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Predicted long-term effects of group selection on species composition and stand structure in northern hardwood forests

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ABSTRACT

The group selection method can potentially increase the proportion of shade-intolerant and midtolerant tree species in forests dominated by shade-tolerant species, but previous results have been variable, and concerns have been raised about possible effects on forest fragmentation and forest structure. Limited evidence is available on these issues for forests managed beyond the first cutting cycle. We used CANOPY, an individual-tree forest dynamics model, to assess long-term effects of group selection methods on tree species composition, fragmentation of the mature forest matrix, and sustainability of size distributions in northern hardwoods. Results were also compared to reference treatments that included a no-cut control, single-tree selection, and clearcutting. Model simulations predicted that group selection would increase midtolerant tree abundance compared to single-tree selection and controls, but magnitude of response was highly variable depending on habitat type and harvest design. All conventional single-tree and group selection designs greatly increased small-scale fragmentation of the mature forest matrix. Group or small patch cutting with area control (constant percent of stand area cut in openings in each cutting cycle with no cutting between groups) produced residual stands with 'rings' of mature and large tree crowns in a 'chain-link fence' pattern. All treatments, however, resulted in sustainable populations; size distributions did not deviate substantially from a descending monotonic distribution over the 300-yr period. Results suggest possible tradeoffs between maximizing midtolerant species composition and minimizing fragmentation of the mature forest matrix, and that the potential for increasing the abundance of midtolerant species can be strongly constrained by habitat type.

1. Introduction

Group selection is receiving renewed attention in situations where foresters seek a partial cutting method that can regenerate species of low to moderate shade tolerance, and yet maintain a fairly high proportion of mature forest cover. Long-term studies have demonstrated that single-tree selection is ineffective for the former purpose, as it typically leads to overwhelming dominance by shade-tolerant species (e.g., Tubbs, 1977a; Leak and Sendak, 2002; Neuendorff et al., 2007). Openings larger than 200–400 m^2, on the other hand, can often foster the regeneration of midtolerant and intolerant tree species (McClure and Lee, 1993; Jenkins and Parker, 1998; Dale et al., 1995). In a 60-year study in New England, harvest openings of about 0.2–0.4 ha maintained forest composition comprised of 25–33% midtolerant and intolerant species (Leak and Filip, 1977; Leak, 1999). In mixed forests managed by group selection in the central U.S., openings included more than 50% midtolerant and intolerant species (Dale et al., 1995).

Although group selection has numerous desirable features, concerns have been raised about potential effects on species composition and forest structure if group selection were to be applied on a much larger scale as a partial replacement for clearcutting or shelterwood systems. In many cases, sizable openings alone may not substantially increase the abundance of less tolerant species. Other factors known to constrain recruitment of the less shade-tolerant species include inherent habitat features (soil, microclimate, local flora and fauna), seed source, seedbed conditions, and degree of vegetative competition (e.g., Tubbs, 1969; Kern et al., 2012, 2013; Walters et al., 2016; Willis et al., 2015, 2016). For example, Shields et al. (2007) reported increases in midtolerant yellow birch (*Betula alleghaniensis* Britt.) within group openings in northern hardwood stands compared to single-tree selection, but birch still comprised less than 10% of the cohort developing in the gaps. In southern Appalachian forests, Beckage et al. (2000) found no

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consistent response to creation of multiple-tree gaps for either intolerant or shade-tolerant species. Group selection harvests in some forest types can actually accelerate the replacement of existing midtolerant canopy species with other, more aggressive competitors. In mixed hardwood forests of the central U.S., formerly dominant oaks (*Quercus* spp.) and hickories (*Carya* spp.) are often among the least abundant species in group selection openings, which become dominated by yellow poplar (*Liriodendron tulipifera* L.) and maples (*Acer* spp.) (Jenkins and Parker, 1998; Weigel, 1999).

Group selection may also have negative impacts on 'sensitive' species requiring shady, mature forest environments. For example, eastern hemlock (*Tsuga canadensis* (L.) Carr.) is a shade-tolerant species of special concern in the Great Lakes region because it is currently limited in abundance and difficult to regenerate. Conventional group selection without intentional scarification can result in poor hemlock establishment even with relatively small openings (350–800 m^2) on favorable hemlock habitats (Webster and Lorimer, 2002; Walters et al., 2016). Group selection may also be detrimental to other, less conspicuous flora and fauna adapted to moist microclimates on the forest floor (Harpole and Haas, 1999; Gundale, 2002). Some field experiments, for example, have reported >80% reductions in salamander abundance after group selection, similar to effects of clearcutting (Homyack and Haas, 2009; Hocking et al., 2013).

A related concern is that group selection may cause excessive fragmentation and edge effects in mature forest (Roach, 1974; Gustafson and Crow, 1996; Bigelow and Parks, 2010), potentially magnifying the direct effects of openings on forest interior species. At the stand level, Roach's conceptual diagrams suggest a surprisingly high degree of small-scale fragmentation of the mature forest matrix even when small groups occupy only 20% of the stand area (e.g., after only two cutting cycles). While Roach (1974) focused only on logistical difficulties of marking and keeping track of numerous unmapped groups, aesthetics and wildlife habitat could also be compromised if the forest matrix has been so fragmented that mature trees exist only as small, dispersed clusters. At a broader landscape level, simulations by Gustafson and Crow (1996) demonstrated substantial reduction in interior forest conditions and increased edge with group selection compared to clearcutting. In New England northern hardwoods, negative effects on salamander populations extended 34 m into the forest matrix from the opening margin, suggesting the potential for substantial edge effects with moderate to large group openings (0.1–0.8 ha; Hocking et al., 2013).

While the use of smaller group selection openings might reduce impacts on flora and fauna that prefer mature forest habitat, smaller openings could theoretically lead to irregular size distributions with fluctuating yields under some conditions. If groups are fairly large (e.g., >0.25 ha), a regulated forest with group selection would probably have a sustainable diameter distribution approaching a negative exponential curve (Leak and Filip, 1977; Leak, 1999), similar to that of a regulated even-aged forest (Assmann, 1970, p. 447). But when openings are small, fast-growing pole and mature trees bordering the gaps often close the gaps laterally before sapling recruits can reach the canopy (Hibbs, 1982; Runkle and Yetter, 1987; Cole and Lorimer, 2005). This could potentially inhibit new recruitment and foster dominance by pole and mature trees, creating a quasi-even-aged stand structure (stem exclusion stage of Oliver and Larson, 1996) that deviates from a negative exponential form (Roach, 1974).

A serious limitation in our understanding of group selection effects is that, aside from the 60-yr study by Leak (1999), most field studies have only examined effects after the first cutting cycle. It is therefore difficult to predict long-term effects of group selection from current evidence. Because of funding and time constraints, field studies have also generally only examined the effects of one or a narrow range of opening size, one implementation of group extent (percent of canopy removed in each cutting cycle), and one habitat type. Comparisons of group selection effects have not usually been made with the current prevailing silvicultural systems on the same habitat. The objectives of this study were to assess long-term ramifications of group selection methods with natural regeneration on tree species composition, cohort structure, and size distributions in forests dominated by shade-tolerant species. We evaluated the following specific questions: (1) How do variations in group selection design and habitat differences influence the abundance of midtolerant as well as exposure-sensitive tree species compared to the alternatives of single-tree selection and even-aged management?; (2) Does group selection lead to excessive small-scale fragmentation of the mature forest matrix after many cutting cycles?; and (3) Does group selection with small to moderate opening sizes (200–2000 m^2) lead eventually to irregular or unsustainable size distributions?

A range of group selection alternatives was simulated using CANOPY (v.3), a crown-based, individual-tree model (Choi et al., 2001; Hanson et al., 2011), on two northern hardwood and hemlock-hardwood habitat types of differing productivity and species diversity. Group selection included two designs: combined group/single-tree selection regulated using a residual diameter distribution (Roach, 1974; Miller et al., 1995), and group selection regulated strictly by area control and with no cutting between the groups or thinning of older cohorts (Miller et al., 1995; Leak, 1999). With the latter approach, called 'patch cutting' or 'group/patch selection' by some investigators, an equal amount of the forest matrix is cut in openings in each cutting cycle. An approximate rotation age, useful for making comparisons with even-aged alternatives, can be computed as the inverse of the mean annualized area of openings created (Miller et al., 1995; Leak, 1999). This 'implicit rotation age' involves a simplifying assumption of non-overlap of group openings. In the simulations, group sizes and the proportion of stand cut in group openings per cutting cycle (hereafter 'group extent') were systematically varied. Single-tree selection, clearcutting, and untreated controls were also simulated for comparative purposes and to provide insights into the implications of shifting management of specific tracts from the existing silvicultural system to group selection.

2. Methods

2.1. Model description

CANOPY is a spatially explicit, individual-tree model designed to simulate the long-term response of tree saplings and mature trees to natural or harvest-created openings (Choi et al., 2001; Hanson et al., 2011). The model simulates the gap-capture process in forest openings by projecting the height growth of saplings in a gap, as well as the height growth and lateral crown growth of mature trees bordering the gap. Crown radial growth is predicted in four cardinal directions for each tree, with the most rapid growth typically in the direction facing a gap (Choi et al., 2001). Sapling height growth is also influenced by gap size, which is monitored annually. Successful gap capture occurs if a sapling or pole tree can reach canopy height before becoming overtopped by the crowns of mature gap-border trees.

The model assesses competition level to predict several processes, including sapling recruitment, tree growth (height, diameter, and crown radius), and mortality. Plot-level competition is evaluated using northern hardwood stocking charts (Tubbs, 1977b), in which plot basal area is compared to average or maximum observed levels in the region for stands with the same mean diameter at breast height (DBH), similar conceptually to self-thinning diagrams (Drew and Flewelling, 1977; Westoby, 1984). In CANOPY, a stand is divided

into a grid of 10 × 10 m cells, and stocking is calculated for each cell. The predicted size distribution is only determined by the sum of the performances of all the individual trees in response to their local competition environment (nine contiguous cells or 900 m^2). Size distributions are not constrained by any *a priori* theoretical assumptions or external empirical evidence of how stand-level distributions change over time.

The number of 2–6 cm DBH saplings recruited in each 10 × 10 m cell is based on stocking level, floristic habitat type, and species composition of that cell and the eight adjoining cells. If fewer saplings than predicted are present on a cell, new recruits are added to make up the difference. In situations where advance regeneration may not be present, recruitment pauses long enough for a sapling or sprout to reach 2 cm DBH. For hemlock, we used the asymptotic recruitment model of CANOPY v.3 (see further details on sapling recruitment and sprouting in Appendix A). While sapling recruitment equations were calibrated from data over a large geographical area, most sites had deer populations typical of the region and considered to be moderate to moderately high (6–10 deer km^{-1}), which may reduce recruitment rates for yellow birch and other species. Because these deer densities are usually sufficient to prevent any hemlock recruitment, however, the hemlock recruitment equations were calibrated from a subset of stands with lower deer populations (≤5 deer km^{-1}).

Because of the complexity and unknown ramifications of global environmental change impacts and interactions, the projections in this paper are not considered to be 'forecasts' of species composition and structure at specific times in the future. Rather, the projections represent the long-term consequences of management practices predicted by the model, given the environmental conditions under which the model was calibrated (ca. 1951–2007). The model does not currently have mechanisms to predict effects and interactions of novel environmental stressors such as climate warming, current or future invasions by exotic insects and diseases, invasive plants, and exotic earthworms.

Calibration data for CANOPY were obtained from 560 permanent and temporary sample plots in 186 northern hardwood and hemlock-hardwood stands in northern Wisconsin and upper Michigan. These stands were located on mesic sites of moderate to high fertility and included a variety of forest structural conditions, ranging from young even-aged stands to uneven-aged old growth. Study sites also incorporated a wide range of past treatments, including unmanaged stands, thinning, selection harvests, group selection openings, shelterwoods, and clearcuts.

Stands in the calibration data set were restricted to three mesic, relatively nutrient-rich habitat types following Kotar et al. (2002): *Acer-Osmorhiza-Caulophyllum* (AOCa; the most productive but intermediate in species diversity), *Acer-Tsuga-Dryopteris* (ATD, moderate in productivity and lowest in species diversity), and *Acer-Tsuga-Maianthemum* (ATM, the least productive but the most diverse). Most stands are dominated by sugar maple (*Acer saccharum* Marsh.) or hemlock with varying amounts of yellow birch, red maple (*Acer rubrum* L.), basswood (*Tilia americana* L.), white and green ash (*Fraxinus americana* L. and *F. pennsylvanica* Marsh.), and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch). Soils are sandy loams and loamy spodosols primarily developed from glacial till, outwash, and lacustrine deposits. Topography is gently rolling, with the elevation of study sites ranging from 200 to 550 m. The climate is humid continental (mean annual precipitation of 80–90 cm and well distributed throughout the year; mean January and July temperatures of −8 to −12 °C and 19–20 °C, respectively).

2.2. Model verification using field data

CANOPY has been tested extensively against field data from independent, long-term silvicultural trials on experimental forests and regional archival data on unmanaged mature and old-growth forests. Tests have indicated good results from both short-term and long-term predictions of various forest attributes in both managed and unmanaged stands. These attributes include sapling recruitment and height growth (Hanson et al., 2011), stem diameter increment and crown growth of individual trees (Choi et al., 2001, 2007), gap-capture processes (Hanson et al., 2011), size distributions (Lorimer and Halpin, 2014; Halpin and Lorimer, 2016a, 2016b; Halpin and Lorimer, 2017) and stand volumes, biomass, annual stand production, and mortality (Choi et al., 2001, 2007; Hanson et al., 2012; Halpin and Lorimer, 2016a).

Predictions of species composition are more difficult to evaluate because few permanent plots of more than 30 years duration are available in stands with large openings. However, a test of observed vs. predicted sapling recruitment over a 23-yr span in old-growth forest gave good predictions of new sapling recruitment (7% error) and species composition (Hanson et al., 2011). Comparisons against 30-yr permanent plot records in mature and old-growth forests also showed that the model correctly predicted increases and decreases for individual species in most cases (Halpin and Lorimer, 2017). Long-term (100–1000 yr) simulations of the natural disturbance regime gave predicted species composition and size distributions similar to that of unmanaged forests in the region, with densities of trees in each size class close to the observed mean (Lorimer and Halpin, 2014; Halpin and Lorimer, 2016a, 2016b; Halpin and Lorimer, 2017). Predicted diameter distributions of all-aged, old-growth stands under small-gap dynamics were rotated sigmoid in form, with basal areas averaging 37 m^2 ha^{-1} and maximum DBH of 80–100 cm. These are consistent with field data collected from uneven-aged, old-growth stands in the region (Goodburn and Lorimer, 1999; Janowiak et al., 2008; Halpin and Lorimer, 2016b).

2.3. Initial conditions for stand simulations

Simulations were conducted on two mapped 1-ha stands not used in model calibration. The first is an even-aged, second-growth northern hardwood stand about 100 years old at the Argonne Experimental Forest near Crandon, Wisconsin. It is a productive site dominated by sugar maple with lesser amounts of hemlock and includes approximately equal proportions of AOCa, ATD, and ATM habitat types. The second site is a mature hemlock-hardwood stand on ATM habitat at the Menominee Indian Reservation and managed by single-tree selection for many decades. On both sites, tree DBHs were measured and stem locations mapped. Heights to the top, widest portion, and bottom of crowns were measured using clinometers, and total and exposed crown radii measured with tapes in the four cardinal directions.

To accommodate simulation of multiple large group selection openings and patch clearcuts, 9-ha stands were constructed by using the 1-ha mapped areas as "tiles" in a 3 × 3 grid. For cells along the boundary of the 9-ha tracts, the tract was treated as a torus, with stocking based partly on cells at the opposite end of the stand. Previous work has indicated that this is among the best methods for minimizing bias of stand edge effects (Yamada and Rogerson, 2003; Pommerening and Stoyan, 2006; Li and Zhang, 2007). Ten replications of each treatment were simulated for 300 years on both sites.

Although two specific stands were selected for initial conditions in the simulations, note that near the end of the 300-yr simulation period, most of the initial stand conditions will have disappeared. The reason is that the 300-yr period exceeds the expected lifespan of most trees in the managed stands and even in the unmanaged control (Lorimer et al., 2001). By the end of the simulation, species composition and structure therefore mainly reflect the dynamics of

many stands on these habitat types in the model's calibration data set, averaged across a broad region.

2.4. Treatment designs

Single-tree selection was simulated by computing allowable cut using a fixed residual diameter distribution of negative exponential form (Marquis, 1978; Nyland, 2016). In each cutting cycle, trees were tallied by 5 cm diameter classes, and surpluses from each class were removed tree by tree as long as the stand basal area did not drop below the specified residual basal area. Within a diameter class, trees growing under the highest stocking levels were removed first to mimic the removal of low-vigor trees (minimum DBH cut = 11.7 cm).

Three variants of single-tree selection were simulated. 'Standard selection' used the recommended residual stand structure values for the region – a maximum diameter (D) of 60 cm, residual basal area (B) of 20.7 m^2 ha^{-1}, and a q-ratio (ratio of number of trees in two successive size classes) of 1.3 for trees > 12 cm DBH (Crow et al., 1981). 'Heavy selection' used the same D and q but a lower residual basal area (B) of 16.1, intended to mimic more intensive management than standard selection while maintaining similar residual structure. 'Industrial selection' used D = 46 cm, B = 16.1 m^2 ha^{-1}, and q = 1.7, representative of more economically-driven management on industrial lands with a higher ratio of medium vs. large trees (Bare and Opalach, 1988; Kaya and Buongiorno, 1989). All single-tree selection treatments used a 15-year cutting cycle.

In all group selection treatments, openings were simulated by removing all trees > 2 cm DBH from a circular area. This has been the recent practice for public lands in the region and is intended to reduce the overwhelming dominance by sugar maple advance regeneration, especially the taller suppressed stems that are often of poor quality (Wisconsin DNR, 2006). Group placement attempted to satisfy three criteria: (1) openings placed preferentially in mature forest (basal area > 20 m^2 ha^{-1} for trees $\geq$ 26 cm DBH), (2) no overlap with other openings installed in the previous two cutting cycles, and (3) a minimum buffer width between openings in the current cycle equal to the radius of a group selection opening. If all placement conditions are not satisfied, the model attempts to satisfy the first two, then the first one, and finally reverts to random placement. In this study, the random placement alternative was never required. All group selection treatments used a 15-year cutting cycle.

After a group selection or clearcut opening is created in CANOPY, stocking is assessed and regeneration simulated in a circular plot centered on the opening. This group-centered stocking assessment prevents the underestimation of sapling density and recruitment of midtolerant species that might occur whenever an opening straddles the boundaries of several 10 × 10 m cells. After this group-centered stocking assessment, regeneration assessment proceeds systematically through the grid and adds more saplings to 10 × 10 m cells if the recruitment equation indicates any remaining deficits, given the subplot structure and composition.

For the first method of group selection, in which group cutting was combined with single-tree selection, group openings were installed first, and then single-tree selection was performed between the openings. Group sizes ranged from 100–2000 m^2 (but of fixed size within each treatment) and occupied 1–9% of the stand area per cutting cycle. Group/single-tree selection used the same residual size distribution as standard single-tree selection.

In the second method of group selection (patch cutting or group/patch selection), the stand was regulated by area control and no cutting was performed between the current groups nor were older openings thinned. This procedure follows prevailing practices in places where group selection has been used for a number of decades, such as northeastern and southeastern Appalachian forests (W.B. Leak and John Blanton, pers. communic.). Group sizes ranged from 200–2000 m^2 (opening width up to twice the dominant tree height), but opening size was constant within a treatment. Three alternative 'implicit rotation ages' were selected: 100, 120, and 135 years, which span a typical range for northern hardwoods on conventional and slightly extended rotations (Leak et al., 1987; Wisconsin DNR, 2006). The proportion of stand area cut in groups in each entry corresponding to these rotation ages was 15%, 12.5%, and 11.1%, respectively.

Simulation of even-aged management was conducted on nine 1-ha compartments, removing all trees larger than 2 cm DBH from one compartment every 15 years. Effects of thinning were also examined because thinning could (and did) affect the shape of the size distribution. When thinning was performed, the minimum residual stocking guideline of Erdmann (1986) was used for maple stands and the B-line of Tubbs (1977b) for hemlock-dominated stands. Each thinning removed a maximum of 25% of the basal area in the compartment. The first thinning was conducted 45 years after overstory removal (Erdmann, 1986), with subsequent thinnings at 15-yr intervals. However, because of limited calibration data on younger even-aged stands that had been thinned more than a decade earlier, no analysis was conducted of thinning effects on recruitment of 2–6 cm DBH saplings in even-aged stands.

In this study, none of the simulated treatments included rules that would favor or prohibit harvesting of particular species.

2.5. Data analysis

One-way ANOVA was used to test for treatment effects on species composition and exposed crown area, followed by multiple comparison tests. Exposed crown area (ECA) was defined as the projection area of the portion of tree crowns exposed to direct skylight (i.e., the portion visible from a low-altitude aerial photo), including gap saplings. Normality of residuals was verified using a Shapiro-Wilk test, and the homogeneity of variance was verified using Levine's test (Steel et al., 1997; Fox, 1997).

The extent to which the mature forest matrix was fragmented by treatments was assessed by the aggregate crown area of mature and large trees and by their statistical spatial pattern. Percent aggregate ECA was calculated as the sum of exposed crown area for trees by size category: saplings (2–11.9 cm DBH), poles (12–25.9 cm), mature trees (26–45.9 cm), large trees ($\geq$46 cm). Comparisons across treatments were conducted using ANOVA and Tukey-Kramer post hoc contrasts. Relative basal area by species for all trees with DBH larger than 12 cm was computed and again compared using Tukey-Kramer contrasts.

The spatial pattern of stem locations was analyzed using the spatial distribution indices F(r), G(r), and K(r) in the R package 'spatstat' (Baddeley and Turner, 2005). F(r) is a distribution of point-to-nearest tree distances in which a grid of sample points is positioned within the stand. G(r) is a distribution of tree-to-tree nearest-neighbor distances. K(r) is a distribution of tree-to-tree distances including all neighbors, rather than just the nearest. G(r) and F(r) both assess local scale spatial pattern, with the former having greater statistical power to detect clustering and the latter having greater statistical power to detect repulsion. K(r) assesses global spatial pattern, and can detect phenomena like clusters that repel each other. F(r), G(r), and K(r) were constructed for all trees as well as for each size category. Complete spatial randomness (CSR; i.e., a uniform Poisson process) is the most common spatial pattern in unmanaged northern hardwoods (Payendeh, 1974; Chokkalingam and White, 2001) and was used as a baseline for comparison in some tests.

The degree to which treated stands maintained a balanced, sustainable size distribution (e.g., Crow et al., 1981; Gronewold et al., 2010) was assessed by means of Weibull models (Bailey and Dell, 1973). Parameters were estimated by maximum likelihood for both a single Weibull model (capable of detecting negative exponential and unimodal structures), and for a finite mixture of two Weibull distributions (capable of detecting rotated sigmoid structure, as in Zhang and Liu, 2006). Both models were fit using the R package 'mixdist' (MacDonald and Du, 2008) with 2 cm diameter classes for all trees above 2 cm. Kolmogorov-Smirnov goodness of fit tests were performed and mean squared errors were calculated for both models.

The effects of treatment on overall stand structure or stand developmental stage were evaluated using the stand-stage classification of Lorimer and Halpin (2014):

Sapling stand: Basal area in pole, mature and large trees < 10 m^2 ha^{-1}.
Pole stand: Basal area in pole, mature, and large trees ≥ 10 m^2 ha^{-1}, and basal area in mature and large trees < 10 m^2 ha^{-1}; OR basal area in mature and large trees 10–20 m^2 ha^{-1}, with ≥ 30% of stand basal area in poles.
Mature-sapling mosaic: Basal area in mature and large trees 10–20 m^2 ha^{-1}, with <30% of the stand basal area in pole trees. Mature-sapling mosaics have more gap area (and therefore more crown area of saplings) than most undisturbed mature stands and usually reflect the influence of recent moderate disturbance.
Mature stand: Basal area of mature and large trees ≥ 20 m^2 ha^{-1}, with < 45% of the stand basal area in large trees.
Old-growth stand: Basal area of mature and large trees ≥ 20 m^2 - ha^{-1}, with ≥ 45% of the stand basal area in large trees. Old-growth stands were considered to have steady-state structure when the size distribution has approached a descending monotonic curve. This additional criterion was satisfied when the ratio of aggregate exposed crown area (ECA) in large to mature trees was at least 1.5, large trees were < 58% of total ECA, and gap saplings comprised at least 3% of total ECA (Lorimer and Frelich, 1998).

Basswood and red maple, two species usually considered to be somewhat shade tolerant (Baker, 1949), both usually appear to require sizable gaps for establishment and long-term survival beneath the densely shaded canopies of sugar maple and hemlock in this region (see also Burns and Honkala, 1990). They are therefore included with the midtolerant species in a category called 'gap-dependent species.'

3. Results

3.1. Treatment effects on species composition

3.1.1. Untreated controls

Without treatment and under a disturbance regime of only small treefall gaps, the model predicted that the fraction of basal area occupied by the dominant shade-tolerant species would remain largely unchanged. Sugar maple continued heavy dominance of the hardwood stand and hemlock and sugar maple shared dominance of the hemlock-hardwood stand (Table 1). Although the fraction of gap species remained fairly stable overall, ash and red maple decreased in the more productive hardwood stand but increased in the less productive hemlock-dominated stand. At the hardwood site, yellow birch was a very minor component initially and showed little further change over time. In the hemlock stand, however, yellow birch initially comprised 15% of the basal area, showing a slow but steady decline to a stable level about 9–10% after 80 years of small gap dynamics. Basswood increased

Table 1
Effects of various reference treatments and combined group/single-tree selection on predicted species percent basal area at simulation year 300.

	Sugar Maple	Hemlock	Yellow Birch	Ash	Basswood	Red Maple	All gap spp.*
	Northern hardwood stand (AOCa-ATD-ATM)						
Initial Conditions	73.4	14.5	1.5	6.1	0.3	3.3	11.2
No treatment	75.4*d*†	13.7*a*	1.6*g*	3.4*ef*	5.1*a*	0.7*b*	10.9*f*
Standard STS	87.2*a*	2.2*b*	2.9*f*	1.7*g*	5.3*a*	0.7*b*	10.6*f*
Heavy STS	87.8*a*	1.1*def*	2.8*f*	3.2*f*	3.9*b*	1.1*b*	11.1*f*
Industrial STS	87.8*a*	1.4*cd*	2.7*fg*	3.3*f*	4.0*b*	0.9*b*	10.8*f*
GS + STS‡ 200 m^2, 3% extent	83.1*b*	1.2*cde*	5.7*e*	4.7*e*	4.0*b*	1.2*b*	15.7*e*
GS + STS 800 m^2, 3% extent	82.1*b*	1.8*bcd*	6.8*d*	4.3*ef*	3.9*b*	1.1*b*	16.2*e*
GS + STS 2000 m^2, 3% extent	82.7*b*	1.9*bc*	6.1*de*	4.3*ef*	3.9*b*	1.2*b*	15.5*e*
GS + STS 200 m^2, 9% extent	77.6*c*	0.6*efg*	7.1*d*	9.9*d*	2.7*c*	2.0*a*	21.8*d*
GS + STS 800 m^2, 9% extent	71.6*e*	0.6*efg*	10.4*c*	12.2*c*	2.9*c*	2.1*a*	27.8*c*
GS + STS 2000 m^2, 9% extent	67.9*f*	0.5*fg*	12.0*b*	14.9*b*	2.7*c*	2.1*a*	31.7*b*
Clearcutting	53.0*g*	0.1*g*	14.2*a*	28.0*a*	2.2*c*	2.5*a*	46.9*a*
	Hemlock-hardwood stand (ATM)						
Initial Conditions	32.7	41.3	15.4	0.3	5.5	0.6	21.8
No Treatment	34.5*e*	39.0*a*	8.7*h*	4.2*f*	12.1*d*	1.4*h*	26.5*h*
Standard STS	39.0*c*	13.7*b*	14.0*f*	10.6*c*	18.5*a*	4.2*fg*	47.3*e*
Heavy STS	47.6*b*	6.7*d*	11.8*g*	12.7*b*	16.4*b*	4.9*f*	45.7*e*
Industrial STS	62.0*a*	6.6*d*	7.6*h*	6.0*e*	14.1*c*	3.6*g*	31.3*g*
GS + STS 200 m^2, 3% extent	47.2*b*	14.1*b*	14.0*f*	9.6*cd*	10.2*e*	5.0*ef*	38.8*f*
GS + STS 800 m^2, 3% extent	37.9*cd*	10.6*c*	24.0*d*	8.8*d*	12.4*d*	6.3*d*	51.5*d*
GS + STS 2000 m^2, 3% extent	35.9*de*	11.5*c*	23.5*d*	9.8*cd*	13.2*cd*	6.1*de*	52.6*d*
GS + STS 200 m^2, 9% extent	46.8*b*	6.5*d*	16.9*e*	14.1*b*	5.6*f*	10.2*c*	46.7*e*
GS + STS 800 m^2, 9% extent	36.1*de*	4.7*e*	27.0*c*	13.9*b*	5.7*f*	12.5*b*	59.1*c*
GS + STS 2000 m^2, 9% extent	30.2*f*	4.2*e*	32.2*b*	13.7*b*	6.3*f*	13.4*b*	65.6*b*
Clearcutting	15.6*g*	0.8*f*	44.0*a*	16.4*a*	3.6*g*	19.6*a*	83.6*a*

* Gap-dependent species: yellow birch, white ash, red maple, and basswood.
† Means followed by different letters within a column were significantly different (Tukey-Kramer tests, $p < 0.05$). Letters are in order such that 'a' represents the group with the highest mean.
‡ GS + STS denotes a group selection treatment which included single-tree cutting between groups. Extent refer to the portion of the stand removed in groups each 15 year cutting cycle.

slowly at both sites, reaching 5% relative basal area (RBA) at the hardwood site and 12% at the hemlock site after 300 years.

3.1.2. General trends across all silvicultural treatments

Sugar maple maintained high dominance on both sites under nearly all treatments. In the hardwood stand, sugar maple eventually comprised 63–88% of the predicted basal area in all treatments except clearcutting. At the hemlock site, sugar maple was initially 33% RBA and generally maintained this level or increased in all treatments except clearcutting, for which yellow birch was the more abundant species. All treatments with small openings, whether or not single-tree selection was part of the mix, increased sugar maple dominance at the expense of hemlock (Tables 1 and 2).

No form of conventional forest management examined here was favorable for hemlock over the 300-year simulation. In the first 40 years, there was often little change in hemlock abundance in many of the treatments. However, in contrast to the stable hemlock populations on the control plots, all treatments on both sites showed drastic declines in hemlock by the end of simulation, even with standard single-tree selection. After three centuries, hemlock was always less than 5% of the basal area in the hardwood stand and less than 15% of the basal area in the hemlock stand (Tables 1 and 2). The rate of hemlock decline depended on the study site, opening size, and group extent. The point at which group selection treatments had reduced hemlock RBA to half of its initial value ranged from 50 to 140 years, with the faster decline occurring on the hardwood site and with smaller opening sizes, shorter rotations, or greater group extent (Fig. 1).

Gap-dependent species were predicted to be much more abundant on the medium-quality hemlock site (ATM habitat) and following treatments that removed higher levels of basal area (Tables 1 and 2). Under various group selection treatments, gap species on the hemlock site comprised 39–69% of the final stand basal area, with all four gap species well represented. In contrast, gap species remained a more modest proportion of stand basal area at the more productive hardwood site (AOCa-ATD-ATM habitats), exceeding 20% RBA only when group extent was 9% or more per cutting cycle. Nevertheless, compared to single-tree selection, group selection with 9% or more group extent doubled or tripled the abundance of gap-dependent species. Clearcutting on the more productive site produced four times the RBA of gap-dependent species compared to single-tree selection. This reflects trends in the calibration data set that show a generally increasing abundance of these species as stocking level decreases or opening size increases (Hanson et al., 2011).

Among gap-dependent species, temporal trends under the various group selection regimes typically showed little change in relative basal area in the first few decades while the new recruits were small. Gap species then increased steadily until about year 90–150, after which they stabilized or declined slightly (Fig. 1).

3.1.3. Single-tree selection and combined group/single-tree treatments

In the more productive hardwood stand, all forms of single-tree selection showed no significant increase in gap-dependent species as a group compared to the untreated controls. However, in the less productive hemlock stand, single-tree selection significantly increased gap species proportion, although increasing the intensity of selection had little additional effect (Table 1).

Group/single-tree selection combinations had significantly higher predicted abundance of yellow birch than single-tree selection methods on both sites. Other gap species showed no consistent response except for increases in ash and red maple at the greater opening extents (Table 1). At a given group extent, increasing the opening size had little effect on the abundance of most gap species, although a few of these differences were statistically significant. At a higher group extent of 9%, however, some substantial

Table 2
Effect of opening size and group extent* on species percent basal area under group selection with area control at simulation year 300.

Opening size (m^2)	Opening extent (%)	Sugar Maple	Hemlock	Yellow Birch	Ash	Basswood	Red Maple	All gap spp.
		Northern hardwood stand (AOCa-ATD-ATM)						
Initial conditions		73.4	14.5	1.5	6.1	0.3	3.3	11.2
200	15.0	76.5*abc*†	0.5*bc*	6.6*de*	11.8*efg*	2.1*b*	2.5*a*	23.1*ef*
200	12.5	77.3*ab*	0.7*abc*	6.3*e*	10.9*fg*	2.3*ab*	2.5*a*	22.0*f*
200	11.1	78.5*a*	0.8*abc*	6.2*e*	9.9*g*	2.7*ab*	1.9*a*	20.7*f*
400	15.0	74.0*cd*	0.4*c*	7.8*cd*	13.2*de*	2.2*ab*	2.4*a*	25.6*de*
400	12.5	74.6*bcd*	0.6*abc*	8.1*c*	11.9*efg*	2.5*ab*	2.4*a*	24.9*de*
400	11.1	73.1*d*	0.9*abc*	8.5*c*	12.8*def*	2.6*ab*	2.1*a*	26.1*d*
800	15.0	67.9*e*	0.4*c*	10.3*b*	16.7*abc*	2.2*ab*	2.5*a*	31.7*bc*
800	12.5	68.0*e*	0.7*abc*	10.3*b*	16.1*bc*	2.5*ab*	2.5*a*	31.3*bc*
800	11.1	68.4*e*	0.9*abc*	10.5*b*	14.9*cd*	2.8*a*	2.3*a*	30.6*c*
2000	15.0	64.7*f*	0.5*bc*	11.6*ab*	18.6*a*	2.3*ab*	2.3*a*	34.8*a*
2000	12.5	65.0*f*	1.1*a*	11.5*ab*	17.3*ab*	2.7*ab*	2.4*a*	33.9*ab*
2000	11.1	63.4*f*	1.0*ab*	12.0*a*	18.2*a*	2.6*ab*	2.7*a*	35.6*a*
		Hemlock-hardwood stand (ATM)						
Initial conditions		32.7	41.3	15.4	0.3	5.5	0.6	21.8
200	15.0	40.8*a*	3.9*bcd*	21.7*e*	16.5*ab*	4.5*ab*	12.6*d*	55.3*d*
200	12.5	41.6*a*	4.5*abc*	19.2*f*	17.0*a*	5.0*a*	12.7*cd*	53.9*de*
200	11.1	42.6*a*	5.8*a*	17.4*f*	16.4*abc*	5.0*a*	12.8*cd*	51.6*e*
400	15.0	36.0*bc*	3.2*de*	26.4*d*	16.0*abcd*	4.5*ab*	13.9*abcd*	60.8*c*
400	12.5	37.7*b*	3.6*cde*	25.5*d*	15.7*abcde*	4.8*ab*	12.7*cd*	58.7*c*
400	11.1	40.8*a*	4.9*ab*	22.3*e*	14.6*cdef*	4.7*ab*	12.7*cd*	54.3*d*
800	15.0	33.1*d*	2.6*e*	32.0*ab*	14.2*def*	4.0*b*	14.0*abcd*	64.2*b*
800	12.5	32.9*d*	3.1*de*	30.9*bc*	14.4*def*	4.5*ab*	14.2*abc*	64.0*b*
800	11.1	34.8*cd*	4.1*bcd*	29.4*c*	13.6*f*	4.9*a*	13.2*bcd*	61.1*c*
2000	15.0	28.3*e*	2.9*de*	34.2*a*	15.0*bcdef*	4.3*ab*	15.3*a*	68.8*a*
2000	12.5	29.0*e*	3.6*cde*	33.8*a*	14.4*def*	4.5*ab*	14.7*ab*	67.4*a*
2000	11.1	28.6*e*	4.1*bcd*	33.2*a*	13.9*ef*	5.1*a*	15.1*a*	67.3*a*

* 'Implicit rotation ages' for 15%, 12.5%, and 11.1% removal over a 15 year cutting cycle are 100, 120, and 135 years.
† Means followed by different letters within a column were significantly different (Tukey-Kramer tests, $p < 0.05$). Letters are in order such that 'a' represents the group with the highest mean.

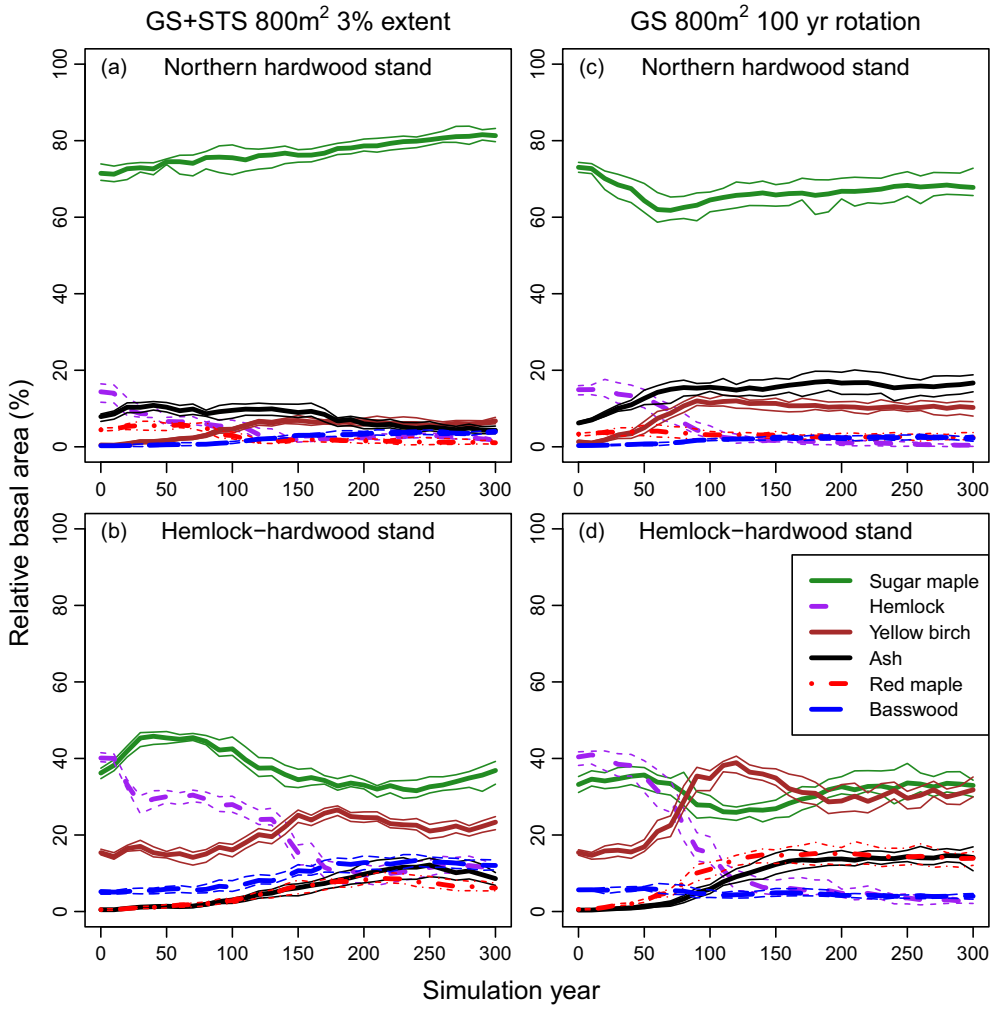

Fig. 1. Temporal trends in the relative basal area for principal species at the two sites over the 300-year simulation period using (a and b) combined group/ single-tree selection with 800 m^2 openings occupying 3% of stand area in each cutting cycle, and (c and d) group/ patch selection on a 100-year rotation. Trend lines show the mean of 10 replications, with bands showing the range of variation.

increases were predicted for yellow birch and white ash as opening size increased from 200 to 2000 m^2 (Table 1).

For a given opening size, an increase in group extent resulted in an increase in the abundance of yellow birch and white ash (and also red maple on the hemlock site). For example, at an opening size of 2000 m^2, yellow birch RBA increased from 6% to 12% on the hardwood site and from 24% to 32% on the hemlock site when opening extent was increased from 3% to 9% (Table 1).

3.1.4. Group (patch) selection and clearcutting

Group selection with area control resulted in higher average gap species abundance across the range of treatments compared to combined group/ single-tree selection (Table 2), primarily because of the higher group extent (11–15% vs. 3–9%). Gap species comprised 21–36% of stand basal area at the hardwood site (compared to 11% initially) and 52–69% of gap species at the hemlock site (compared to 22% initially). Increasing gap size resulted in higher abundance of yellow birch and white ash at one or both sites. Decreasing the rotation age from 135 to 100 years had little or no effect on gap-species abundance at the hardwood site but resulted in slight increases at the hemlock site.

Despite the relatively long 135-yr rotation, the 1 ha clearcuts on both sites had higher abundance of gap species than any of the group selection treatments with area control, including the 2000 m^2 patch cuts on a 100-yr rotation (Tables 1 and 2).

3.2. Demographic structure and spatial patterns

3.2.1. Untreated stands

After 300 years in untreated stands, gap saplings and poles that had regenerated in small treefall gaps made up about 20% of the aggregate exposed crown area of trees. Mature and large tree crowns were predicted to dominate the canopy and formed a fairly continuous matrix (Fig. 2b), comprising about 80% of the aggregate exposed crown area of trees (Table 3). Stem patterns for all trees and for 'mature + large only' were not statistically different from a random pattern based on all three spatial statistics F(r), G(r), and K(r).

Untreated stands at both sites met the criteria of steady-state, old-growth stands at the end of the simulation, with ≥50% of the stand basal area and aggregate exposed crown area in large trees, and a ratio of exposed crown area in large to mature trees of 1.7–1.8. Diameter distributions at both sites were rotated sigmoid in form on semilogarithmic axes (cf. Goff and West, 1975), with two abrupt changes in slope at about 16 and 68 cm DBH (Fig. 3). Q ratios decreased from about 2.9 in the 6 cm class to about 1.2 in the 32 cm class and then rose to 1.4–2.1 in classes larger than

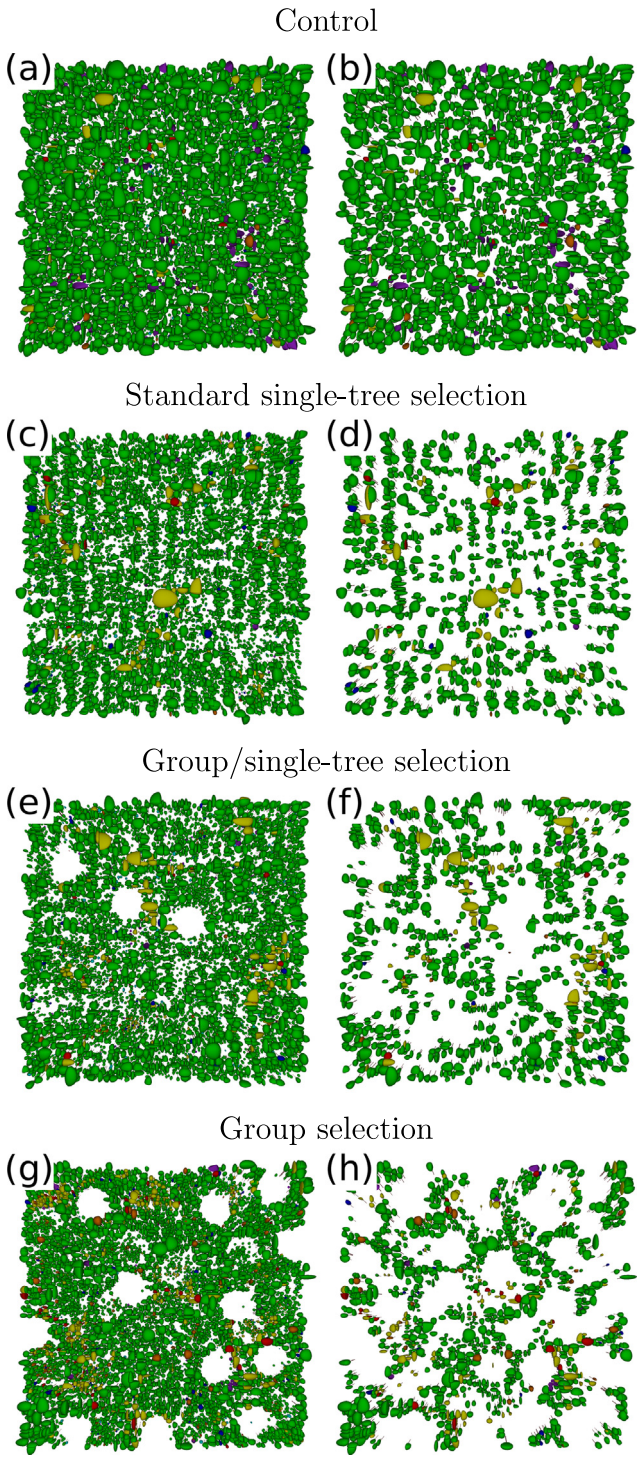

Fig. 2. Crown maps of selected treatments at the end of a 300 year simulation. Area shown is 9 ha. Panels a, c, e, g: all trees. Panels b, d, f, h: mature and large trees only (DBH > 26 cm). In group/single-tree selection (e, f), 800 m^2 openings occupied 3% of the stand area per cutting cycle. In group selection with area control (g, h), 800 m^2 openings occupied 11.1% of the stand area per cutting cycle ('implicit rotation age' of 135 years). Green: sugar maple; Purple: hemlock; Yellow: yellow birch; Red: red maple; Orange: white ash; Dark blue: basswood; Light blue: eastern hop-hornbeam.

62 cm DBH. The predicted percent aggregate exposed crown area in mature (30%) and large trees (50%) agrees well with mean field observations from 14 old-growth, all-aged northern hardwood stands (29% and 50%, respectively; Lorimer and Frelich, 1998 and unpublished data).

Single Weibull diameter distribution models in year 300 had R^2 of 0.73 and double Weibull models had R^2 of 0.98, with double Weibull models having less than half the RMSE of single Weibull models. The double Weibull also had better fit statistics and residual patterns than the negative exponential distribution, although both fitted distributions failed to capture the steep drop-off in the number of trees between 85 and 95 cm DBH. Based on 10 replicates of 1000 1-ha subsamples of the 9 ha tract, the Kolmogorov-Smirnov test indicated that 100% of the negative exponential fits were significantly different ($p < 0.05$) from the simulated diameter distribution, indicating a poor fit. In contrast, 63% of the double Weibull fits were not significantly different from the simulated distribution.

3.2.2. Single-tree selection and combined group/single-tree treatments

The standard and heavy single-tree selection treatments had 17–21% of the aggregate exposed crown area in large trees (compared to 50% in old growth) and a substantially higher fraction in sapling, pole, and mature trees. Because the selection stands had more ECA in saplings and poles and less in mature trees compared to untreated mature stands, the standard and heavy selection stands met the criteria of 'mature-sapling mosaics.' The industrial selection stands had lower basal area with no ECA in large trees, and were classified as pole stands (Table 3).

Mature and large trees in the standard selection treatments were predicted to comprise 57–62% of the aggregate exposed crown area, compared to 75–90% in the initial mature stands and 78–80% in the all-aged, old growth control treatment. Compared to the untreated control, the mature forest matrix was fragmented at a small scale, with mature and large trees occurring in small, isolated clusters of typically 1–10 trees (Fig. 2d). Under standard single-tree selection, the spatial pattern for trees of all size classes showed no difference from the control treatment based on K(r) or F(r), but G(r) showed significant clustering at short distances of <5 m. However, for mature and large trees only, both K(r) and F(r) detected significant clustering across a range of scales of <10 m (Fig. 5a and c).

Diameter distributions under single-tree selection were regulated to follow a negative exponential form with constant slope for trees above 12 cm in diameter, but the slope of the distribution was much steeper for trees < 12 cm DBH in the unregulated portion of the curve (Fig. 3b). For all trees > 2 cm, a double Weibull model was a better fit in terms of RMSE than a single Weibull with a negative exponential distribution (shape parameter of 1.0). For trees > 12 cm, a straight-line pattern on a semi-log plot was observed for all selection stands ($R^{2>}0.97$, $p < 0.001$), in conformity with the marking guidelines. The diameter distribution remained stable over the 300-yr period with only minor fluctuations (Fig. 4).

The combined group/single-tree selection treatments were cut to the same residual diameter distribution as standard single-tree selection, and so aggregate ECA among size categories typically was similar across these treatments. Group/single-tree treatments were classified as mature-sapling mosaics under most conditions of percent group extent. However, treatments removing 9% of the stand area in openings were classified as pole stands, with poles occupying significantly more growing space than in standard selection (21–31% of the aggregate ECA vs 16–18% for standard selection) and large trees occupying less (5–13% vs. 18–21%).

Based on all three spatial metrics, none of the combined group/single-tree selection treatments had stem spatial patterns different from standard single-tree selection, either overall or within any tree size category.

Although diameter distributions in combined group/single-tree selection with 9% group extent did not generally differ from standard single-tree selection, larger opening sizes had less steeply

Table 3
Effects of combined group/ single-tree selection and reference treatments on stand structure and degree of fragmentation of the mature forest matrix in simulation year 300.

Treatment	Sapling	Pole	Mature	Large		Mat + Lg cover	Stand stage*
				46–66 cm	66 + cm		
	Percent of aggregate exposed crown area						
	Northern hardwood stand						
Initial Conditions	2.7	6.9	44.0	34.9	11.5	90.4	Mature
No treatment	11.0*h*†	9.5*e*	29.8*e*	33.9*a*	15.8*a*	79.5	Old Gr.
Standard STS	25.2*de*	17.5*d*	39.5*bc*	17.8*b*	0.0*b*	57.3	MSM
Heavy STS	30.9*b*	16.0*d*	35.8*d*	17.3*b*	0.0*b*	53.1	MSM
Industrial STS	26.2*cd*	39.0*a*	34.8*d*	0.0*f*	0.0*b*	34.8	Pole
GS + STS 200 m^2, 3% extent	25.1*de*	17.8*d*	40.2*abc*	16.9*b*	0.0*b*	57.1	MSM
GS + STS 800 m^2, 3% extent	25.9*cd*	17.7*d*	38.9*c*	17.5*b*	0.0*b*	56.4	MSM
GS + STS 2000 m^2, 3% extent	25.4*de*	17.9*d*	38.9*c*	17.7*b*	0.0*b*	56.6	MSM
GS + STS 200 m^2, 9% extent	22.5*f*	30.4*b*	40.9*ab*	6.2*e*	0.0*b*	47.1	Pole
GS + STS 800 m^2, 9% extent	24.8*e*	29.5*b*	34.9*d*	10.8*d*	0.0*b*	45.7	Pole
GS + STS 2000 m^2, 9% extent	26.7*c*	20.9*c*	39.3*bc*	13.2*c*	0.0*b*	52.5	Pole
Clearcutting	19.3*g*	38.3*a*	41.8*a*	0.6*f*	0.0*b*	42.4	Pole
	Hemlock-hardwood stand						
Initial Conditions	6.6	18.4	50.7	20.4	3.9	75.0	Mature
No treatment	11.5*i*	10.9*h*	27.8*f*	29.1*a*	20.7*a*	77.6	Old Gr.
Standard STS	22.5*d*	15.7*f*	40.6*c*	21.2*b*	0.0*b*	61.8	MSM
Heavy STS	27.9*b*	13.7*g*	37.5*d*	21.0*b*	0.0*b*	58.5	MSM
Industrial STS	25.3*c*	39.3*a*	35.5*e*	0.0*h*	0.0*b*	35.5	Pole
GS + STS 200 m^2, 3% extent	22.0*de*	15.9*f*	42.8*ab*	19.3*c*	0.0*b*	62.1	MSM
GS + STS 800 m^2, 3% extent	22.1*d*	15.8*f*	41.4*bc*	20.7*bc*	0.0*b*	62.1	MSM
GS + STS 2000 m^2, 3% extent	22.3*d*	15.9*f*	41.3*bc*	20.5*bc*	0.0*b*	61.8	MSM
GS + STS 200 m^2, 9% extent	20.5*g*	30.6*b*	44.1*a*	4.9*f*	0.0*b*	49.0	Pole
GS + STS 800 m^2, 9% extent	20.9*fg*	29.1*c*	41.3*bc*	8.7*e*	0.0*b*	50.0	Pole
GS + STS 2000 m^2, 9% extent	21.3*ef*	27.2*d*	41.2c	10.3d	0.0*b*	51.5	Pole
Clearcutting	16.2*h*	39.4*a*	44.1a	0.3*h*	0.0*b*	44.4	Pole

Diameter categories: sapling: 0–12 cm DBH, pole: 12–26 cm, mature: 26–46 cm, large: 46–66 cm, very large: 66+ cm

* Developmental stages evaluated over the entire 9 ha area. For clearcutting treatments, the reported stage is effectively an average over all compartments. Notation: MSM: Mature-sapling mosaic; Old Gr.: old growth.

† Means followed by different letters within a column were significantly different (Tukey-Kramer tests, $p < 0.05$). Letters are in order such that 'a' represents the group with the highest mean.

descending diameter distributions. Single Weibull shape parameters decreased by ~10% as opening size increased from 200 to 2000 m^2. Mean diameters in this treatment were slightly higher than with standard selection; scale parameters increased by ~15% as opening sizes increased from 200 to 2000 m^2. Double Weibull models had lower RMSE than single Weibull models, but above 12 cm DBH, straight line fits on semilog scales at year 300 were very good ($p < 0.001$), suggesting structural sustainability.

3.2.3. Group (patch) selection and clearcutting

These treatments had the lowest proportions of ECA in large trees, ranging from 0.2 to 10%, with the lower values in treatments with smaller openings and shorter rotations. At the rotation ages and 'implicit rotations' investigated here (100–135 years), all group selection treatments with area control, as well as clearcut stands, were classified as pole stands when evaluated across the entire 9 ha stand area. The reason was that all patches or compartments cut in the previous 60 years were still dominated by saplings or poles, and only the older patches qualified as mature forest. Mature and large tree crowns occupied as little as 28% of the aggregate ECA in the 200 m^2 group selection treatments (Table 4). In all the group selection treatments with area control, contiguous 'rings' of mature trees were broken up by group openings, leading to a residual mature forest matrix in a distinctive 'chain-link fence' pattern (Fig. 2h). Under most conditions of opening sizes, group extent, and size class combinations, the K(r) statistic indicated significant clustering of trees across a wide range of distances (4 to >20 m) when compared to single-tree selection (Fig. 5f). The F(r) and G(r) statistics were not as consistent in detecting departures from randomness, but clustering was often detected for size class combinations that included sapling and pole trees. The F(r) statistic detected clustering in mature and large trees, but only at the 15% group extent.

Diameter distributions under group selection with area control consistently had descending monotonic forms for all group sizes and extents (Fig. 3). Curves remained stable over time with no evidence of substantial fluctuations (Fig. 4). However, compared to single-tree selection, there were more trees per ha in the 15–30 cm classes and fewer in the 45–60 cm classes, even for the lower 11% group extent. The additional recruitment delays imposed in forest patches with higher pole or mature basal area (see Appendix A) did not cause further departures from the negative exponential form, even in the 200 m^2 openings that are most susceptible to lateral closure.

Both group size and extent, however, did have some effect on tree densities, slope of the curve, and maximum tree diameters. As group size increased from 200 to 2000 m^2, maximum tree size increased and the predicted curve shape shifted more in the direction of a negative exponential curve (single Weibull scale parameters increased from 12 to 15 cm and shape parameters decreased from 1.4 to 1.2). Decreasing the group extent from 15% to 11% had similar effects on the distribution (Halpin, 2009). Group selection with area control was the only treatment in this study, other than the untreated control, in which trees >66 cm DBH were present, although the frequency was very low (1% or less of aggregate exposed crown area; Table 4).

Diameter distributions of clearcut stands (composite of the nine 1-ha compartments) were generally descending monotonic in form, although the unthinned even-aged stands had a slight peak in the 28 cm class (Fig. 3a). As in group selection treatments with area control, clearcutting produced stands with more trees in the 15–30 cm classes and fewer trees in the 45–60 cm classes when compared with single-tree selection.

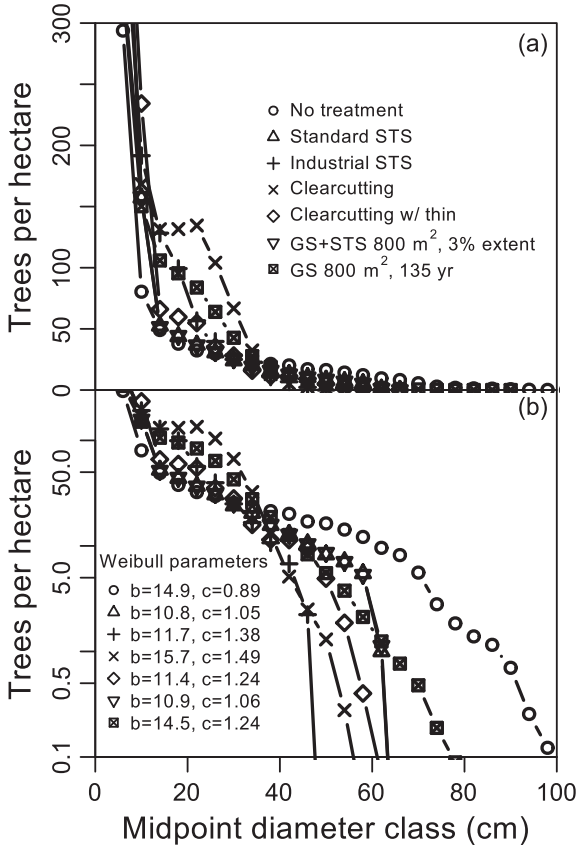

Fig. 3. Final diameter distributions for selected treatments. Plotted curves are the average of 10 replications. Maximum likelihood estimates for a Weibull distribution fit to each replication were performed at year 300; parameters shown are averages of the 10 estimates. (a): arithmetic scale; (b): semi-logarithmic scale.

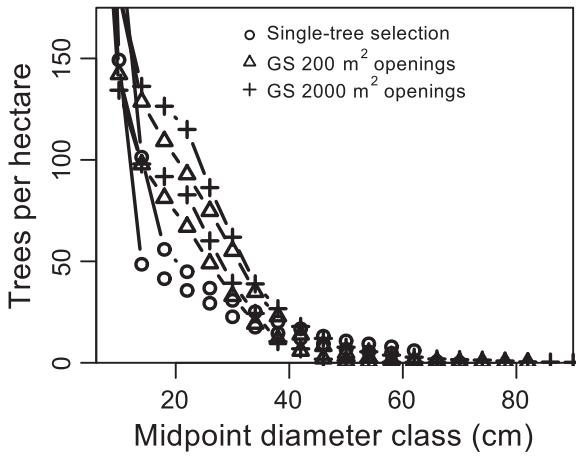

Fig. 4. Range of variation in diameter distributions for selected treatments across 10 replicates over the last 150 years of simulation. Envelopes denote the maximum and minimum number of trees observed in each size class among all replicates.

4. Discussion

4.1. Responses of gap-dependent and gap-sensitive species to group creation

Over the long time horizon of this study, group selection resulted in greater predicted regeneration of gap-dependent species than single-tree selection, though differences were often small and varied across sites, species, and styles of group selection (e.g., patch cutting with area control vs. group/single-tree combination). These results are consistent with several shorter-term field studies of group selection in Great Lakes northern hardwoods demonstrating minimal or modest increases in natural regeneration of the less shade- tolerant species (Shields et al., 2007; Bolton and D'Amato, 2011; Kern et al., 2013; D'Amato et al., 2015). It is widely recognized that tall and abundant advance regeneration of shade-tolerant species can obstruct the regeneration of midtolerant and intolerant species in forest openings (e.g., Brokaw and Busing, 2000; Webb and Scanga, 2001). But the CANOPY model predicts that even with removal of all advance regeneration > 2 cm DBH in group openings, shade-tolerant species are still likely to dominate heavily, especially on the more productive habitats. This prediction is in line with results of a recent field experiment by Gauthier et al. (2016).

However, local habitat variation had a strong influence on the efficacy of group selection in fostering greater abundance of these species in both the underlying calibration data and in the simulations. Group selection benefitted gap-dependent species substantially on the less fertile habitat type (*Acer-Tsuga-Maianthemum* or ATM) but had minimal effects on one of the more fertile habitats (*Acer-Tsuga-Dryopteris* or ATD). Comparisons of prior field studies also suggest evidence of strong habitat-related variation in abundance of gap-dependent species. As in the simulations, group selection openings with up to 40% relative density of yellow birch have been observed on ATM habitat even without intentional scarification (Webster and Lorimer, 2005). On ATD habitat, in contrast, yellow birch comprised <6% even when yellow birch seed trees were left in the openings (Shields et al., 2007; see also Kern et al., 2013). Low abundance of yellow birch is also typical of old-growth stands on ATD habitat affected only by natural disturbances (mostly windthrow and drought-related mortality), despite a wide range in opening size and an abundance of suitable seedbeds such as mossy logs and exposed soil on tip-up mounds. Among 49 randomly-selected stands on ATD habitat in primary northern hardwood forest reserves of upper Michigan, 77% had less than 15% yellow birch basal area. Only 12% had more than 20% yellow birch, and all of these occurred in only one of the three landscape reserves (Sylvania Wilderness; data base of Frelich and Lorimer, 1991). The fact that even the old-growth stands have only modest levels of yellow birch suggests that yellow birch abundance was strongly limited on some habitats long before the recent increases in deer populations.

Landscape-level or regional studies of species diversity in temperate forest have often reported maximum species richness on moderately fertile sites and decreased richness on more productive sites (Mittelbach et al., 2001; Dupré et al., 2002; Schuster and Diekmann, 2005). Similar trends are evident in our calibration data set; the moderately fertile ATM habitat typically has higher tree-species diversity (richness and equitability) than the two more productive habitats (see also Kotar et al., 2002). However, for northern hardwoods in this region, the lowest diversity is typically not on the richest sites (*Acer-Osmorhiza-Caulophyllum* or AOCa habitat) but on the somewhat less productive ATD habitat type. These ATD habitats are above-average sites but often located on outwash or ice-contact features with well-drained, sandy loam soils. A single species (sugar maple) strongly dominates all foliar strata (Fassnacht and Gower, 1998; Kotar et al., 2002). ATD habitat typically has low abundance of the more nutrient-demanding (and less shade-tolerant) species like white ash or basswood, but it also has lower abundance of the less nutrient-demanding species like yellow birch, red maple, white pine (*Pinus strobus* L.) and hemlock (Kotar et al., 2002; Kern et al., 2013).

While causes of the species richness-site productivity trend have been debated (cf. Abrams, 1995; Waide et al., 1999;

Table 4
Effects of opening size and group extent* on stand structure and degree of fragmentation under group selection with area control in simulation year 300.

Opening size (m^2)	Opening extent (%)	Sapling	Pole	Mature	Large		Mat + Lg Cover	Stand Stage
					46–66 cm	66 + cm		
		Percent of aggregate exposed crown area						
		Northern hardwood stand						
Initial Conditions		2.7	6.9	44.0	34.9	11.5	90.4	Mature
200	15.0	29.3*a*†	41.1*a*	29.0*h*	0.5*g*	0.0*e*	29.5	Pole
200	12.5	25.7*b*	36.3*cd*	35.9*ef*	2.1*f*	0.1*de*	38.1	Pole
200	11.1	23.9*c*	34.0*e*	38.7*bcd*	3.4*e*	0.1*de*	42.2	Pole
400	15.0	26.2*b*	38.8*b*	33.4*g*	1.6*f*	0.0*e*	35.0	Pole
400	12.5	23.1*c*	34.8*de*	37.7*cde*	4.1*de*	0.2*cde*	42.0	Pole
400	11.1	21.3*d*	31.4*g*	40.8*a*	6.1*b*	0.4*cde*	47.3	Pole
800	15.0	23.7*c*	36.9*c*	35.6*f*	3.6*e*	0.3*cde*	39.5	Pole
800	12.5	21.3*d*	33.2*ef*	39.5*abc*	5.7*bc*	0.5*bcd*	45.7	Pole
800	11.1	19.4*e*	30.3*g*	40.7*a*	8.5*a*	1.2*a*	50.4	Pole
2000	15.0	21.5*d*	36.0*cd*	37.4*def*	4.7*cd*	0.5*bc*	42.6	Pole
2000	12.5	19.3*e*	31.8*fg*	39.8*ab*	8.2*a*	0.8*ab*	48.8	Pole
2000	11.1	19.2*e*	30.8*g*	39.7*ab*	9.2*a*	1.1*a*	50.0	Pole
		Hemlock-hardwood stand						
Initial Conditions		6.6	18.4	50.7	20.4	3.9	75.0	Mature
200	15.0	29.3*a*	42.6*a*	27.9*g*	0.2*f*	0.0*d*	28.1	Pole
200	12.5	25.1*b*	37.8*cd*	36.1*e*	1.0*ef*	0.0*d*	37.1	Pole
200	11.1	23.3*c*	35.5*ef*	38.9*d*	2.4*d*	0.0*d*	41.3	Pole
400	15.0	25.4*b*	40.6*b*	33.2*f*	0.8*f*	0.0*d*	34.0	Pole
400	12.5	22.2*d*	36.3*ef*	39.4*cd*	2.1*d*	0.1*d*	41.6	Pole
400	11.1	20.6*e*	33.0*g*	42.4*b*	3.9*c*	0.1*d*	46.4	Pole
800	15.0	22.8*cd*	39.0*c*	36.4*e*	1.8*de*	0.1*d*	38.3	Pole
800	12.5	20.5*e*	35.2*f*	40.5*c*	3.8*c*	0.1*d*	44.4	Pole
800	11.1	18.8*f*	30.8*h*	44.1*a*	5.8*b*	0.5*bc*	50.4	Pole
2000	15.0	20.0*e*	36.7*de*	39.5*cd*	3.7*c*	0.2*cd*	43.4	Pole
2000	12.5	17.9*g*	32.0*gh*	42.9*ab*	6.4*ab*	0.9*ab*	50.2	Pole
2000	11.1	17.5*g*	31.4*h*	43.2*ab*	6.9*a*	1.0a	51.1	Pole

* 'Implicit rotation ages' for 15%, 12.5%, and 11.1% removal over a 15 year cutting cycle are 100, 120, and 135 years.
† Means followed by different letters within a column were significantly different (Tukey-Kramer tests, $p < 0.05$). Letters are in order such that 'a' represents the group with the highest mean.

Mittelbach et al., 2001), these relationships appear to impose inherent restrictions on the degree to which large openings can stimulate species diversity and midtolerant species abundance on some habitats. Under a prolonged regime of single-tree gap formation, all three of these northern hardwood habitat types become strongly dominated by the one or two most shade-tolerant species (Tubbs, 1977a; Kotar et al., 2002; Neuendorff et al., 2007; Gronewold et al., 2010). The potential for modifying these trends with group selection is more substantial for the less fertile ATM habitat, and probably also for the richest AOCa sites if seed sources of basswood and white ash are present (Guldin and Lorimer, 1985). It is also widely recognized that soil scarification can increase the proportion of gap-dependent species (e.g., Godman and Krefting, 1960; Tubbs, 1969; Willis et al., 2015; Gauthier et al., 2016).

The shade-tolerant hemlock was predicted to remain at near-current levels in untreated stands but to show very steep declines under all the uneven-aged treatments after the first 40 years. This occurred regardless of treatment design and even though all simulations were based on recruitment data from sites with low levels of deer browsing. An 'ecological forestry' variant of single-tree selection with higher residual basal area and larger maximum DBH did result in higher predicted hemlock abundance than reported here, but only if half the allowable cut of hemlock was reserved from harvesting. Even in this treatment, hemlock declined moderately compared to no cutting (Hanson et al., 2012).

Hemlock is a small-seeded species with short dispersal distances (Ribbens et al., 1994) and is known in this region to recruit poorly in large openings with unscarified soil (McClure and Lee, 1993; Webster and Lorimer, 2002; Walters et al., 2016). The level of decline predicted after single-tree selection, however, was surprising. While single-tree and group selection maintained stand-wide stocking above the critical 80% threshold for fostering good hemlock regeneration (see Appendix A), model output showed that stocking was often far lower than that at the plot level. Neuendorff et al. (2007) found that single-tree selection did not result in hemlock decline over four decades on a site in northern Michigan, and this was also generally true for CANOPY predictions in the first 40 years. The predicted decline appears to reflect a longer-term negative feedback loop between reduced recruitment under low stocking levels and subsequent seed-source limitations, and it may not be pronounced until after more than one generation of this long-lived species. Some states in the region already have an unofficial moratorium on cutting hemlock on public lands because of regeneration difficulties. The results here suggest that the caution may be warranted and that population trends of hemlock should be monitored closely. Hemlock appears to be able to maintain or increase its prominence in untreated stands under current conditions, although future spread of the exotic hemlock woolly adelgid *(Adelges tsugae)* into this region is likely to have devastating effects (Orwig et al., 2008).

4.2. Does group selection cause fragmentation of the mature forest matrix?

While group selection caused only modest reductions in the fraction of the stand occupied by mature (medium-sized) trees relative to the initial conditions, it caused major decreases in the fraction occupied by large trees. A modest component of large trees was maintained in the combined group/single-tree treatments as specified by the residual diameter distribution. But they were mostly eliminated in group selection with area control because the implicit rotation ages of 100–135 years were too short to produce many large trees. The occasional trees >66 cm DBH in these treatments after 300 years, in contrast to the group/single tree

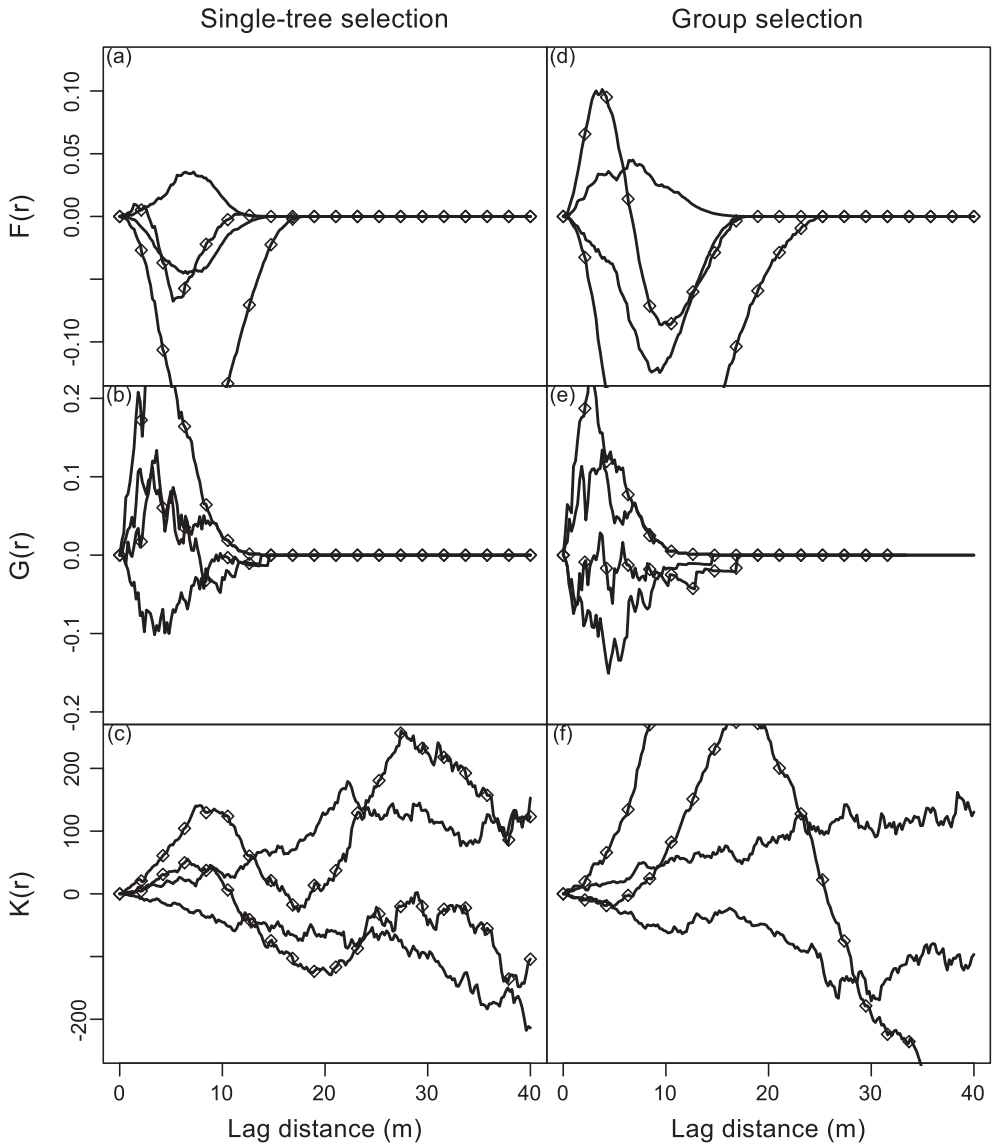

Fig. 5. Spatial metrics for stem patterns of mature and larger trees. Panels a–c: Comparison of standard single-tree selection (envelope with diamond symbols) with complete spatial randomization (envelope without symbols; y = 0 on the graph corresponds to the average value for CSR). Panels d–f: Comparison of group selection (envelope with diamond symbols) with single-tree selection (envelope without symbols; y = 0 on the graph corresponds to the average value for single-tree selection). Envelopes give range of variation across 10 replications. Where ranges overlap, there is no statistically significant difference. For G(r) and K(r), positive differences represent clustering and negative differences represent repulsion. For F(r), the interpretation is reversed (Kalunzy et al., 1998).

combinations, was due to the lack of single-tree cutting between the openings in the group/patch selection treatments. This allowed occasional large trees to go unharvested if they were not located within the boundaries of a new discrete circular patch scheduled for harvesting.

Consequently, the model predicted that all of these group selection designs would cause substantial small-scale fragmentation of the mature/large tree matrix compared to the initial mature stands and untreated controls. Under group selection with area control (the most extreme selection treatment), mature and large trees usually comprised less than half of the aggregate exposed crown area, compared to ~80% in the initial conditions and the all-aged, untreated controls. The all-aged, old-growth stands also contained sapling and pole groups from recurrent natural treefall gaps, but the openings were small and scattered, resulting in a fairly continuous mature forest matrix (Fig. 2b). While there was no prohibition against cutting older buffer strips in the group/patch selection treatment, mature and large trees were dispersed in irregular clusters or loosely connected 'rings' representing buffer strips from the two most recent cutting cycles. These rings are not fixed in place but shift throughout the stand as new patches are harvested, and so they do not reduce the area available for harvest in each cutting cycle. Loosening of restrictions against cutting buffer strips could break up this pattern, but as demonstrated in the single-tree and combined group/single tree treatments, this would merely result in even greater isolation of mature and large trees. The connectivity of the 'rings' could possibly aid foraging of mature-forest animal species and the dispersal or survival of arboreal lichens and bryophytes (Sillett et al., 2000; Root et al., 2007; Miller et al., 2007; Bigelow and Parks, 2010).

Potential effects of these spatial patterns on biological diversity will require further study and will likely vary among different organisms. Some neotropical migrant songbirds that prefer mature forest habitat, for example, appear to make little distinction between pole and mature forests when selecting breeding sites (Welsh and Healy, 1993; Howe and Mossman, 1995). Field studies

have suggested that a number of neotropical migrant species preferring mature forest habitat may be as abundant or more abundant in group selection stands than in undisturbed mature forests (Costello et al., 2000; Moorman and Guynn, 2001; Campbell et al., 2007). Thus, they may not perceive conventional group selection stands as highly fragmented. A replicated field experiment with group selection in northern hardwoods (9% of stand area in group openings) has not yet indicated significant effects on nesting behavior of flying squirrel populations (*Glaucomys volans*) in the first two years after treatment (Steinhoff et al., 2012). In small group selection openings with adequate coarse woody debris, salamanders may be little affected (McKenny et al., 2006). But in larger group openings, salamanders have experienced drastic population declines that may require 60 years for recovery (Homyack and Haas, 2009; Hocking et al., 2013). Large gap creation can also cause substantial declines in some lichen and bryophyte species (Rheault et al., 2003; Miller et al., 2007)

In this study, it was never the case that the stand became so fragmented by group selection as to be impossible for the simulator to locate and mark suitable patches of mature trees (unlike the field-based impressions of Roach, 1974). Also, the search algorithm could always locate groups in a way that satisfied other placement constraints involving buffer strips and non-overlap with groups from the previous two cutting cycles. Aesthetically, however, forests managed by group selection do not resemble natural mature stands very closely, despite the common expectation that group selection retains a largely mature forest canopy with only scattered openings. This is because after many cutting cycles, sapling and poles usually occupied 40–70% of the canopy compared to <25% in the initial mature stands and in the all-aged, old-growth controls, supporting other concerns raised by Roach (1974). Mature and large tree crowns still made up 40–60% of the stands under most treatments. Nevertheless, all group selection treatments with area control, and all group/ single-tree selection treatments with at least 9% group extent per cutting cycle, were classified structurally as pole stands rather than mature forest or mature-sapling mosaics. When evaluated across the entire 9 ha stand, size distributions under these conditions differed little from stands managed by industrial uneven-aged management, except for a modest representation of large trees in the combined group/ single-tree treatments.

4.3. Does small group selection cause irregular structure?

Although small canopy openings surrounded by vigorous pole and mature trees can close rather quickly and impede sapling recruitment (Hibbs, 1982; Cole and Lorimer, 2005), the model did not predict that small-group selection would produce unimodal or 'hybrid' unimodal/descending monotonic diameter distributions (*sensu* Roach, 1974). Residual distributions in these group selection treatments had more poles and fewer large trees than single-tree selection, but they were all steeply descending monotonic curves that maintained this shape with minimal fluctuation over many cutting cycles. While the stable negative exponential form in the combined group/ single-tree treatments partly reflected the periodic removal of surplus trees above the target distribution, there was no pre-specified or regulated residual size distribution in group selection with area control. Possibly the impact of rapid lateral gap closure in small-group selection was minimized by the frequent creation of new openings with new sapling recruitment. Leak (1999) did not report problems with irregular diameter distributions or fluctuating yields with patch cuts 3000–4000 m^2 in size over a span of more than 60 years. In the current study, similar stability was predicted for smaller group sizes as well. Nevertheless, group selection stands with ≥9% group extent per cutting cycle failed to meet the structural criteria of mature forest or mature-sapling mosaics. Trials with the smallest openings (200 m^2) also had the largest proportion of pole trees and greatest departures from a negative exponential distribution (higher Weibull shape parameters). It would be advisable to examine and monitor these processes more closely in long-term group selection field experiments (e.g., Kern et al., 2013; Fassnacht et al., 2015).

5. Conclusions

Results of this study suggest likely tradeoffs between the objectives of increasing midtolerant species composition and that of minimizing small-scale forest fragmentation under group selection regimes. The advisability of any treatment design may be heavily constrained by inherent habitat limitations. In cases where increased tree species diversity and minimal fragmentation are both important goals, combined group/ single-tree selection with a small group extent (e.g., 1–3% per cutting cycle) may be one of the better alternatives in this forest type and region. On some of the more fertile sites such as ATD, an aggressive approach to group selection with large openings and greater group extent appears to substantially increase fragmentation of the mature forest matrix without markedly increasing midtolerant species proportions. For example, yellow birch under those conditions is only expected to increase from 6% to 12% of the stand basal area, and the comparable increase in white ash is likely to be prevented by eradication of ash species by the exotic emerald ash borer (*Agrilus planipennis*). Group selection with 9% or greater opening extent per cutting cycle may also thwart aesthetic objectives of group selection, potentially converting mature stands to pole stands that differ little in structure from those under industrial uneven-aged management. On moderately fertile sites such as ATM, a substantial proportion of midtolerant species (e.g., >20% yellow birch) may be attainable even under conservative treatments with small 800 m^2 openings and only 3% group extent per cutting cycle (Table 1).

Soil scarification or retention of legacy trees capable of creating uprooted mounds of soil and mossy logs may further increase abundance of midtolerant species (Shields et al., 2007; Bolton and D'Amato, 2011). Even with conservative group selection designs, however, special measures may be needed to protect populations of hemlock and other species sensitive to creation of sizable openings. Novel environmental stressors such as invasive species, high deer populations, and climate change will likely create even greater obstacles. Long-term experiments in this region and forest type (e.g., Kern et al., 2013; Fassnacht et al., 2015; Walters et al., 2016) recently have been established for operational field tests of some of these questions. Long-term experiments in other forest types (e.g., Treiman et al., 2005) will help determine the degree to which conclusions in this study may apply over a broader range of conditions.

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Appendix A. Additional details on sapling and sprout recruitment in the CANOPY model

The most recent version of CANOPY (v. 3) has a recruitment option in which further delays in sapling recruitment can occur in addition to delays already imposed by the competition metric. Based on a significant negative correlation in the calibration data between sapling density and percent basal area of mature trees (Halpin and Lorimer, 2016a), this additional delay is activated whenever the surrounding 0.25 ha patch has ≥20% of the basal area in pole trees (10–25 cm DBH) or ≥35% in mature trees (26–45 cm DBH). A sensitivity analysis was conducted to determine if this additional 'stem exclusion' mechanism would alter the predicted diameter distributions. As reported in Section 3.2.3, this additional stem exclusion mechanism did not cause diameter distributions to depart from a negative exponential form or fluctuate over time.

The relationship between recruitment of hemlock saplings and forest composition and structure in the calibration data set has much scatter, and so there is some ambiguity concerning the underlying functional form. The equation form with the highest overall fit statistics (R^2 = 0.59) shows a continually increasing trend of hemlock relative abundance as stocking level and relative basal area of hemlock increase (Hanson et al., 2011). The underlying scatter diagram, however, seems more consistent with an asymptotic model because hemlock recruitment does not increase significantly (P = 0.30–0.47) above a level of 80% stocking or 60% relative basal area of hemlock. In this paper, an alternative model used categorical variables to reflect the apparent asymptote beyond those threshold levels:

$$P_{Hem} = 1/(1 + \exp(-x)) \quad (1)$$

$$x = -4.725 + 1.021\ S_{80} + 4.105\ RB_{Hem60} + (0.759 * (1 - RB_{Hem60}) * \ln RB_{Hem})$$

Where

P_{Hem} = the probability that a new sapling recruit is a hemlock
x = the logit or exponent of the logistic regression equation
S_{80} = '1' if stocking is > 80% and '0' otherwise
RB_{Hem} = relative basal area of hemlock (%).
RB_{Hem60} = '1' if percent hemlock basal area is >60% and '0' otherwise
R^2 is only slightly lower (0.55) in this model, and habitat type was not a significant variable.

Although sprouts are well represented in the calibration data set, CANOPY does not model stump sprouting as a distinct process due to insufficient data on sprout frequency and long-term survival. Effects of mineral soil seedbeds from intentional soil scarification treatments are also not considered because such treatments were not performed in stands in the calibration data set. Any mineral soil seedbeds resulted only from incidental scuffing of the ground during harvests or by uprooting of mature trees from natural or harvest-induced mortality.

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