Forest Ecology and Management 448 (2019) 174–186

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Can group selection with legacy retention change compositional trajectories in conventionally managed hardwoods?

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ABSTRACT

Group selection has been proposed as a complementary system to conventional, uneven-aged management in temperate hardwoods (i.e. single-tree selection) to counteract declines in overstory diversity and growing importance of shade-tolerant species caused largely by past management activities. Mixed results from experimental group selection harvests in eastern North America and growing interest in retention forestry have led some scientists and managers to apply ideas from retention forestry into group selection systems. The Yellow Birch Legacy-Tree Project is a group selection experiment established in 2003, which incorporates single, dominant/co-dominant yellow birch (*Betula alleghaniensis* Britt.) legacy-trees into the centers of harvested canopy gaps in a northern hardwoods forest in the Upper Peninsula of Michigan. Group selection openings (n = 49) in three size classes based upon radii—small (11 m, n = 16), medium (16.5 m, n = 17), and large (22 m, n = 16)—were surveyed alongside single-tree selection reference sites (n = 20) 15 years post-harvest. Our goals were to (1) examine long-term trends in seedling and sapling abundance and diversity, (2) evaluate the initial and contemporary effects of gap size on regeneration, and (3) assess the overall efficacy of group-selection with legacy-tree retention in regenerating mid-tolerant and intolerant species, especially yellow birch. At 15 years post-harvest, we found that shade-tolerant sugar maple (*Acer saccharum* Marsh.) dominated regeneration layers across all treatments, but we observed modest increases in seedling and sapling diversity within openings that may alter long-term canopy composition over several cutting cycles. We found that gains in diversity and evenness in canopy gaps persisted through time and that large gaps (22 m radius) had the most species-rich and diverse regeneration compared to reference sites. Canopy gaps contained significantly higher densities of shade-intolerant and mid-tolerant seedlings and saplings compared to reference sites, namely red maple (*Acer rubrum* L.), black cherry (*Prunus serotina* Ehrh.), and yellow birch; however, most diversity occurred in shorter height classes. Nevertheless, legacy retention within group selection systems holds promise for maintaining ecological memory and structural complexity through time, but further treatments such as scarification may be necessary to shift compositional trajectories in favor of shade-intolerant and mid-tolerant species.

1. Introduction

In a changing climate, forest managers face ever-increasing challenges to meet timber production goals while simultaneously preserving biodiversity, ecosystem services, and future productivity (Creutzburg et al., 2017). These challenges are further compounded by the legacy effects of past management, which can detrimentally affect outcomes of silvicultural treatments (Puettmann et al., 2009). Within the temperate-boreal ecotone of North America, losses of ecological memory have resulted from widespread exploitive timber harvesting, recurrent slash fires, and land clearing for agricultural use circa 1850–1920 (Johnstone et al., 2016; Webster et al., 2018). In some cases, forest stands have not regained their historic structural or compositional trajectories (Puettmann et al., 2009). Variants of disturbance-based management techniques have been used from decades to centuries, depending on location, to maintain timber productivity by more-closely emulating natural disturbance regimes (Schütz, 1997; Johann, 2006; North and Keeton, 2008). However, some disturbance-based techniques such as selection systems have tended to homogenize forests directly and indirectly over time (Crow et al., 2002; Schulte et al., 2007).

Selection systems are forms of disturbance-based management that approximate blowdowns and/or natural senescence to create small openings while maintaining continuous canopy coverage (Hupperts et al., 2018). Variants of selection harvest systems have been applied widely to temperate forests (O'hara et al., 2007; Schütz, 1997; Seymour et al., 2006; Pond et al., 2013). For hardwoods in the Lake States, USA, selection systems were designed to supply a continuous stream of high-quality timber from uneven-aged stands (Eyre and Zillgitt, 1953; Arbogast, 1957; Nyland, 1998). Single-tree selection—where single trees or small groups are removed to produce gaps in the forest canopy $< 400\ \text{m}^2$ until a target level of residual stocking is reached (Wisconsin Deparment of Natural Resources, 2013)—has been commonly applied to hardwoods since the mid-20th century in this region (Neuendorff et al., 2007; Schulte et al., 2007). However, it is well known that sole reliance on single-tree selection favors regeneration of shade-tolerant species over those less tolerant of shade by producing

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https://doi.org/10.1016/j.foreco.2019.06.005
Received 29 March 2019; Received in revised form 31 May 2019; Accepted 3 June 2019

relatively homogeneous low-light conditions at ground level (Angers et al., 2005; Yoshida et al., 2006; Thurnher et al., 2011; Keyser and Loftis, 2012). Single-tree selection also reduces the abundance of large-diameter trees through time (Angers et al., 2005), which leads to smaller crowns and canopy openings upon harvest, further limiting recruitment opportunities for shade-intolerant and mid-tolerant species (Hupperts et al., 2018).

Group selection has been suggested as a supplemental system to single-tree selection to improve overstory diversity while maintaining productivity in uneven-aged systems (Tubbs, 1977; Brang et al., 2014). Group selection is another form of uneven-aged, disturbance-based management, which removes groups of trees to create canopy openings ranging 400–2000 m^2 at regular harvest intervals, and can be used in conjunction with single-tree selection to promote mid-tolerant regeneration (Wisconsin Deparment of Natural Resources, 2013). Gap partitioning theory predicts that the light, moisture, and heat gradients present between gap centers and forest edges should promote shade-intolerant and mid-tolerant regeneration within sufficiently large canopy openings (Denslow, 1980; Poulson and Platt, 1989). However, results from experimental group selection harvests in northern hardwoods have been mixed (Kern et al., 2017). In some cases, regeneration of intolerant and mid-tolerant species increased within group selection openings (Leak, 1999, 2003; Webster and Lorimer, 2005; Raymond et al., 2006; Gauthier et al., 2016). Numerous other studies resulted in group selection openings that remained dominated by shade-tolerant regeneration (Arseneault et al., 2011; Bolton and D'Amato, 2011; Forrester et al., 2014) or that failed to regenerate to target stocking levels (Kern et al., 2013).

Study duration may be an additional factor influencing results from group selection experiments. Results from long-term experiments (Eyre and Zillgitt, 1953), retrospective studies (Leak, 2003; Webster and Lorimer, 2005), and model simulations (Lafond et al., 2014; Halpin et al., 2017) suggest that group selection promotes increased abundance of intolerant and mid-tolerant species in forests with primary management histories of single-tree selection. Group selection openings in New England lasting over multiple decades and cutting cycles resulted in over 20% of basal area in birches (*Betula* spp., mid-tolerant and intolerant) within large gaps (~2000 m^2) (Leak and Filip, 1977; Leak, 1999, 2003), whereas single-tree selection led to marked declines in birch abundance in the same region (Leak and Smith, 1996; Leak and Sendak, 2002). In contrast, results from short-term group selection experiments (< 12 years) vary widely. One-, 3-, and 5-year studies in eastern Canada regenerated yellow birch and other mid-tolerant species in high abundance within large canopy gaps (1000–2000 m^2) (Raymond et al., 2003; Falk et al., 2010; Gauthier et al., 2016). Studies from the western Great Lakes region ranging from 6 to 12 years post-harvest found canopy gaps were dominated by shade-tolerant regeneration (gap areas ranged 80–700 m^2 and 30–1600 m^2) (Bolton and D'Amato, 2011; Kern et al., 2013). Given these discrepancies, more long-term experiments of group selection openings are needed, especially as climate change alters underlying abiotic conditions and forest compositional trajectories (Swanston et al., 2018).

Stressors that reflect degradation of ecological memory and growing resilience debts in contemporary forests—e.g. declining species richness, competition from understory vegetation, overabundance of herbivores, and the presence invasive species—are some of the proposed explanations for unmet regeneration goals in group selection experiments (Kern et al., 2017; Webster et al., 2018). The framework of ecological memory has been used to describe an ecosystem's ability to recover its trajectory following disturbances via material and informational legacies (Johnstone et al., 2016; Jõgiste et al., 2017; Webster et al., 2018). Material legacies—e.g. available seeds and advance regeneration—enable local plant communities to reestablish following disturbance. Processes that remove material legacies create resilience debts that reduce an ecosystem's ability to maintain a given state or trajectory. Consequently, a reduction of available propagule material from one species or over representation from another may slowly shift an ecosystem towards an alternate state, especially if one species' contribution to forest structure or ecosystem function is disproportionately high (e.g. eastern hemlock [*Tsuga canadensis* (L.) Carr.]) (Davis et al., 1994; Ellison et al., 2005). Furthermore, other material legacies such as living trees, standing snags, down deadwood, soil organic materials, and soil biota, may directly and/or indirectly influence post-disturbance community structure and trajectory. As awareness of these legacies has grown, interest in explicitly retaining aspects of ecological memory within silvicultural systems has increased (Lindenmayer et al., 2012). Retention forestry is one silvicultural approach that aims to maintain function and biodiversity in managed forests by retaining some of the structural and biological complexity common to old-growth (Lindenmayer et al., 2012). Legacy retention is not a new concept in silviculture and follows logically from disturbance-based silvicultural approaches (Franklin et al., 1997). However, it remains unclear how preserving ecological memory via legacy retention affects long-term diversity and recruitment within group selection openings (D'Amato et al., 2014).

The Yellow Birch Legacy-Tree Project is a group selection experiment which incorporates co-dominant yellow birch (*Betula alleghaniensis* Britt.)—an important but declining mid-tolerant species in the western Great Lakes region (Godman and Krefting, 1960; Schulte et al., 2007)—into harvested canopy gaps of varying size (400–1800 m^2) to promote natural yellow birch regeneration. Established in 2003, the experiment was inspired by Eyre and Zillgitt (1953) and Arbogast (1957) who proposed retaining yellow birch seed trees within or near group selection openings to encourage natural regeneration. In this experiment, yellow birch were retained to maintain a permanent structural and biological feature within openings (Keeton, 2006). In addition to enhancing stand structure and seed availability, yellow birch retention may also moderate extreme temperature, light, and moisture fluctuations to improve seedling germination and survival (Godman and Krefting, 1960; Gustafsson et al., 2010; Poznanovic et al., 2014) and increase resource heterogeneity to promote regeneration diversity (Denslow, 1980). Intentional retention of living trees goes by several synonyms—e.g. green tree retention, variable retention, retention felling (Gustafsson et al., 2010)—but will be referred to as "legacy-tree retention" here.

Earlier results from this experiment at 2 and 9 years post-harvest (2005 and 2012) suggested that although some shade-intolerant and mid-tolerant species benefited from canopy gaps, sugar maple (*Acer saccharum* Marsh., shade-tolerant) dominated all regeneration layers (see Shields et al., 2007; Klingsporn Poznanovic et al., 2013). Our objectives at 15 years post-harvest (2018) were to (1) examine long-term trends in seedling and sapling abundance, richness, and diversity; (2) evaluate the initial and contemporary effects of gap size on regeneration, and (3) assess the overall efficacy of group selection with yellow birch legacy-tree retention in regenerating mid-tolerant and intolerant species, especially yellow birch.

2. Materials and methods

2.1. Study site

The study site is a northern hardwoods forest in the western Upper Peninsula of Michigan, USA, near the village of Alberta, Baraga County (46° 37 ′N, 88° 29′ W) at the Michigan Technological University Ford Center Research Forest. The landscape is characterized by rolling upland moraines with shallow, poorly drained silt loams (Soil Survey Staff, 2017). Total annual precipitation is 87 cm, including an average 382 cm of snowfall, and average temperatures range from 17.4 °C in summer to −9.8 °C in winter (Berndt, 1988). The primary habitat type is *Acer saccharum-Tsuga canadensis/Dryopteris spinulosa* (Kotar and Burger, 2003). Sugar maple dominates the canopy with lesser amounts of eastern hemlock, red maple (*Acer rubrum* L.), and yellow birch and with occasional inclusions of ironwood (*Ostrya virginiana* (Mill.) K. Koch), black cherry (*Prunus serotina* Ehrh.), American basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), black ash (*Fraxinus nigra* Marsh.), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), northern white-cedar (*Thuja occidentalis* L.), and white spruce (*Picea glauca* (Moench) Voss.). Prior to this study, the site had been managed with single-tree selection since in the 1960s on 10–15 year cutting cycles (Neuendorff et al., 2007), with the goal of producing high-quality sugar maple for sawlogs and veneer. Stands in the Ford Research Forest had been managed with the BD*q* method, with target residual basal areas of 16.1 $m^2 ha^{-1}$ (70 $ft^2 ac^{-1}$) and maximum diameter limits of 51–56 cm (20–22 in.) at a *q*-ratio of 1.3 (2 in. diameter classes) (Schwartz et al., 2005).

2.2. Study design

The current study is an addition to the Yellow Birch Legacy-Tree Project, testing the effects of group selection with legacy-tree retention on forest biodiversity and productivity. In the winter of 2003, 49 group selection openings, each centered upon a single dominant/co-dominant yellow birch, were created. Yellow birch legacy-trees averaged 41.0 ± 1.4 cm dbh with crown areas of 57.4 ± 3.0 m^2 at the time gap creation. At the time of harvest, legacy-trees were 103 ± 4 years-old in canopy gaps and 90 ± 8 years-old in reference sites. Canopy gaps were cut to three size classes with gap diameter scaled to mean canopy height (22 m): Small = 1 × *canopy height* ($n = 16$); Medium = 1.5 × *canopy height* ($n = 17$); Large = 2 × *canopy height* ($n = 16$). A minimum buffer of 60 m was set between openings to minimize edge effects. All trees > 10 cm diameter at breast height (dbh, 1.4 m) were cut within the prescribed diameters (excluding legacy-trees), producing roughly circular openings. Merchantable trees were removed, while non-merchantable trees were left onsite as coarse woody debris. The harvest occurred during a period of deep snowpack, but as is common within snowbelt areas of Lake Superior, the underlying ground was not frozen and incidental rutting occurred within and between canopy gaps (Shields and Webster, 2007; Shields et al., 2007). Expanded gap areas (see Section 2.3 for definition) immediately following harvest were 400–720 m^2 for small gaps, 740–1210 m^2 for medium gaps, and 1270–1840 m^2 for large gaps. Two years post-harvest, effective gap areas were 200–420 m^2 in small gaps, 500–810 m^2 in medium gaps, and 890–1460 m^2 in large gaps.

Reference conditions were established around co-dominant yellow birch trees in the adjacent managed forest matrix. Concurrent with canopy gap creation in 2003, a single-tree selection harvest occurred in the forest matrix (*q* factor of 1.3 (2 in. diameter classes) and 16.1 $m^2 ha^{-1}$ (70 $ft^2 ac^{-1}$) residual basal area) surrounding the experimental openings. Twenty co-dominant yellow birch were randomly selected within the forest matrix no closer than 60 m from the edge of a canopy gap to serve as the study's reference sites.

The study used a nested sampling design comprised of 12 subplots per canopy gap or reference site. All subplots were placed at random distances (integers in meters) from the yellow birch legacy-tree. Four subplots were placed under the yellow birch crown along cardinal directions between 1 and 3 m from the legacy-tree's approximate point of germination, while eight subplots were placed between the legacy-tree crown (dripline) and the forest edge (boles) on cardinal and sub-cardinal directions.

2.3. Field sampling

Subplots were initially surveyed 2 and 9 years post-harvest (2005 and 2012), and we revisited all subplots in the 15th growing season (summer 2018) to tally and measure woody regeneration. Seedlings were classified as woody stems ≤50 cm height (unstretched). All seedlings with points of germination within 1 m^2 quadrats centered on subplots were tallied by species. Saplings (woody stems > 50 cm tall) were measured for height and dbh (if applicable) if their points of germination fell within a 1 m radius (3.14 m^2) of subplot centers. Saplings less than 8.2 m height were measured with a telescoping height pole (Sokkia Corporation, Olathe, Kansas, USA), while a clinometer and tape were used for measuring taller heights. Species nomenclature followed the USDA Plants Database (USDA, 2019). Canopy gap area was defined as the area lying within the dripline of the surrounding forest canopy, while expanded gap area included adjacent areas between the forest dripline and the boles of trees marking the boundary between canopy gaps and the forest matrix (expanded edge) (Runkle, 1982). To measure expanded gap area, radial distances between the legacy-trees and expanded edge were measured (Haglöf DME Range Finder, Haglöf Sweden AB, Långsele, Sweden) along the eight cardinal and sub-cardinal directions, and areas were calculated as eight-sided polygons. Canopy gap areas and yellow birch crown areas were measured in a similar manner, measuring from the legacy-tree's approximate point of germination to the driplines of the forest matrix and yellow birch legacy-tree crown, respectively. Driplines were defined as the outermost branch of the crown (or interpolation between branches) measured at 90° vertical with a clinometer.

2.4. Data analysis

For assigning shade-tolerance classes to regeneration, we adjusted the tables of Niinemets and Valladares (2006) to define trees as shade-intolerant, mid-tolerant, and tolerant species (see Table 1) (Niinemets and Valladares, 2006). Certain species were infrequently found throughout the study site and were categorized as "other", including American basswood, American elm, black ash, pin cherry (*Prunus pensylvanica* L.), quaking aspen (*Populus tremuloides* Michx.), serviceberry (*Amalanchier* spp.), and white spruce. Species categorized as "shrubs" included American fly honeysuckle (*Lonicera canadensis* W. Bartram ex Marsh.), Canada yew (*Taxus canadensis* Marsh.), willows (*Salix* spp.), beaked hazelnut (*Corylus cornuta* Marsh.), and speckled alder (*Alnus incana* (L.) Moench.). In all cases, seedling and sapling counts were converted to densities in stems ha^{-1}. Unless otherwise noted, means are presented plus or minus standard error of the mean.

Generalized linear mixed-effects models were used in R version 3.5.0 (R Core Team, 2019) to examine effects of treatment (i.e. gap size or reference) on regeneration density 15 years post-harvest. Because models of count data often experience over-dispersion—when model variance exceeds the mean—appropriate distribution families for our models had to be determined. Typically, Poisson and negative binomial distributions are used to model count data, but negative binomial distributions contain an extra term in the variance function that explicitly accounts for over-dispersed data and are more often appropriate (Zuur et al., 2009). To check for over-dispersion, we used the R packages *msme* (v. 0.5.3) (Hilbe and Robinson, 2016) and *MASS* (v. 7.3–51.1) (Ripley, 2002) to calculate Pearson's chi-square dispersion parameter for generalized linear models of stem density by species predicted by treatment (seedlings and saplings analyzed separately). For all species, we found that generalized linear models using negative binomial distributions produced dispersion parameters closer to 1 than those with Poisson distributions, indicating negative binomial distributions were more appropriate for our dataset (Hilbe, 2011). We then used the *lme4*

Table 1
Shade-tolerance categories of tree species present at study site.

Shade-Tolerance	Species
Tolerant	Balsam fir, eastern hemlock, ironwood, sugar maple
Mid-tolerant	American basswood, American elm, eastern white pine, northern white-cedar, red maple, white spruce, yellow birch
Intolerant	Black ash, black cherry, paper birch, quaking aspen, willows

Table adapted from Niinemets and Valladares (2006). Latin species names appear in text.

Table 2

Mean densities (stems ha^{-1} ± SE) of saplings (stems ≥ 50 cm tall) in group selection openings and single-tree selection reference sites 15 years following opening creation.

Species	Single-tree selection	Group selection openings		
	Reference sites (n = 20)	Small (n = 16)	Medium (n = 17)	Large (n = 16)
Sugar maple	9019 ± 2536^{a}	10,859 ± 1657^{a}	9549 ± 667^{a}	9251 ± 1471^{a}
Red maple	133 ± 62^{a}	2537 ± 1349^{b}	1264 ± 455^{ab}	3929 ± 1132^{b}
Black cherry	146 ± 65^{a}	647 ± 250^{ab}	1030 ± 443^{b}	497 ± 164^{ab}
Yellow birch	27 ± 27^{a}	249 ± 158^{ab}	515 ± 215^{ab}	729 ± 267^{b}
Balsam fir	212 ± 121^{a}	182 ± 149^{a}	62 ± 48^{a}	149 ± 68^{a}
Ironwood	93 ± 29^{a}	133 ± 84^{a}	47 ± 34^{a}	50 ± 36^{a}
Eastern hemlock	53 ± 41^{a}	33 ± 23^{a}	31 ± 21^{a}	50 ± 36^{a}
Other[1]	159 ± 83	332 ± 142	421 ± 135	696 ± 205

Superscript letters indicate significant differences in species density between treatment using generalized linear mixed-effects models with a nested design framework. All species were modeled with negative binomial distributions, and the significance level (α = 0.05) was adjusted with a false discovery rate of 0.25 for Tukey's multiple comparison of means.

[1] Other species include American basswood, American elm, black ash, pin cherry, quaking aspen, serviceberry, and white spruce.

package (v. 1.1–19) (Bates et al., 2014) to create generalized linear mixed-effects models (with negative binomial distributions) of regeneration density by species predicted by treatment (seedlings and saplings analyzed separately). Treatment was treated as a fixed effect, while individual canopy gaps/reference sites were treated as random effects. To perform Tukey's method of multiple comparisons between treatments, estimated marginal means derived from the mixed-effects models were calculated with the *emmeans* package (v 1.3.1) (Searle et al., 1980), and pairwise comparisons were made using the *multcomp* package (v. 1.4–8) (Hothorn et al., 2008). To account for the increased chance of committing a type I error with multiple comparisons, we used the Benjamini-Hochberg procedure to set a false-discovery rate (the chance accepting "false-positive" results as significant) of 0.25 (Benjamini and Hochberg, 1995).

To gain insights into the overall richness and proportional abundance of regeneration, species richness, evenness, and Shannon's diversity index for the seedling and sapling layers were calculated for each canopy gap ($n = 49$) and reference site ($n = 20$) in PC-ORD version 6.20 (McCune and Mefford, 2011) excluding shrub species. To test for treatment effects within a given sampling year, we created generalized linear models in R version 3.5.3 (R Core Team, 2019) of diversity metrics at the gap/reference site-level predicted by treatment. Gaussian models were used, and model assumptions were checked graphically. The *multcomp* package (v. 1.4–8) (Hothorn et al., 2008) was used to perform Tukey's method of multiple comparisons between treatment levels, and the Benjamini-Hochberg procedure was used to correct for multiple comparisons with a false discovery rate of 0.25 (Benjamini and Hochberg, 1995).

Nonmetric multidimensional scaling (NMS) ordinations were used to visualize the compositional trajectories of tree regeneration (excluding shrubs) in canopy gaps and reference sites through time. Canopy gaps and reference sites from each sampling year (2, 9, and 15 years post-harvest) were used as plots ($n = 207$), and species counts were used in the primary matrix. Ordinations were run in autopilot mode in PC-ORD version 6.20 from a random starting configuration and using the Sørenson (Bray-Curtis) distance measure (McCune and Mefford, 2011). Acceptable values for stress—the inverse of model fit—were less than 20, and the instability criterion—the standard deviation of stress over the final 10 iterations—was set to 1×10^{-6} (McCune and Grace, 2002). Monte Carlo tests were used to determine the appropriate number of ordination axes (dimensionality) by comparing resultant stress from 250 runs with both real and randomized data. Pearson's correlation coefficient was used to evaluate relationships between species, environmental variables, and the final NMS axes. Reference sites were not included in correlation calculations for variables that did not apply to reference sites (i.e. expanded and effective gap areas).

To test for different species assemblages of seedlings and saplings between treatments, we used multiple response permutation procedures (MRPPs), creating pairwise comparisons of treatments within each survey year, in R version 3.5.3 and the Vegan package v. 2.5–4 (Oksanen et al., 2019; R Core Team, 2019). The Sørenson (Bray–Curtis) distance measure was used, and groups were defined by treatment (small, medium, large, reference). The calculated statistic A is known as the "chance-corrected within-group agreement" and describes heterogeneity within a group compared to what is expected by chance. If $A = 0$, then within-group heterogeneity is random; if $A = 1$, all members within a group are equal. The p-value describes the likelihood that species assemblages within one or more groups are distinct (McCune and Grace, 2002). To reduce the chance of committing a type I error with multiple comparisons, the Benjamin-Hochberg procedure was used within sets of comparisons for each survey year with a false-discovery rate of 0.25 (Benjamini and Hochberg, 1995).

3. Results

After 15 growing seasons, lateral crown closure reduced the area of all group-selection openings. Small gaps ranged from 180 to 370 m^2, medium gaps from 530 to 790 m^2, and large gaps from 1000 to 1400 m^2 effective gap area. Most yellow birch legacy-trees had larger crown areas in year 15 than in year 2. Legacy-trees crowns in canopy gaps averaged 69 ± 4 m^2 and increased 11 ± 2 m^2 since year 2, while those in single tree-selection reference sites averaged 47 ± 4 m^2 and increased 5 ± 3 m^2 since year 2. As of 15 years post-harvest, 9 of 49 (18%) legacy-trees died within canopy gaps, while only 1 of 20 (5%) legacy-tree died in a reference site.

3.1. Regeneration density and composition

Shade-tolerant sugar maple dominated the regeneration layers across all treatments, but the highest densities of mid-tolerant and intolerant regeneration were found within canopy gaps (Tables 2 and 3). Across the study, sugar maple comprised 82% of seedling stems (≤50 cm) and 74% of sapling stems (> 50 cm); whereas, the shade mid-tolerants red maple and yellow birch accounted for 10% and 3% of seedlings and 22% and 3% of saplings, respectively. Sugar maple density did not differ between treatments but was markedly higher than any other species. Shade-intolerant black cherry saplings were most abundant in medium gaps ($p = 0.02$, Table 2), but black cherry seedling density did not differ by treatment (Table 3). Red maple regeneration density was higher in canopy gaps than single-tree selection reference sites except for saplings in medium gaps (seedlings: $p < 0.006$, saplings: $p < 0.019$). Yellow birch regeneration was more abundant in large gaps than in reference sites (seedlings: $p < 0.009$, saplings:

Table 3
Mean densities (stems ha^{-1} ± standard error) of seedlings (stems ≤ 50 cm tall) in group selection openings and single-tree selection reference sites 15 years following opening creation.

Species	Single-tree selection	Group selection openings		
	Reference sites (n = 20)	Small (n = 16)	Medium (n = 17)	Large (n = 16)
Sugar maple	4591 ± 1601^a	3301 ± 604^a	2145 ± 620^a	1406 ± 378^a
Red maple	62 ± 43^a	817 ± 283^b	475 ± 245^b	462 ± 160^b
Yellow birch	2 ± 2^a	91 ± 44^{ab}	193 ± 108^b	264 ± 103^b
Black cherry	125 ± 79^a	104 ± 51^a	162 ± 58^a	80 ± 22^a
Shrubs[1]	85 ± 46	127 ± 44	184 ± 63	94 ± 47
Other[2]	83 ± 47	62 ± 16	12 ± 7	46 ± 23

Superscript letters indicate significant differences in species density between treatments using generalized linear mixed-effects models with a nested design framework. All species were modeled with negative binomial distributions, and the significance level (α = 0.05) was adjusted with a false discovery rate of 0.25 for Tukey's multiple comparison of means.

[1] Shrubs species included American fly honeysuckle, Canada yew, *Salix* spp., beaked hazelnut, and speckled alder.

[2] Other species include American basswood, American elm, balsam fir, black ash, eastern hemlock, ironwood, pin cherry, quaking aspen, serviceberry, and white spruce.

$p = 0.007$), with the highest densities occurring in medium and large gaps for saplings and large gaps for seedlings.

Regeneration density categorized by height class followed an expected pattern of change for recently harvested stands, but patterns of composition and recruitment differed between canopy gaps and reference sites. Red maple, black cherry, and yellow birch stems > 1 m were rare in reference sites, while red maple and black cherry stems > 1 m were common throughout canopy gaps. Although yellow birch regeneration was common within canopy gaps, stems over 2 m height were rarely found. Between 9 and 15 years post-harvest attrition occurred in the lower height classes as stems competed for limited resources (Fig. 1). Exceptions were yellow birch between 1 and 3 m in medium gaps, black cherry ≤50 cm in medium and large gaps, and sugar maple between 1 and 3 m in reference sites which increased in stem density. More stems were present in taller height classes (> 5 m) within canopy gaps than in reference sites (151 ± 10 stems ha^{-1} compared to 50 ± 8 stems ha^{-1}). Of stems > 5 m height, sugar maple comprised 67 ± 3% and 88 ± 5% in canopy gaps and reference sites respectively.

3.2. Regeneration diversity

Differences in the Shannon's diversity index and evenness widened between reference sites and large gaps between year 9 and year 15 (Figs. 2 and 3). Seedling richness in canopy gaps decreased between year 2 (5.4 ± 0.3 species) and year 15 (4.3 ± 0.3 species) and was no longer statistically different from the reference (Fig. 2). Sapling richness increased from year 2 (2.6 ± 0.2 species) to year 9 (4.7 ± 0.4 species) in canopy gaps as the new seedling cohort grew above 0.5 m height (Fig. 3) but marginally decreased between year 9 and year 15 (4.3 ± 0.3 species) to no longer statistically differ from the reference. However, marginally more sapling species were found in large gaps than in reference sites in year 15 ($p = 0.042$). Shannon's diversity index persisted for the seedling and sapling layers in canopy gaps between year 9 (seedlings: 0.61 ± 0.10; saplings: 0.63 ± 0.09) and year 15 (seedlings: 0.69 ± 0.11; saplings: 0.63 ± 0.09), and large gaps became more diverse than reference sites 15 years post-harvest (seedlings: $p = 0.02$, saplings: $p = 0.05$). Evenness was maintained in canopy gaps between year 9 (seedlings: 0.37 ± 0.06; saplings: 0.39 ± 0.05) and year 15 (seedlings: 0.45 ± 0.06; saplings: 0.41 ± 0.05) but decreased in reference sites (seedlings: 0.23 ± 0.06; saplings: 0.26 ± 0.05) to become statistically lower than in medium and large gaps for the seedling layer ($p = 0.003$) and in large gaps for the sapling layer ($p = 0.04$).

3.3. Compositional trajectories

The NMS ordination of sapling density over time revealed that canopy gaps, regardless of size, followed similar successional trajectories that were distinctly different from reference sites (Fig. 4). The final NMS ordination had a 2-dimensional solution with a final stress and instability of 10.7 and $< 1 \times 10^{-6}$, respectively, after 69 iterations. The ordination explained 83% of the variation in species composition, with axis 1 explaining the most variation ($r^2 = 0.71$) followed distantly by axis 2 ($r^2 = 0.12$). Effective and expanded gap areas were not correlated with species compositional gradients, as neither variable correlated with ordination axes (Table 4). In the ordination space, canopy gaps moved collectively towards the region correlated with increased sapling density and species richness between 2 and 9 years post-harvest (Fig. 4). Between 9 and 15 years post-harvest, canopy gaps rebounded slightly from their initial trajectories towards regions correlated with increased Shannon's diversity and evenness. Conversely, reference sites moved away from regions of increased Shannon's diversity and evenness between year 9 and year 15. Yellow birch legacy-tree crown area, total sapling density, and species richness showed significant negative correlations with axis 1, while evenness was positively correlated. Sapling density, richness, Shannon's diversity index, and evenness were negatively correlated with axis 2. Axis 1 scores for principal species were as follows: red maple (−0.80) < sugar maple (−0.75) < yellow birch (−0.64) < black cherry (−0.60). Species scores and significant environmental correlations are shown in an inset joint plot (Fig. 4), while species and environmental correlations with ordination axes may be found in Table 4.

The MRPP results revealed that community compositional differences in group selection openings and reference sites continued developing over the 15 years post-harvest in both the seedling and sapling layers (Table 5). The composition of seedlings in canopy gaps differed from that in reference sites in all three surveys ($p < 0.047$, Supplemental Table A), whereas compositional differences for saplings only developed between canopy gaps and reference sites in years 9 and 15 ($p = 0.001$, Supplemental Table A). Relative compositional differences for seedlings showed continued development for 15 years between treatments (Table 5). Small gaps and reference sites had similar seedling compositions in year 9 ($A = -0.005$, $p = 0.544$). Medium and large gaps were also compositionally similar in year 9 ($A = -0.006$, $p = 0.591$). However in year 15, seedling composition in small gaps separated from reference sites ($A = 0.043$, $p = 0.009$) while maintaining differences with composition in medium and large gaps ($p \leq 0.014$). Sapling compositional differences between treatments also developed through time but more slowly (Table 5). Between year 2 and year 9, sapling composition within canopy gaps developed differences with composition in reference sites ($A = 0.067$, $p = 0.001$) and

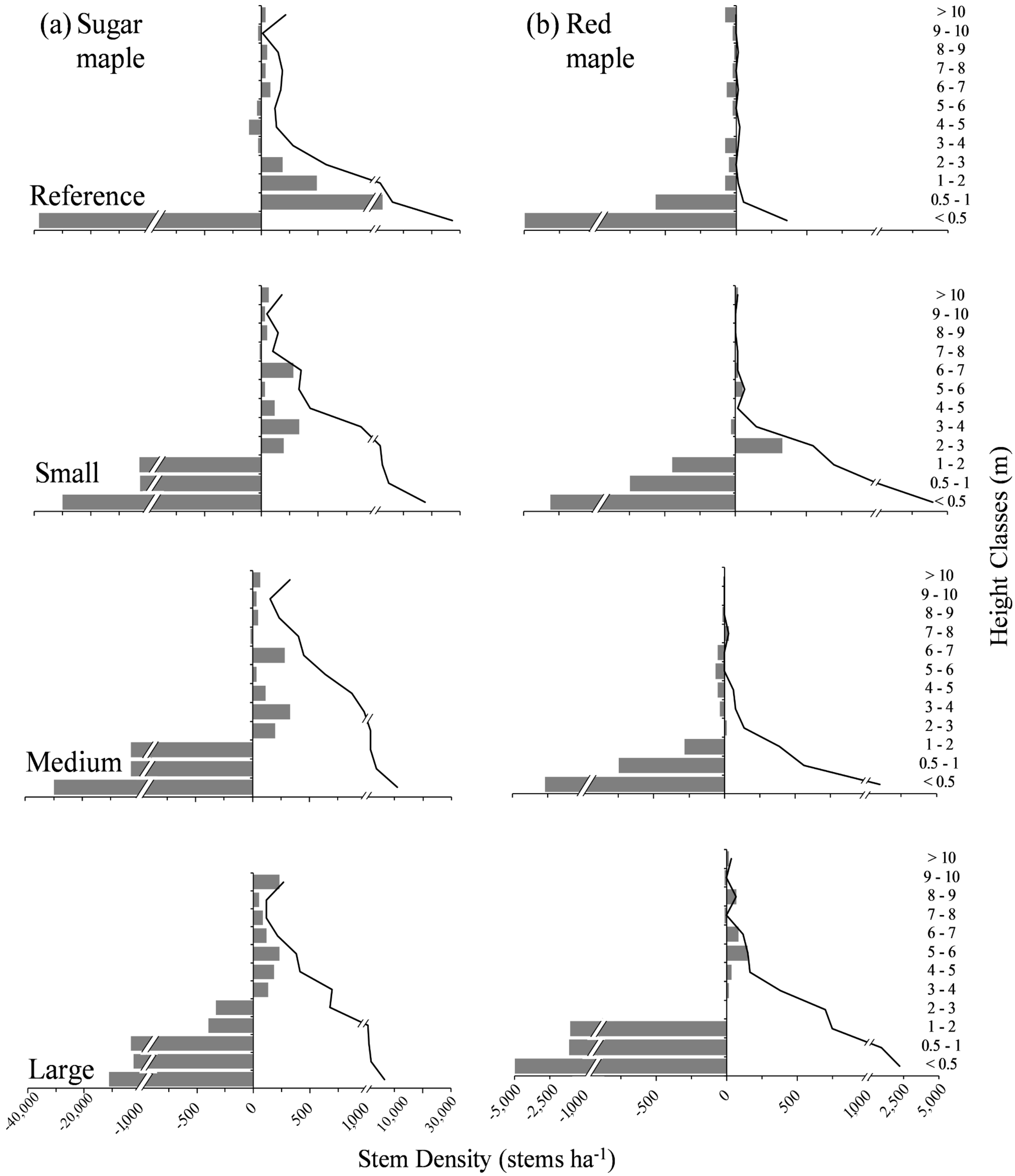

Fig. 1. Regeneration stem density (stems ha^{-1}) by height class bins (m) within experimental group selection openings and single-tree selection reference sites in a northern hardwood forest in Michigan, USA. Bars depict absolute change in stem density between 9 and 15 years post-harvest (2012 and 2018). Black lines depict stem density from the year 15 (2018) survey. Rows correspond to treatments: single-tree selection reference sites ($n = 20$) and small ($n = 16$), medium ($n = 17$), and large ($n = 16$) group selection openings. Columns correspond to species: (a) sugar maple, (b) red maple, (c) yellow birch, (d) black cherry, and (e) other species. Other species include American basswood, American elm, balsam fir, black ash, eastern hemlock, ironwood, pin cherry, quaking aspen, serviceberry, and white spruce. Note axis breaks and scale changes where applicable and differences between horizontal axis scales for different species.

retained differences to year 15 ($A = 0.070$, $p = 0.001$). Sapling composition did not differ by opening size in year 9 ($p \geq 0.357$) but differed between medium and large gaps in year 15 ($A = 0.041$, $p = 0.017$).

4. Discussion

Despite shade-tolerant sugar maple dominating regeneration across treatments, we observed modest increases in diversity within artificial openings of varying size 15 years after harvest that may alter long-term

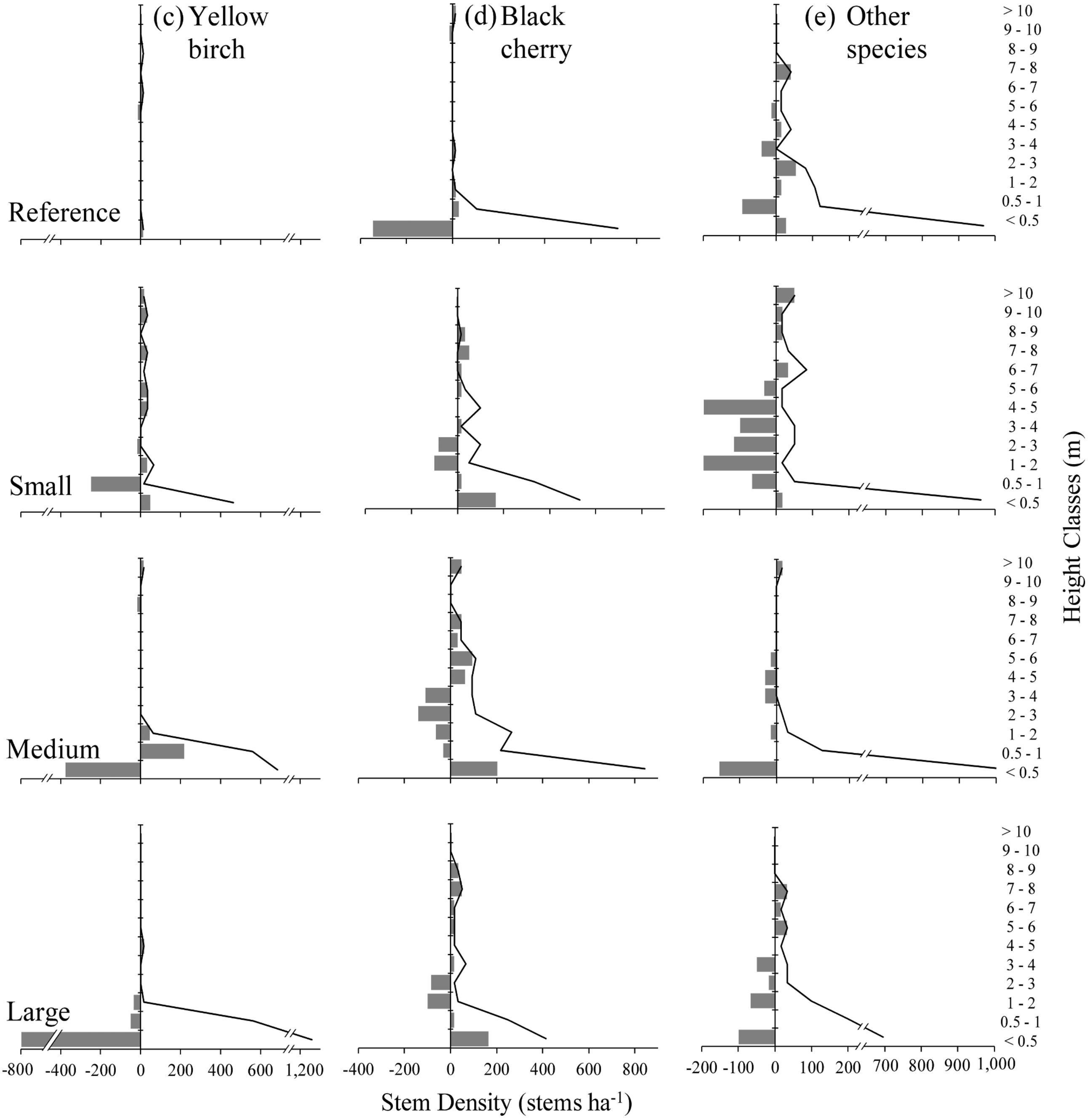

Fig. 1. (*continued*)

canopy composition over several cutting cycles. A common goal of group selection is often to counteract the decline in canopy tree diversity associated with single-tree selection (Neuendorff et al., 2007; Brang et al., 2014; Kern et al., 2017). Broadly, we found that Shannon's diversity and evenness were highest in large gaps (radius ~22 m), and some shade-intolerant and mid-tolerant species (i.e. black cherry, red maple, and yellow birch) benefited from group selection openings. Shade mid-tolerant yellow birch regeneration was most prevalent in large gaps (22 m radius), while mid-tolerant red maple regeneration favored small (11 m radius) and large gaps. Medium gaps (16.5 m radius) contained the highest density of shade-intolerant black cherry saplings. Overall, canopy gaps had distinct species trajectories compared to single-tree selection reference sites that continued developing between 9 and 15 years post-harvest, illustrating the importance of continued monitoring of silvicultural trials.

4.1. *Effects of canopy gaps on species composition over time*

At 15 years post-harvest, we found that gains in Shannon's diversity and evenness in canopy gaps persisted through time and that tree species large gaps were more equitably represented compared to reference sites. At 9 years post-harvest, we saw few statistical differences between the regeneration diversity metrics of canopy gaps and reference sites (except in sapling richness), whereas at year 15, large gaps had distinctly higher Shannon's diversity (seedlings: $p = 0.020$; saplings $p = 0.023$) and evenness (seedlings: $p = 0.003$; saplings $p = 0.015$) than reference sites. We also observed a slight reduction (roughly one species) in richness between 9 and 15 years post-harvest, and shade-tolerant sugar maple continued to dominate across regeneration layers. Long-term (> 20 years) retrospective studies of canopy gaps in northern hardwoods have found that regeneration diversity markedly increases through time and scales positively with gap

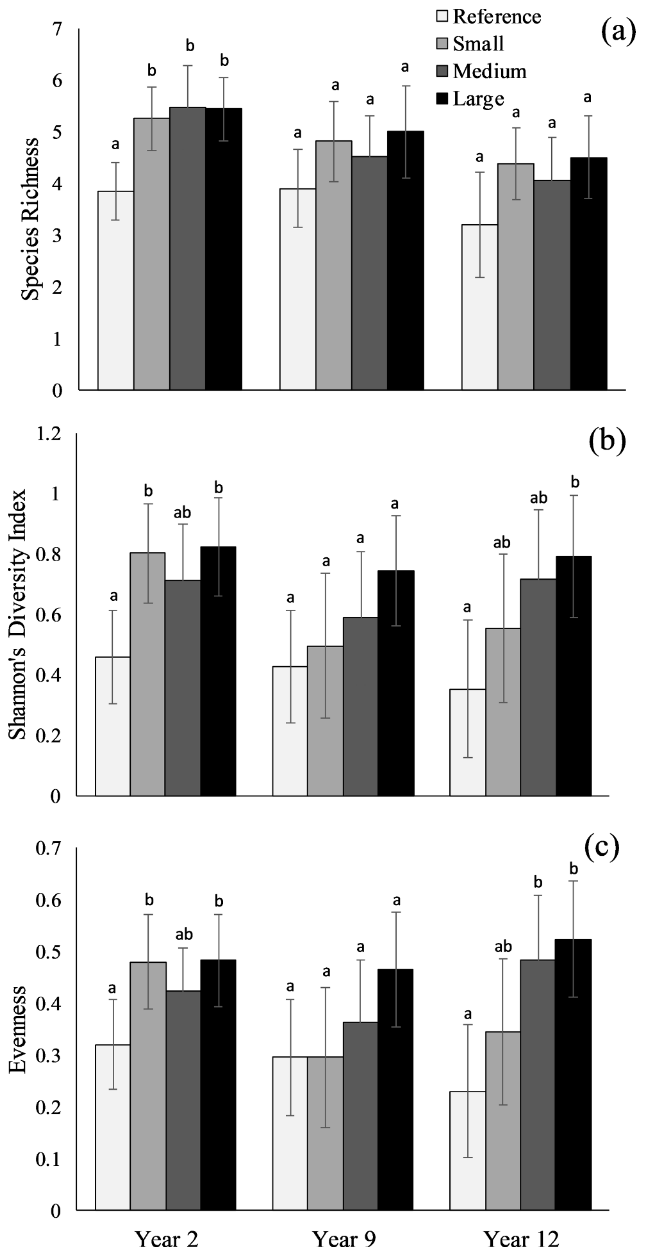

Fig. 2. Diversity metrics for seedlings (stems ≤ 50 cm) from surveys at 2, 9, and 15 years post-harvest (2005, 2012, and 2018 respectively) within experimental group selection openings and single-tree selection reference sites in a northern hardwood forest in Michigan, USA: (a) species richness, (b) Shannon's diversity index, and (c) evenness. Lowercase letters indicate treatment differences within a given year as determined with one-way ANOVA and Tukey's HSD tests ($\alpha = 0.05$), correcting for multiple comparisons with a false discovery rate of 0.25.

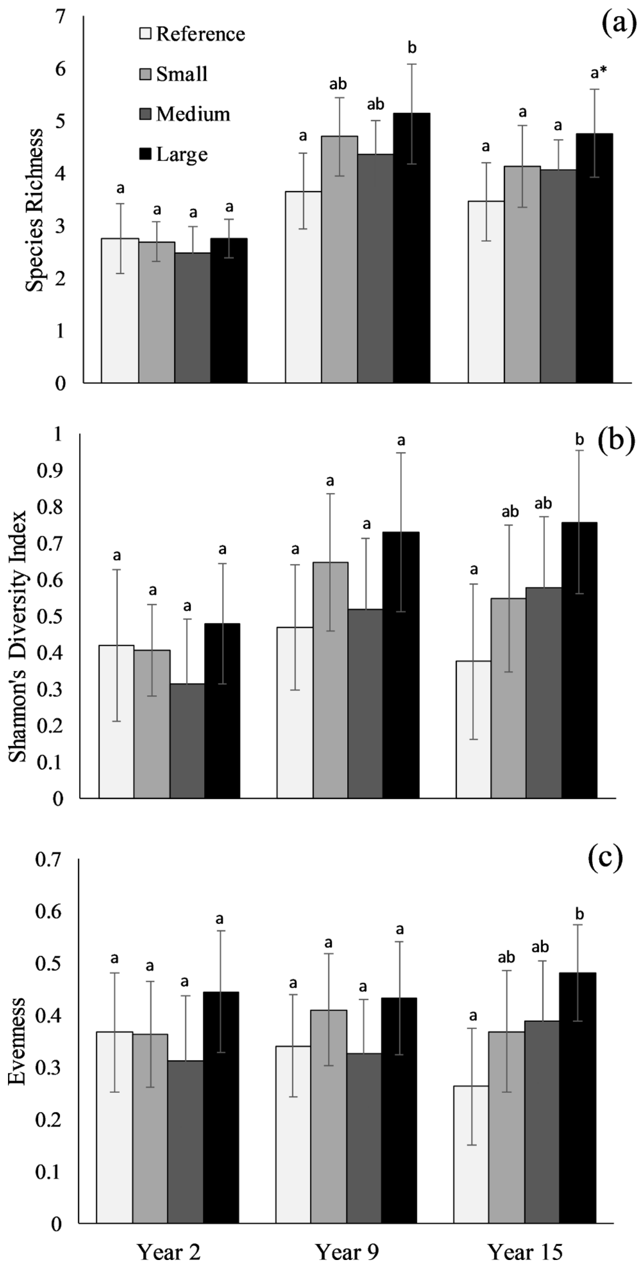

Fig. 3. Diversity metrics for saplings (stems > 50 cm) from surveys at 2, 9, and 15 years post-harvest (2005, 2012, and 2018 respectively) within experimental group selection openings and single-tree selection reference sites in a northern hardwood forest in Michigan, USA: (a) species richness, (b) Shannon's diversity index, and (c) evenness. Lowercase letters indicate treatment differences within a given year as determined with one-way ANOVA and Tukey's HSD tests ($\alpha = 0.05$), correcting for multiple comparisons with a false discovery rate of 0.25. $^{*}p = 0.08$.

size (Leak, 1999, 2003; Webster and Lorimer, 2005). In contrast, some short-term studies (< 12 years) have found that canopy gaps do little to abate dominant shade-tolerant species (Mcclure and Lee, 1993; Bolton and D'Amato, 2011; Kern et al., 2013; Forrester et al., 2014). Our results 15 years post-harvest show that diversity is not static within individual gaps and that long-term monitoring is necessary to capture late-developing patterns of compositional change.

We found that canopy gaps contained significantly higher densities of shade-intolerant and mid-tolerant seedlings and saplings than reference sites, although most diversity occurred in shorter height classes (i.e. < 3 m) at 15 years post-harvest. Shade mid-tolerant yellow birch seedlings and saplings were the most dense in large (seedlings: 264 stems ha^{-1}; saplings: 729 stems ha^{-1}) and medium (seedlings: 193 stems ha^{-1}) gaps, which was consistent with the year 9 results (Klingsporn Poznanovic et al., 2013). Similar studies of group selection openings in northern hardwoods also found the most abundant yellow birch saplings in gaps with effective areas between 1000 and 2000 m^2 (Falk et al., 2010; Gauthier et al., 2016). However, a study examining survival rates of planted yellow birch seedlings found low survival (< 20%) and no differences between gap sizes 30–1500 m^2 (Kern et al., 2012). In the current study, shade-intolerant black cherry saplings were densest in medium gaps and were well represented in taller height classes in both medium and large gaps (Fig. 1). In addition to high-light

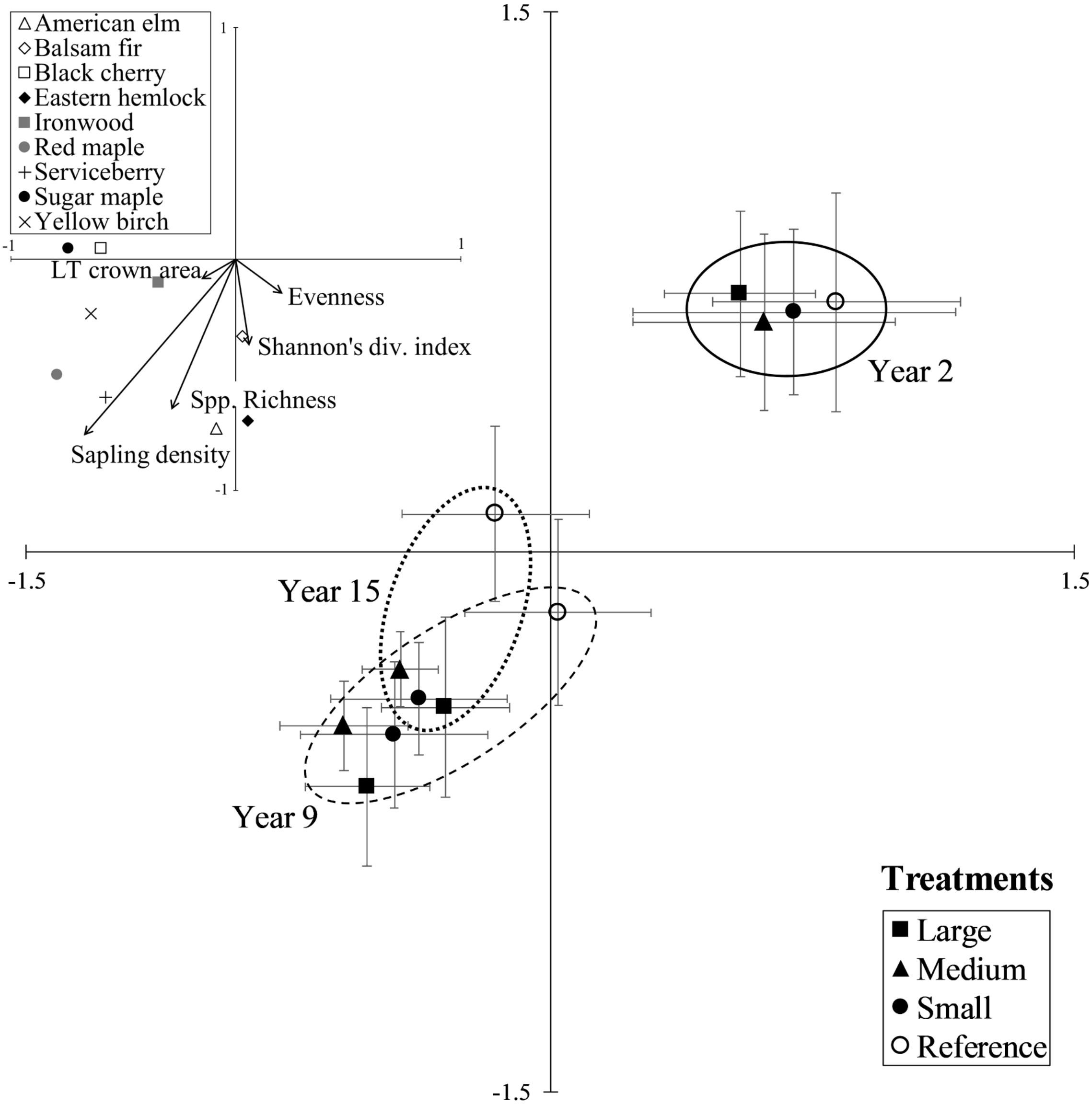

Fig. 4. Plot showing the movement through time of group selection openings and single-tree selection reference sites in a northern hardwood forest in Michigan, USA, within the NMS ordination space of sapling density. A joint plot showing the locations of select species and significantly correlated ($\alpha = 0.05$) environmental variables (Table 4) appears as an inset in the upper left. Error bars around points represent 95% confidence intervals, and overlaid ovals group treatments by time (year) post-harvest. Treatments are labeled separately as: (a) single-tree selection "reference" sites ($n = 20$), and group selection openings with size (b) "small" ($n = 16$), (c) "medium" ($n = 17$), and (d) "large" ($n = 16$). Collectively, ordination axes explained 83% of the data variation (axis 1: 73%, axis 2: 12%). Axes correlated significantly with both environmental variables and regeneration species (see Table 4). Legacy-tree abbreviated as "LT" in the inset.

conditions within canopy gaps, the success of black cherry in our experiment may reflect predicted expansions along its northern range; forest composition models predict increased importance of black cherry in our region due to climate change (Prasad et al., 2014) and especially at disturbed sites (Woodall et al., 2013). Shade mid-tolerant red maple were most abundant in large and small gaps as saplings (3929 and 2537 stems ha^{-1}, respectively) and equally abundant in canopy gaps as seedlings, although small gaps contained the greatest mean density (817 stems ha^{-1}). Red maple has physiological characteristics common to both shade-tolerant and mid-tolerant species (Abrams, 1998), principally a low light compensation point (although not as low as sugar maple) and relatively high net photosynthesis. Results from 44 to 48 year-old experimental canopy gaps in New Hampshire demonstrate red maples' vigor, as red maple maintained the most constant growth rates through time and were the tallest of any species that captured canopy openings (McClure et al., 2000). Our results suggest that group selection may promote the reestablishment of species with wide ecological aptitude, such as red maple, into areas with long management histories of single-tree selection.

Dominance by shade-tolerant sugar maple within canopy gaps after 15 years was not unexpected given previous results from 2 to 9 years post-harvest (Shields et al., 2007; Klingsporn Poznanovic et al., 2013). Sugar maple density was unaffected by treatment, but more sugar maple saplings entered taller height classes (i.e. > 5 m) in canopy gaps than in reference sites (Fig. 1). The mean densities of sugar maple saplings > 5 m were 47 ± 7 stems ha^{-1} and 85 ± 8 stems ha^{-1} in reference sites and canopy gaps, respectively. Even under excellent conditions, it would be unusual for 15 year-old sugar maple to exceed 7.5 cm (~3 in.) dbh (Kiernan et al., 2008). The relatively high density of sugar maple saplings with dbh > 7.5 cm (~3 in.) in gaps and reference sites (309 ± 49 stems ha^{-1} and 172 ± 65 stems ha^{-1}, respectively) suggests that cohorts of sugar maple advance regeneration were released at the time of harvest. Data from the year 2 survey also support this interpretation (Shields et al., 2007). Sugar maple

Table 4
Pearson’s correlations between species, environmental variables, and ordination axes for the NMS ordination of sapling densities within canopy gaps and reference sites.

	Axis 1 (r^2 = 0.701)		**Axis 2** (r^2 = 0.119)	
	r	*p*-Value	r	*p*-Value
Environmental Variables				
Effective gap area (m^2)	0.052	0.528	0.054	0.519
Expanded gap area (m^2)	−0.006	0.946	−0.015	0.860
Legacy-tree crown area (m^2)	**−0.154**	**0.027**	−0.087	0.214
Legacy-tree status (live/dead)	0.059	0.396	0.084	0.227
Total sapling density (stems ha^{-1})	**−0.676**	**< 0.001**	**−0.763**	**< 0.001**
Total seedling density (stems ha^{-1})	−0.075	0.285	0.004	0.950
Species richness	**−0.287**	**< 0.001**	**−0.652**	**< 0.001**
Shannon's Diversity Index	0.059	0.395	**−0.376**	**< 0.001**
Evenness	**0.209**	**0.002**	**−0.150**	**0.031**
Species				
American basswood	−0.017	0.808	−0.02	0.742
American elm	−0.011	0.875	**−0.24**	**0.001**
Balsam fir	0.019	0.786	**−0.39**	**< 0.001**
Black ash	−0.002	0.977	−0.11	0.128
Black cherry	**−0.263**	**< 0.001**	−0.01	0.853
Eastern hemlock	0.019	0.786	**−0.42**	**< 0.001**
Ironwood	−0.111	0.111	−0.03	0.637
Quaking Aspen	−0.068	0.330	−0.07	0.323
Red maple	**−0.359**	**< 0.001**	**−0.44**	**< 0.001**
Serviceberry	−0.138	0.047	**−0.27**	**< 0.001**
Sugar maple	**−0.772**	**< 0.001**	0.094	0.178
White spruce	−0.079	0.258	−0.02	0.753
Yellow birch	**−0.287**	**< 0.001**	**−0.2**	**0.004**

Bold values indicate significant correlations between variables and ordination axes at α = 0.05.

Table 5
Results of multiple response permutation procedure (MRPP) pairwise comparisons from experimental group selection openings and single-tree selection reference sites. Pairwise comparisons only applied within survey years. Significance (α = 0.05) was adjusted for multiple comparisons using the Benjamini-Hochberg procedure with a false-discovery rate of 0.25.

	Year 2	**Year 9**	**Year 15**
Seedlings			
Reference (*n* = 20)	a	a	a
Small (n = 16)	b	a	b
Medium (n = 17)	b	b	c
Large (n = 16)	b	b	c
Saplings			
Reference (n = 20)	a	a	a
Small (n = 16)	a	b	bc
Medium (n = 17)	a	b	b
Large (n = 16)	a	b	c

regeneration has declined in some regions and has been attributed to nutrient leaching from acid rain (Cleavitt et al., 2017), invasive earthworm invasion (Bal et al., 2018), reduced snow pack depth (Comerford et al., 2013), and high deer densities (Matonis et al., 2011). Given the high success of sugar maple in our canopy gaps and others (Bolton and D’Amato, 2011; D'Amato et al., 2014; Forrester et al., 2014), group selection may be an option for releasing new cohorts of advance regeneration of shade tolerant seedlings, such as sugar maple, especially where competition with *Rubus* spp. and other vegetation is a concern (Widen et al., 2018).

We found that all canopy gaps had different species compositional trajectories than reference sites after 15 growing seasons. MRPPs revealed that sapling species compositions were similar for all gap sizes at both 9 and 15 years post-harvest (with the exception of medium and large gaps in year 15) (Table 5). Regeneration in reference sites, however, did not experience the same compositional shifts exhibited in canopy gaps and retained distinct species assemblages after 9 and 15 years post-harvest. This same pattern was observed for saplings within 3 year-old group selection openings with legacy-tree retention in Massachusetts (D'Amato et al., 2014). However, it is worth noting that our study did not exhibit these same differences at 2 years post-harvest. In our study, we observed that the compositional development of the sapling layer lagged behind the seedling layer. Kern et al. (2013) also observed this pattern in similar group selection openings in Wisconsin, and it likely reflects the time required to recruit seedlings to taller height classes.

NMS ordinations revealed that sapling community composition in openings shifted away from high stem density and species richness in favor of increased Shannon’s diversity and evenness between year 9 and year 15. It is unclear whether these patterns will persist into the future. Currently, stems between 0.5 and 5 m height comprise 86% of saplings across treatments, and high mortality rates can be expected in the coming years (Oliver, 1980). Ultimately, differential rates of survival between species will determine future canopy composition (Chesson, 2000). The NMS ordination also revealed that legacy-tree crown area correlated with similar regions in the ordination space as sapling stem density (Fig. 4). This may indicate that retaining yellow birch legacy-trees did not negatively affect regeneration density in our study. In the previously mentioned group-selection experiment with legacy-tree retention in Massachusetts, canopy gaps with legacy-retention contained lowered stem densities of certain species including striped maple (*Acer pensylvanicum* L., mid-tolerant) and quaking aspen (intolerant) after 3 years (D’Amato et al., 2014). However, striped maple did not appear at our study site, and quaking aspen was very poorly represented. Legacy tree crown area also correlated with a similar region in the ordination space as species richness. Increased richness could presumably result from greater seed production resulting from larger crowns and lead to more yellow birch seedlings (Bjorkbom, 1979), but our study design did not allow us to test this idea explicitly.

Our study site also exhibits spatially uneven patterns of regeneration, with areas of persistent and dense shrubs (e.g. red raspberry [*Rubus idaeus* L.]) common in canopy gaps (Widen et al., 2018). Over half of canopy gaps contained areas 10–310 m^2 devoid of regeneration over 1.4 m height (Knapp et al., unpublished). Competing vegetation may pose serious problems for regenerating certain species, especially yellow birch (Cameron, 1996). This phenomenon of patchy and delayed regeneration has been observed in similar forests in Wisconsin (Metzger and Tubbs, 1971; Kern et al., 2013), and adds additional uncertainty to the timing, composition, and structure of tree recruitment within harvested openings.

4.2. *Effects of ecological memory on canopy gap success*

Ecological memory may be an important factor deciding the successional trajectory of this and other group selection studies (Webster et al., 2018). Two proposed reasons for unmet biodiversity targets are the continuing reductions in overstory species richness and increased competition from understory vegetation (Kern et al., 2017). These largely result from the material legacies of human activities on the landscape. In the Great Lakes region of eastern North America, decades of single-tree selection have homogenized forest composition towards maple dominance at the expense of shade-intolerant and mid-tolerant species (Neuendorff et al., 2007; Schulte et al., 2007). Reduced overstory richness limits seed availability for declining species and diminishes the likelihood that seeds reach and germinate within canopy gaps, especially for large-seeded species (Willis et al., 2016). Additionally, prolific seed banks of highly competitive understory vegetation (e.g. red raspberry) formed following intensive clear-cut logging in the late 19th and early 20th centuries in the upper Great Lakes (Whitney, 1987; Donoso and Nyland, 2006). These seed banks readily germinate in the light- and nutrient-rich environments created during canopy removal (Marks and Bormann, 1972; Jobidon, 1993). Within our study sites, red raspberry negatively affected recruitment in areas without advanced regeneration (Widen et al., 2018), and has severely challenged regeneration in other group selection studies in the region (Metzger and Tubbs, 1971; Kern et al., 2012).

Herbivory and effects of invasive earthworms are additional factors hampering regeneration success within harvested canopy gaps and reflect degradation of local and/or regional ecological memory (Kern et al., 2017; Webster et al., 2018). Harvested canopy gaps where white-tailed deer (*Odocoileus virginianus*) populations are high have experienced alteration of regeneration composition towards unpalatable and browse-tolerant species (e.g. black cherry, balsam fir, white pine, white spruce) (Walters et al., 2016) or suffered losses of planted seedlings (Kern et al., 2012). In our study, we suspect that deer browse may be a primary reason for low recruitment of yellow birch into height classes > 2 m (personal observation). Invasive, exotic earthworms may also negatively affect natural regeneration and alter plant community composition and structure in northern hardwoods (Bal et al., 2018). Although we did not observe earthworm invasion within our study site, the potential for significant ecosystem alteration is nevertheless concerning.

Group selection may be more successful at promoting canopy diversity in areas where ecological memory is more intact. One example comes from canopy gaps in the Menominee Indian Reservation in central Wisconsin. There, forests largely avoided the severe disturbances (e.g. clearcutting, agricultural clearing, and wildfires) that accompanied European settlement circa 1880–1920, have a long history of sustainable management (Webster and Lorimer, 2005; Menominee Tribal Enterprises, 2012; Mausel et al., 2016), and have substantially lower deer populations than in surrounding areas (Alverson et al., 1988). Harvested canopy gaps within Reservation boundaries regularly regenerate species-rich cohorts of shade-intolerants and mid-tolerants, including yellow birch (Webster and Lorimer, 2005). Other examples come from New England where regional forests have experienced more recovery time since clearing and/or agricultural abandonment compared to those further west, and experimental canopy gaps have successfully regenerated intolerant and mid-tolerant species (Leak, 1999, 2003).

4.3. Implications for management

Our results suggest that large (22 m radius) group selection openings with yellow birch legacy-trees may recruit more diverse cohorts of regeneration in northern hardwoods managed primarily with single-tree selection, but the gains are modest. The compositional trajectories of canopy gaps and single-tree selection reference sites have separated over 15 growing seasons, but shade-tolerant sugar maple continues to dominate the regeneration layers under both group and single-tree selection. We did not intentionally scarify or remove advance regeneration within our group selection treatments during or following harvest. Thus, preexistent maple dominance—caused largely by past management—perpetuated within our experimental gaps. Arbogast (1957) suggests intentionally thinning sugar maple around developing yellow birch, and this release method, although labor intensive, might also be applied to other desired but underrepresented species. Other group selection experiments in northern hardwoods have shown that scarification increases recruitment of mid-tolerants, such as yellow birch and eastern white pine (Godman and Krefting, 1960; Raymond et al., 2003; Willis et al., 2015; Gauthier et al., 2016). Scarification may also improve mid-tolerant recruitment by damaging shade-tolerant advance regeneration and reducing advanced competition (Zaczek, 2002). Forest simulation models suggest that group selection may increase overstory diversity over several cutting cycles when supplementing single-tree selection systems (Halpin et al., 2017). Climate change may also significantly alter future forest composition and diversity, with some models predicting reduced importance of sugar maple and increased importance of shade mid-tolerant white pine in our study region (Duveneck et al., 2014; Prasad et al., 2014). The full effects of legacy retention in our study remain unclear. However, legacy retention within group selection holds promise for maintaining ecological memory and structural complexity through time within conventionally managed temperate forests, and we suggest further experimentation to better understand the specific effects of legacy retention on regeneration dynamics in group selection systems.

Acknowledgements

Funding supporting this research came from the McIntire-Stennis Cooperative Forestry Research Program, USDA Forest Service, and Michigan Technological University's School of Forest Resources and Environmental Science. We thank Kaylie Butts and Russell Lipe for their help with field data collection and entry, and the Michigan Technological University's Ford Research Center and Forest for hosting the research site and field crews. We also thank Dr. Yvette Dickinson and Dr. Erik Lilleskov for their helpful comments on earlier drafts of this manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.06.005.

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