image]

(2013) and for those differences to persist to year 23. However, we found that compositional differences among opening sizes for trees >0.61 m height found in year 13 (Kern et al. 2013) were only present in small saplings 0.61–2.13 m height at that time, not in large saplings >2.13 m height. Even so, the general compositional patterns present in year 13 persisted to year 23, with no compositional differences among opening sizes found for large saplings. Thus, the compositional differentiation among opening sizes found for small saplings in year 13 did not translate into the large sapling height class by year 23. In contrast with other studies showing that late-developing compositional changes can sometimes occur within harvested openings (Leak 2003, Knapp et al. 2019a), our openings developed a relatively homogenous early cohort of regeneration that remained relatively static over time and largely failed to recruit new species into taller height classes.

Shade-tolerant sugar maple and ironwood and shade-midtolerant white ash were the most abundant species year 13 and persisted to year 23 in our experiment. These three species composed the majority of the advance regeneration remaining after stems >2.5 cm dbh were removed and the majority of saplings likely to recruit into the canopy (Knapp et al. 2019b). They have also been found as the predominant species in other regional group-selection experiments (Reuling et al. 2019). Theoretically, harvested openings that emulate intermediate-scale disturbances enhance the recruitment of shade-intolerant and -midtolerant species (Denslow 1980), and this enhanced recruitment, unlike in our study, has been commonly observed in both natural and harvested canopy gaps in temperate forests (Runkle 1982, Dale et al. 1995, Webster and Lorimer 2005, Zhu et al. 2014). Thus, compositional patterns in our study and others have not always followed the patterns expected by theory, suggesting that other factors may be affecting results.

In our experiment and others, factors such as availability of propagules and appropriate substrates may be collectively limiting the efficacy of group-selection openings to recruit more light-demanding species (Willis et al. 2016, Kern et al. 2017, Webster et al. 2018). Furthermore, homogenization of regional forest composition resulting from historic and contemporary forest management (Neuendorff et al. 2007, Schulte et al. 2007) may be limiting local seed availability and recruitment opportunities for poorly-represented species in harvested canopy openings (Willis et al. 2016, Webster et al. 2018). Even if seeds are present, many small-seeded species require specific substrate

**Table 2**
Linear mixed-effects model results of large sapling (>2.1 m height) density in year 23 predicted individually by density or cover of vegetation present in year 2—tree stems, ferns, forbs, graminoids, and shrubs—in experimental group-selection openings in the Chequamegon-Nicolet National Forest, USA. Separate models were created for each predictor, and all density and percent cover data were $\log_{10}$ transformed to meet assumptions of linearity and homoscedasticity. All models used plots (i.e. individaul openings/reference plots) within experimental blocks as random effects. Significant predictors appear in bold.

| Fixed Effect | Estimate | Standard Error | df | t value | Pr (>\|t\|) | Random Effect | Std Dev of Intercept | Std Dev of Residual |
|---|---|---|---|---|---|---|---|---|
| **Tree density, year 2** | 0.041 | 0.009 | 287 | 4.60 | **<0.0001** | Gap in Block | 0.048 | 0.064 |
| Fern % Cover, year 2 | −0.009 | 0.008 | 287 | −1.11 | 0.270 | Gap in Block | 0.045 | 0.067 |
| Forb % Cover, year 2 | 0.007 | 0.008 | 287 | 0.84 | 0.403 | Gap in Block | 0.045 | 0.067 |
| Shrub density, year 2 | −0.012 | 0.032 | 287 | −0.37 | 0.712 | Gap in Block | 0.046 | 0.067 |
| Graminoid % Cover, year 2 | 0.001 | 0.008 | 287 | 0.16 | 0.877 | Gap in Block | 0.046 | 0.067 |

conditions for successful germination (i.e. exposed mineral soils for birches [*Betula* spp.]; Willis et al. 2015, Willis et al. 2016), and many examples of successful shade-intolerant and -midtolerant recruitment exist in canopy openings intentionally scarified during harvest (Raymond et al. 2003, Prevost et al. 2010, Willis et al. 2015, Gauthier et al. 2016, Shabaga et al. 2019). Canopy openings in our study were harvested during winter months and were not intentionally scarified; thus, certain species, such as yellow birch, may have struggled to regenerate due to a lack of appropriate substrates. Advance regeneration in our study site also appeared to be a major driver of composition in openings (see Knapp et al. 2019b).

Site quality may also be a factor limiting regeneration diversity in our study. In contrast to similar forests in the Great Lakes region, ATD (*Acer saccharum-Tsuga canadensis/Dryopteris spinulosa*) habitat types are often heavily dominated by sugar maple in all regeneration layers (Kotar et al. 2002). ATD habitats are classified as having medium-to-rich soils, which may provide a niche for sugar maple to dominate compared to other mesic types with lower and/or higher productivity (Kotar and Burger 2003). Difficulty regenerating diverse cohorts with group selection has been common on medium-to-rich soils in northern hardwoods (Kotar et al. 2002, Forrester et al. 2014, Halpin et al. 2017). Another study of group-selection openings on ATD sites in northern Wisconsin, USA, found that neither removing advance regeneration nor scarifying the soil abated sugar maple dominance, and they speculated that this may be inevitable for medium-to-rich, mesic northern hardwoods (i.e. ATD) (Reuling et al. 2019). Several other studies have noted that species richness in deciduous forests tends to peak at intermediate productivity and decline as nutrient richness increases or decreases (Dupré et al. 2002, Schuster and Diekmann 2005, Halpin et al. 2017) and may support this interpretation. In our study, sugar maple was the most abundant species but not totally dominant across regeneration layers, suggesting that factors in addition to the ATD habitat type may have influenced overall composition within openings.

Deer herbivory may be one additional factor influencing patterns of regeneration in harvested openings in the upper Great Lakes region, USA (Matonis et al. 2011, Kern et al. 2017, Webster et al. 2018). High white-tailed deer abundance—at least 7.6 ± 0.6 deer $\text{km}^{-2}$ documented in autumn 2018 (WI DNR 2019)—may be increasing white ash and ironwood relative abundance above normal levels for ATD habitats (Kotar et al. 2002, Knapp et al. 2019b). This is possibly due to the relatively high browse-tolerance of white ash (Long et al. 2007) and the unpalatability of ironwood to white-tailed deer (Hurley and Flaspohler 2005). In our study site 22 ± 1% of tree stems were browsed within openings during the fourth growing season following harvest (Kern et al. 2012), suggesting a high likelihood that deer affected regeneration composition and development. Other studies from this region have found that heavy browsing can alter regeneration composition in canopy openings in favor of unpalatable ironwood (Matonis et al. 2011, Forrester et al. 2014). Deer browsing has also been shown to nullify the effects of canopy opening size on regeneration richness (Walters et al. 2016), and this may be occurring in our study site too. A similar experiment in northern Wisconsin, USA, found that the species richness of saplings within harvested canopy gaps 200–380 $\text{m}^2$ more than doubled when white-tailed deer were excluded (Sabo et al. 2019), and this phenomenon has not been limited to North American forests (Tamura and Nakajima 2017).

### 4.2. Developmental patterns

We expected declines in stem density and diversity in smaller openings between years 13 and 23, signifying ongoing self-thinning, but presented competing hypotheses for larger openings. If cohort development in large openings had progressed beyond sapling recruitment, we expected increasing stem density and decreasing diversity metrics. In contrast, we expected to find static stem density and diversity metrics if self-thinning was not occurring in large openings after 23 years. The majority of canopy openings in our experiment were undergoing self-thinning at 23 years post-harvest. However, some openings—especially 30 m and 46 m treatments—contained areas where sapling recruitment was delayed and/or arrested (Fig. 5). In smaller openings (6–20 m diameter), large sapling density declined between years 13 and 23 as expected due to competitive attrition. Species richness and evenness were also largely static in smaller openings during this time period, supporting our hypothesis that cohort development in small openings would continue with self-thinning. In larger openings we found mixed results counter to either of our expectations. Large sapling density declined in 46 m openings but remained static in 30 m openings between years 13 and 23. Thus, regeneration dynamics in 46 m openings were largely indicative of active self-thinning, while 30 m openings showed evidence of either protracted sapling recruitment or ongoing self-thinning. However, we suspect that declining stem density inside "normally developing" areas masked effects of delayed development and/or regeneration failure elsewhere. In year 23, 42% and 23% of subplots met our definition of regeneration failure in 46 m and 30 m openings, respectively. Thus, self-thinning was occurring in some areas within larger openings while other areas experienced impaired or delayed sapling recruitment.

To better address our hypotheses about delayed cohort development (H3a–b), we subdivided the data to include only subplots that met our definition of regeneration failure in year 13. Our definition of regeneration failure translates to <952 stems $\text{ha}^{-1}$ for tree stems >1.37 m height (dbh) and is less stringent than minimum stocking guidelines defined by Leak et al. (1987) and used by Bilodeau-Gauthier et al. (2020) in northern hardwoods (>1,000 saplings $\text{ha}^{-1}$). We found no changes in stem density within subplots meeting our definition of failure between years 13 and 23. This suggests that although some areas dominated by understory vegetation may have infilled from below, the majority of these areas remained free of stems >2.13 m height. Thus, it is more likely that H3b is correct for harvested openings in our study: most areas with impaired sapling recruitment have not infilled from below and are still delayed after 23 years. However, our results suggest regeneration failures, although common, were not the norm in large canopy openings, and that the majority of subplots in larger canopy openings were well stocked after 23 years.

As expected, most subplots meeting our definition of regeneration failure in year 13 continued to meet this definition by year 23, and we found that the largest (46 m) openings had the highest prevalence of regeneration failures in year 23 (Fig. 4). These results provide another

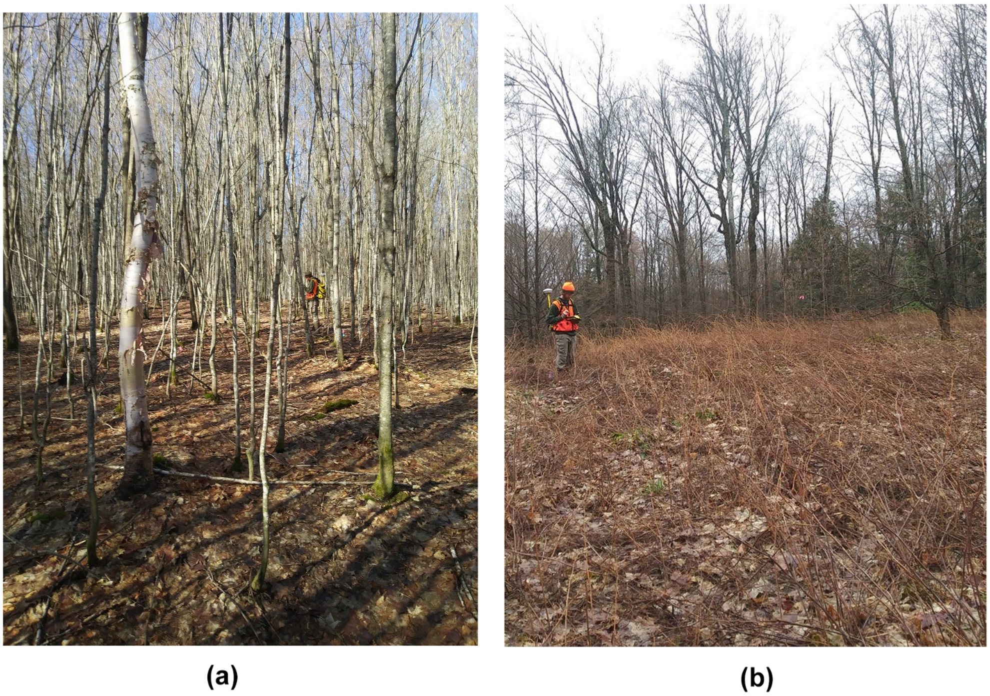

**Fig. 5.** Examples of regeneration success (a) and failure (b) in 23-year-old ,46 m diameter experimental group-selection openings in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA.

example of the risks of dominant ruderal species emerging in large harvested openings (Metzger and Tubbs 1971, Engelman and Nyland 2006, Widen et al. 2018). Although not the definitive cause for the protracted stand development, many areas with delayed regeneration were also found to be dominated by understory shrubs and herbaceous plants, chiefly *Rubus* spp. in year 13 (Kern et al. 2013). *Rubus* abundance in particular has been shown to increase along gradients of light availability in hardwood forests (Ricard and Messier 1996), which may be one explanation for the high likelihood of regeneration failures in 46 m canopy openings in our study.

The development of recalcitrant understories—those forming dense and competitive layers that inhibit natural tree regeneration following disturbance—has also been linked to increased browse pressure and past management activities such as widespread and repeated canopy removals (Royo and Carson 2006). *Rubus* spp. have been particularly troublesome to seedling success in our sites (Kern et al. 2012) and other group-selection openings in our geographic region (Metzger and Tubbs 1971, Widen et al. 2018). *Rubus* spp. may be especially abundant in the local seed pool due to the regional history of exploitive logging in the early 20th century (Whitney 1987), enabling dense germination and growth following canopy disturbances (Donoso and Nyland 2006, Kern et al. 2017, Knapp et al. 2019a). After 23 years, *Rubus* spp. continued to dominate some large openings (Fig. 5) with additional colonization from aggressive herbs such as *Cirsium* spp. These results demonstrate the potential longevity of regeneration failures following intermediate-scale canopy removals and stand in contrast to predictions that shade-tolerant seedlings should outgrow dense *Rubus* within a decade (Donoso and Nyland 2006).

### 4.3. Predicting delayed regeneration

We expected that high densities of herbaceous vegetation and shrubs at 2 years post-harvest would negatively correlate with large sapling density after 23 years. Instead, we found that only seedling/sapling-stem density in year 2 predicted the density of large saplings >2.13 m height after 23 years. No measures of herbaceous or shrub density were indicative of long-term regeneration success within openings (Table 2). In similar harvested openings in Ontario, Canada, Shabaga et al. (2019) also noted a positive relationship between post-harvest stem density and long-term sapling density which strengthened over time. Bilodeau-Gauthier et al. (2020) noted a similar relationship between year 2 stocking and year 15 stocking in both group-selection and patch cuttings in northern hardwoods in Quebec, Canada. Previous findings at our site suggested that seedling/sapling-stem density and *Rubus*-stem density were negatively correlated (Kern et al. 2013). It may be that advance regeneration can overcome competition from aggressive understory vegetation and, where advance regeneration is absent, seedlings not established within 2 years post-harvest cannot germinate and/or survive under recalcitrant understory layers. Thus, advance regeneration may be vital for preventing regeneration delays and/or failures where recalcitrant understories commonly form.

In our study, all advance regeneration >2.5 cm dbh were cleaned from openings shortly following harvest, which may have left some areas vulnerable to future regeneration failure. Some regional studies have found that shade-tolerant advance regeneration dominate in group-selection openings when left onsite (Bolton and D'Amato 2011), but others have found that some shade-intolerant and -midtolerant species recruit successfully even when advance regeneration ≤10 cm dbh remains post-harvest (Knapp et al. 2019a). Even though shade-tolerant species comprise a large part of advance regeneration in second-growth and uneven-aged managed northern hardwoods (Webster and Lorimer 2005), retaining at least some advanced regeneration may be advantageous where competition from understory vegetation is a concern and when adequate stocking is a goal.

### 4.4. Management implications

Results from this study and others indicate that good stocking and enhanced diversity in group-selection openings under current conditions may be hindered on some sites by a variety of factors. In some forests, group-selection openings may modestly increase future canopy diversity (Knapp et al. 2019b), or add meaningful richness to the canopy over several cutting cycles (Halpin et al. 2017). In others, such as our study, a combination of factors may act to dampen resource partitioning (Bolton and D'Amato 2011) or worse, encourage developmental delays and/or regeneration failures within harvested openings (Matonis et al. 2011). Despite having a high representation of shade-tolerant species (Webster and Lorimer 2005, Royo and Carson 2006), advance regeneration might be vital for adequate stocking within large canopy openings that may harbor competitive understory vegetation or have overly-abundant deer populations (Forrester et al. 2014). Overstory diversity might, therefore, be increased by targeting the placement of group-selection openings to areas where shade-intolerant and/or -midtolerant advance regeneration already exists (Eyre and Zillgitt 1953). Future studies might also investigate the effects of delaying advance regeneration removal to prevent slowed cohort development when timely and adequate stocking is a primary goal.

Results from this study and others suggest that long-term regeneration success can be evaluated in the first few years following harvest (Shabaga et al. 2019) and that appropriate actions such as installing exclusion fencing, applying herbicides, or selectively thinning shade-tolerant regeneration might prevent long-term failures (Thiffault and Roy 2011, Frank et al. 2018). Intentional soil scarification or autumn harvesting also appears to increase the recruitment of certain shade-intolerant and -midtolerant species (Gauthier et al. 2016, Shabaga et al. 2019); however, the likelihood for damaging advance regeneration (Zaczek 2002) and the additional operational costs potentially make these options unsuitable. Consequently, achieving diversity and stocking goals in uneven-aged silvicultural systems, in light of contemporary challenges, may require investments beyond the current status quo (Webster et al. 2018). Maintaining the status quo in uneven-age temperate hardwood management presents potential risks for forest homogenization, resource loss, and diminished ecosystem function. Managers should take site-specific factors into consideration when weighing goals of maintaining stocking and tree diversity against potential delays and/or failures in natural tree regeneration.

## CRediT authorship contribution statement

**Samuel P. Knapp:** Investigation, Data curation, Formal analysis, Visualization, Writing - original draft. **Christel C. Kern:** Funding acquisition, Supervision, Methodology, Writing - review & editing. **Christopher R. Webster:** Funding acquisition, Supervision, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118804.

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