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REGENERATION PATTERNS IN SILVICULTURAL OPENINGS OF WESTERN GREAT LAKES NORTHERN HARDWOOD FORESTS 15-24 YEARS POST-HARVEST

Matthew S. VanderMolen
Michigan Technological University, matthewv@mtu.edu

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Recommended Citation

VanderMolen, Matthew S., "REGENERATION PATTERNS IN SILVICULTURAL OPENINGS OF WESTERN GREAT LAKES NORTHERN HARDWOOD FORESTS 15-24 YEARS POST-HARVEST", Open Access Master's Thesis, Michigan Technological University, 2021.
<https://doi.org/10.37099/mtu.dc.etdr/1164>

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REGENERATION PATTERNS IN SILVICULTURAL OPENINGS OF WESTERN
GREAT LAKES NORTHERN HARDWOOD FORESTS 15-24 YEARS POST-
HARVEST

By

Matthew S. VanderMolen

A THESIS

Submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

In Forest Ecology and Management

MICHIGAN TECHNOLOGICAL UNIVERSITY

2021

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This thesis has been approved in partial fulfillment of the requirements for the Degree of
MASTER OF SCIENCE in Forest Ecology and Management.

College of Forest Resources and Environmental Science

Thesis Advisor:	<i>Christopher Webster</i>
Committee Member:	<i>Yvette Dickinson</i>
Committee Member:	<i>Christel Kern</i>
College Dean:	<i>Andrew Storer</i>

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Author Contribution Statement

The chapters within this thesis include work from multi-authored, peer-reviewed journal articles in various stages of submission and review.

Chapter 2, Influence of deer herbivory on regeneration dynamics in experimental gaps, 18 years post-harvest: in preparation for submission to the peer-reviewed journal *Forest Ecology and Management*. Christopher Webster and Matthew S. VanderMolen conceived the study. Study design by C. Webster. Field work, data analysis, and original manuscript preparation performed by M.S. VanderMolen. Input and edits for manuscript provided by C. Webster.

Chapter 3, Spatial patterning of low-density tree regeneration in experimental canopy gaps 15-24 years post-harvest: in preparation for submission to the peer-reviewed journal *Forest Ecology and Management*. Samuel Knapp, Christopher Webster, and Matthew S. VanderMolen conceived the study. Study design by C. Webster and Christel Kern. Field work completed by S. Knapp. Data analysis and original manuscript preparation performed by M.S. VanderMolen. Input and edits for manuscript provided by C. Webster, S. Knapp, C. Kern, and Yvette Dickinson.

Acknowledgements

I am exceptionally grateful for the frequent counsel and encouragement from my advisor, Christopher Webster, and current committee members, Yvette Dickinson and Christel Kern. Their support has been instrumental in the formation and completion of this work. Thank you to Samuel Knapp and Stefan Hupperts for their willingness to answer my numerous questions and for laying the foundational research groundwork I feel privileged to build upon. I am grateful to Claudia Bartlick for the opportunity to work at NHSEED for a summer season and the experience, enlightening conversations that helped guide this research work. I am fortunate to have an incredible cohort of graduate student peers and friends that have enriched this work with their experiences and enthusiasm. Thank you to the McIntire-Stennis Cooperative Forestry Program and Michigan Technological University's College of Forest Resources and Environmental Science for providing the funding for these projects. Thank you to my parents, siblings and extended family members who have supported and encouraged me along every part of my personal development and career path. Finally, an enormous and sincere thank you to my wife, Christine, for supporting me in this journey.

Abstract

In managed northern hardwood forests, successful forest regeneration can depend on the application of silvicultural methods tailored to stand-specific recruitment limitations. The objective of this research is to develop a deeper understanding of the factors that interfere with tree regeneration at three long-term, well-replicated experimental canopy gap studies in the upper Great Lakes region, USA. Chapter 2 examines regeneration at a hemlock canopy gap study 18 years post-harvest that included deer exclosures and a gradient of gap sizes. Chapter 3 investigates the spatial patterns of low-density regeneration along gradients of gap size and different levels of legacy-tree retention at two canopy gap studies, 15 and 24 years post-harvest. Our findings indicate that deer exclusion in larger gap sizes may promote the recruitment of browse sensitive species, such as yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock (*Tsuga canadensis* L.), into the tallest layers of the regeneration response (Chapter 2). Furthermore, spatial patterns of low-density regeneration did not follow resource gradients at the gap level and legacy-tree retention appeared to moderate the extent of low-density regeneration (Chapter 3). Collectively, these studies suggest that reducing herbivory and retaining legacy-trees where appropriate may help secure a timely and species-rich regeneration response.

1 Introduction

Natural forest regeneration faces many challenges at global and local scales. Climate change threatens to push many forest systems beyond critical thresholds of forest regeneration cycles (Mok et al. 2012; Anderson-Teixeira et al. 2013; Boucher et al. 2020). Massive anthropogenic land-use changes and major changes to forest management methods have altered forest structure and diminished species diversity (Riitters et al. 2000; Wade et al. 2003; Cyr et al. 2009; Schuler 2011). Furthermore, these changes coupled with other factors, such as invasive species introductions and overabundant herbivores, can catalyze precarious shifts of the disturbance regimes critical for maintaining forest resiliency and natural regeneration capabilities (Stromayer and Warren 1997; Moser et al. 2009; Johnstone et al. 2016; Shive et al. 2018). Many of these obstacles cooccur and are interrelated in complex relationships at multiple spatial scales (Messier et al. 2013). Therefore, to overcome these challenges, a context-specific understanding of the interplay of any limiting factors will aid in the application of successful forest management techniques (Webster et al. 2018).

In managed northern hardwood forests, the factors limiting regeneration can be numerous and difficult to tease apart. Exploitive timber harvests and subsequent high-intensity slash fires in the 1800s removed a significant portion of biological legacies and altered soils (Whitney 1987). The pre-settlement prominence of windthrow and fire disturbances have diminished under widespread use of single-tree selection and efforts in fire suppression (Kern et al. 2014; Hupperts et al. 2018). The result has been a homogenization of forest structure and diversity that favors shade-tolerant species like sugar maple (*Acer saccharum* Marsh.) and therefore an underrepresentation of many valuable and ecologically important tree species (Angers et al. 2005; Neuendorff et al. 2007). The shift in disturbance regime and the relative dominance of a few forest species can further diminish the seed sources and available microsites vital for the regeneration of less-abundant tree species (Caspersen and Saprundoff 2005; Willis et al. 2015). Moreover, overabundant deer populations can exert a strong filtering effect on tree regeneration, in some cases, only allowing the recruitment of less palatable or browse tolerant species (Sage et al. 2003; Rooney and Waller 2003; Walters et al. 2016). Often

coinciding with historically high rates of herbivory, competing vegetation may further interfere with seedling establishment by the formation of dense shrub layers (Royo and Carson 2006; Nuttle et al. 2011). Invasive forest pathogens and pests, such as beech bark disease complex (*Cryptococcus fagisuga* Lindinger – *Neonectria* spp. Woollenweber) and hemlock woolly adelgid (*Adelges tsugae*) further threaten tree species and can have reverberating ecological consequences (Case et al. 2017; Cale et al. 2017). At the landscape and stand scale, these factors may act simultaneously and/or generate complex feedback relationships (Millington et al. 2013; Henry et al. 2021). Therefore, to achieve recruitment goals in many northern hardwood forest stands, silvicultural approaches must be tailored to stand-specific suites of limiting factors.

Although silviculture in northern hardwood forests has been dominated by single-tree selection for many decades, there are promising modifications and alternatives. Gap-based silviculture is a method that models a medium-intensity windthrow disturbance by harvesting all trees within areas of varying sizes (Coates and Burton 1997; Hanson and Lorimer 2007). Often combined with single-tree selection, these canopy gaps are harvested in an attempt to create opportunities for less shade-tolerant species to recruit into the overstory (Leak et al. 2014). However, experimental results have been mixed and the modification of gap size alone may not be enough to recruit a diverse cohort of trees (Kern et al. 2017). Variable retention is another method seeking to restore material and biological legacies that may enhance the regeneration response (Franklin et al. 1997; Shields et al. 2007). The retention of dead wood to promote the availability of coarse woody debris can be instrumental in providing microsites for the regeneration of tree species such as yellow birch (*Betula alleghaniensis* Britton) (Fraver et al. 2002; Bolton and D'Amato 2011). Live tree (or green tree) retention can provide valuable seed sources for underrepresented species (Shields et al. 2007; Willis et al. 2016). However, although retention harvests can enhance regeneration in northern hardwoods, further modifications to the regeneration environment may be needed to satisfy recruitment goals for forest production and diversity (Poznanovic et al. 2013; D'Amato et al. 2015; Roberts et al. 2017; Knapp et al. 2019a).

Silvicultural strategies such as group selection and variable retention introduce spatial heterogeneity at the stand scale. In many forest systems, the spatial patterns of disturbance and remaining legacies exert a strong influence on the pattern of forest regeneration (Beckage and Clark 2003; Getzin et al. 2008). For example, in pine forests of northern Minnesota, Boyden et al. (2012) found spatial patterns of retained trees after harvest to predict spatial patterns of light and soil resource availability. These patterns of resource availability, such as light patterns in temperate old-growth forests, can be strong determinants for spatial distributions of understory vegetation and tree regeneration (Tinya and Ódor 2016). Moreover, canopy gaps introduce resource gradients of light and soil moisture at the gap scale and can pattern tree regeneration and growth (Denslow 1980; Gray and Spies 1996; Raymond et al. 2006; Poznanovic et al. 2014). Therefore, identifying spatial patterns of tree regeneration may shed light on the underlying drivers or limitations of the regeneration response.

This thesis includes research that aims to develop a deeper understanding of the factors that interfere with tree regeneration at long-term, well-replicated experimental canopy gap studies in northern hardwood forests. Chapter two describes regeneration dynamics at a hemlock northern-hardwood gap experiment 18 years post-harvest that included deer exclosures and a gradient of gap sizes. Chapter three includes results from a spatial analysis of low-density regeneration along gradients of gap size and different levels of legacy-tree retention at two experimental gap studies, 15 and 24 years post-harvest. The goal of this research is to further illuminate the limitations of forest regeneration in these systems and to enlighten the application of forest management actions that may enhance forest productivity and resiliency amid growing challenges.

2 Influence of deer herbivory on regeneration dynamics in experimental gaps, 18 years post-harvest

2.1 Introduction

The successful management of productive and resilient forest systems is often met with significant challenges. In northern hardwood forests, the critical loss of structural and species diversity is the result of complex combinations of local and landscape factors (Webster et al. 2018). The fundamental shift of disturbance regime during the last 200 years (Hupperts et al. 2018) followed by increases in deer herbivory (Rooney 2001) and invasive species introductions (Moser et al. 2009) have all contributed to a simplification of northern hardwood forests (Schulte et al. 2007; Neuendorff et al. 2007). In addition, the growing threat of climate change may further erode remnants of ecological memory in forest systems (Groffman et al. 2012; Johnstone et al. 2016). Therefore, the implementation of management strategies that can overcome these challenges is imperative to ensure a future with productive and resilient forests.

Land-use change has led to the loss of biological and material legacies vital for the maintenance of resilient forest systems in many regions. In the northern Lake States, prior to widespread European settlement, windthrow events were the primary disturbance type in mesic forests (Canham and Loucks 1984; Frelich and Lorimer 1991). These events created the structural, microsite, and resource heterogeneity requisite for the regeneration of species with contrasting suites of life-history traits (Peterson and Pickett 2000; Hanson and Lorimer 2007). Major land-use change started in the late nineteenth century with the ‘cutover’ which removed substantial proportions of several dominant tree species including eastern hemlock (*Tsuga canadensis* L.). Subsequent high-intensity slash fires degraded soil fertility and diminished the regeneration of selectively harvested species by the removal of advance regeneration, coarse woody debris, and seed banks (Whitney 1987). In recent decades, the widespread use of single-tree selection timber harvests has further homogenized forest structure and diversity, leading to stands dominated by the shade-tolerant sugar maple (*Acer saccharum* Marsh.) (Angers et al. 2005).

Alternative silvicultural methods have been predicted to help restore species diversity, yet experimental outcomes have not always satisfied regeneration objectives. Gap-based silviculture emulates intermediate natural disturbances like windthrow (Coates and Burton 1997; Raymond et al. 2018). Artificial canopy gap openings of various sizes can increase resource heterogeneity and are hypothesized to diversify the regeneration response (Halpin et al. 2017). However, it has become increasingly clear that modifying harvest gap size alone is unlikely to overcome a lack of certain biological and material legacies needed for the successful recruitment of a diverse species cohort (Kern et al. 2017). These legacies include propagule availability such as nearby seed sources (Willis et al. 2016) and/or advance regeneration (Widen et al. 2018), opportunity for release from intense herbivory pressure (Rooney and Waller 2003), and suitable substrates for seedling establishment (Caspersen and Saprunoff 2005).

Regional trends in forest floor conditions have limited successful seedling establishment for many tree species. Among species, there is variation in the range of soil microsite conditions suitable for germination and establishment (Shields et al. 2007). Many small-seeded species (e.g. yellow birch [*Betula alleghaniensis* Britton]) usually prefer moist bare mineral soil and coarse woody debris (CWD) and seldom establish on undisturbed litter layers (McGee and Birmingham 1997; Barras and Kellman 1998; Lorenzetti et al. 2008). Conversely, large-seeded species (e.g. sugar maple) often establish successfully on a wider range of microsite conditions including hardwood litter layers (Shugart et al. 2005). In managed forests, dense litter layers are seldom disturbed as a result of winter timber harvests on snowpack and CWD is less abundant due to the iterant harvest and removal of mature trees (Hura and Crow 2004; Willis et al. 2015). Therefore, the bottleneck of limited available microsites can pose significant challenges for the successful recruitment of economically and ecologically important forest species.

Deer herbivory can act as strong filter on forest regeneration by preferentially suppressing the growth of some species and enabling the success of others. During the past century, predator decline and hunting regulations have spurred historic high densities of white-tailed deer populations (Rooney 2001). This has coincided with high rates of herbivory on woody stems particularly in winter when herbaceous species are unavailable

to deer (Stromayer and Warren 1997; Rooney and Waller 2003). Palatable species, such as eastern hemlock and northern white cedar (*Thuja occidentalis* L.), are especially browse sensitive and regeneration is nearly eliminated in areas of high deer densities (Rooney et al. 2002; Parikh and Webster 2019). Other palatable hardwood species (e.g. sugar maple) can tolerate browse pressure by re-sprouting and persisting in the regeneration environment (Holmes and Webster 2010). Less palatable species such as ironwood (*Ostrya virginiana* Mill.) can dominate compositional trajectories where herbivory exerts a very strong influence (Matonis et al. 2011). Moreover, indirect effects of herbivory including soil compaction (Sabo et al. 2017) and increased cover of shrubs, ferns, and graminoids may further limit seedling establishment (Royo and Carson 2006; Frerker et al. 2014). The combined influence of herbivory and microsite limitation may be the primary impediments to the recruitment of underrepresented tree species in managed northern hardwood forests.

The main objective of this study was to investigate the long-term influence of deer herbivory and gap size on tree regeneration in hemlock northern hardwood forests. We revisited an experimental canopy gap study 18 years post-harvest that included deer exclosures and a range of gap sizes. We hypothesized a homogenization of the regeneration response due to high levels of historic deer browsing and microsite limitations would prevent browse sensitive species from successfully regenerating. Specifically, given the lack of CWD and limited disturbance to the forest floor when the gaps were created using a winter harvest, we hypothesized that small-seeded, browse sensitive species such as eastern hemlock and yellow birch would be uncommon in both exclosures and controls. Similarly, since previous research in these gaps noted intense browsing in small gaps (Tahtinen et al. 2014), we expected heights of browse-tolerant species to be suppressed in small gaps.

2.2 Materials and Methods

2.2.1 Study site

This study was conducted at the Michigan Technological University Ford Center and Forest (46°37'N, 88°29'W) located in the western portion of the Upper Peninsula of Michigan, USA. We reexamined forest regeneration at a gap study within a hemlock-

hardwood forest (see Homes and Webster, 2010; Tahtinen et al., 2014). Dominant canopy tree species at this research site included sugar maple, yellow birch, and eastern hemlock. The primary habitat type across this study area was *Acer-Tsuga/Maianthemum* (ATM) (Burger and Kotar 2003). Less common canopy tree species included balsam fir (*Abies balsamea* L.), red maple (*Acer rubrum* L.), white spruce (*Picea glauca* [Moench] Voss), black cherry (*Prunus serotina* Ehrh.), American basswood (*Tilia americana* L.), and American elm (*Ulmus americana* L.) (Tahtinen et al. 2014). Historical forest management at this site is comprised of a partial timber harvest in the 1930s and subsequent single-tree selection (Arbogast 1957) on ~10 year harvest cycles starting in the 1960s (Neuendorff et al. 2007). Mean daily temperatures range from 17.7°C in the summer to -9.2°C in winter. Annual mean precipitation is 84 cm which includes 363 cm of snowfall (Arguez et al. 2010). Soil types consist primarily of moderately well-drained Kallio cobbly silt loams with minor inclusions of poorly drained Pickford mucky silt loams (Soil Survey Staff 2007). White-tailed deer densities vary by season, which can range from 6.5 deer km⁻² in spring to 9.3 deer km⁻² in the fall (Mayhew 2003). In a previous study, Tahtinen et al. (2014) found high winter deer use within canopy gaps at this site (893 ± 238 pellet groups ha⁻¹) and a trend of higher deer use in smaller gap sizes.

2.2.2 Study design

The hemlock canopy gap study was established in the winter of 2002/03. A total of 20 artificial gaps were harvested in three size classes: small (50-150 m², $n = 7$), medium (151-250 m², $n = 7$), and large (251-450 m², $n = 6$) (Table 2.1). The range of gap sizes were based on recommended minimum opening sizes to successfully regenerate yellow birch and eastern hemlock (Webster and Lorimer 2002, 2005). Gap areas were calculated as eight-sided polygons determined from field-measured gap center to gap edge radii (see Holmes and Webster, 2010). At the time of harvest, all trees >1 m tall and all coarse logging slash were removed from gaps. Permanent sampling plots ($n = 4$ to 12 per gap) were installed at random spatial locations within each gap. In 2005, one to three plots per gap were selected at random and enclosed in 1.52 m tall fencing. Fencing mesh size (~15 cm²) prevented deer from entering fenced plots but permitted small herbivore entry (e.g., small rodents and snowshoe hares [*Lepus americanus* Macfarlani]). Deer exclosures were

circular and measured approximately 3.14 m² (1 m radius). A previous study excavated 6 sugar maple saplings in each gap at year 5 post-harvest: 3 from exclosure plots and 3 from control plots (see Holmes and Webster, 2010). Given the high abundance of sugar maples in gaps and the elapsed time, the effect of this removal on the current study should be negligible.

2.2.3 Field sampling

During the summer of 2020 (18 years post-harvest), we sampled regenerating stems in all 20 gaps. For each 1 m radius exclosure plot ($n = 46$) and control plot ($n = 93$), we tallied all individual stems of tree species capable of reaching overstory canopy heights. One exclosure plot fence was compromised by a fallen tree and excluded from sampling. Each stem was identified to species and placed into one of six height classes: ≤ 0.5 m, >0.5 to ≤ 1 m, >1 to ≤ 2 m, >2 to ≤ 4 m, >4 to ≤ 8 m, and >8 m. Maximum stem height (unstretched) was measured with a ruler (≤ 2 m) or a telescoping height pole (>2 m) (Sokkia Corporation, Olathe, Kansas, USA). For all stems in control plots, we counted the number of stems with any evidence of browse from the second terminal bud scar (two years previous) to the terminal ends of shoots. We did not differentiate between deer and other small mammal browse because previous research at this study noted only infrequent and minor rates of herbivory from small mammals (i.e. snowshoe hare) on tree regeneration (Holmes and Webster 2010) and many of the stems examined were now above the reach of smaller herbivores.

2.2.4 Data analyses

To examine differences in regeneration abundance between treatments, we used generalized linear mixed-effects models (GLMM) with negative binomial distributions. To test the influence of deer herbivory on regeneration height, exclosure and gap size treatments were included as fixed effects and gap identity (ID) was included as the random effect to account for multiple subplots within each gap. For analysis, count data were aggregated into three height classes: seedlings (≤ 1 m), small saplings (>1 to ≤ 4 m), and large saplings (>4 m). Models were built with the *glmmTMB* package v. 1.0.2.1 (Brooks et al. 2017) in R version 4.0.3 (R Core Team 2020). Separate models were run

for each of the three stem height classes. Post-hoc pairwise comparisons with Tukey's HSD correction were performed with the *emmeans* package v. 1.5.4 (Lenth 2021). To test the influence of deer herbivory on browse sensitive and browse tolerant species groupings (Table 2.2), count data were aggregated into two species groups and three height classes (as noted above). Species were designated browse sensitive or tolerant based on palatability classes reported in the literature (Dahlberg and Guettinger 1956; Bradshaw and Waller 2016) and the ability of a species to recover (resprout) after repeated browsing events (Anderson and Katz 1993; Salk et al. 2011). Black cherry was characterized as browse tolerant based on recent regeneration studies (Miller et al. 2009; Nuttle et al. 2011). Models were built with identical parameters as the models described above, but in this case six separate models were run for each stem height class and species grouping.

To visualize trends in species composition among treatments, we used a nonmetric multidimensional scaling (NMS) ordination run in PC-ORD version 6.22 (McCune and Mefford 2016). In the main matrix, variables were species subsets of three height classes (as noted above). Five species subsets that were not observed in any sampling plot were removed from the analysis. Count data values were averaged by gap and exclosure treatment. We performed a relativization by species subset maximum to accommodate variability in abundances (McCune and Grace 2002). Environmental variables included exclosure treatment type, gap size class, and gap areas measured in 2005 - year 3 after harvest. We ran the ordination in autopilot mode using the Sørensen (Bray-Curtis) distance measure for 250 runs of real data and 250 runs of randomized data. Monte Carlo tests were used to determine dimensionality of the data. Pearson and Kendall correlations were used to examine the relationship of gap area to ordination axes.

Differences in species composition between treatments were tested with multiple response permutation procedures (MRPP) using Sørensen (Bray-Curtis) distance measures in PC-ORD version 6.22 (McCune and Mefford 2016). MRPP is a non-parametric procedure that tests the observed compositional differences of groups (i.e. treatments) against the random expectation due to chance (i.e. null-hypothesis) of no differences between groups (McCune and Grace 2002). This test used the same main

matrix and relativized values as the NMS ordination. To test the influence of deer herbivory, we defined groups as enclosure or control and compared compositions between groups for all gaps. To test the influence of gap size, we defined groups as small, medium, or large gap size classes. We ran two separate MRPPs to compare gap size treatments: one with all enclosure plots and another with all control plots. For the two procedures comparing gap size treatments, species height class subsets containing no observations were removed from the analysis. This resulted in the removal of 8 species subsets from the gap size MRPP for enclosure plots and the removal of 13 species subsets from the gap size MRPP for control plots.

To investigate the regeneration response to treatments at the species level, we used an indicator species analysis (ISA) in PC-ORD version 6.22 (McCune and Mefford 2016). Based on the work of Dufrêne and Legendre (1997), this method compares the performance of species between groups by combining metrics of abundance and frequency (McCune and Grace 2002). Indicator values (IV) are calculated for each species relative to composition data within each grouping and range from 0 to 100. A perfect indicator ($IV = 100$) is a species always present and exclusive within a group, whereas a species with a lower IV would not be as frequent nor abundant within that particular group. We used a Monte Carlo test of observed maximum IV with 4999 iterations to compare differences between treatments. To describe the species-specific response to deer herbivory, we defined groups as enclosure or control and each species was subset into three height classes (as noted above). To describe the species-specific response to gap sizes, we first isolated enclosure plots and control plots into two separate matrices, then compared IV maximum values between gap size groups within each treatment. All count values were relativized by species maximum and five species subsets with no observations were removed from the analysis.

Table 2.1. Gap size and sampling subplot attributes of a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Area values represent mean \pm standard deviation (SD).

Gap size class	Replicates (<i>n</i>)	Area 2005 (m ²)	Area 2020 (m ²)	Sampling subplots	
				Exclosure (<i>n</i>)	Control (<i>n</i>)
Small	7	114.97 \pm 31.53	68.86 \pm 32.62	13	24
Medium	7	199.32 \pm 31.11	134.81 \pm 34.24	16	28
Large	6	325.83 \pm 66.41	280.95 \pm 64.97	17	41

Table 2.2. Browse sensitive and browse tolerant species groupings of forest regeneration in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Species codes match USDA nomenclature, symbols are used in following tables and figures.

Latin name	Common name	USDA Code	Symbol
Browse sensitive species			
<i>Betula alleghaniensis</i> Britton	yellow birch	BEAL2	BETALL
<i>Tilia americana</i> L.	American basswood	TIAM	TILAME
<i>Thuja occidentalis</i> L.	northern-white cedar	THOC2	THUOCC
<i>Tsuga canadensis</i> (L.) Carrière	eastern hemlock	TSCA	TSUCAN
Browse tolerant species			
<i>Abies balsamea</i> (L.) Mill.	balsam fir	ABBA	ABIBAL
<i>Acer rubrum</i> L.	red maple	ACRU	ACERUB
<i>Acer saccharum</i> Marsh.	sugar maple	ACSA3	ACESAC
<i>Fraxinus nigra</i> Marsh.	black ash	FRNI	FRANIG
<i>Ostrya virginiana</i> (Mill.) K. Koch	ironwood	OSVI	OSTVIR
<i>Picea glauca</i> (Moench) Voss	white spruce	PIGL	PICGLA
<i>Populus grandidentata</i> Michx.	bigtooth aspen	POGR4	POPGRA
<i>Prunus serotina</i> Ehrh.	black cherry	PRSE2	PRUSER

2.3 Results

2.3.1 Abundance

At 18 years post-harvest, deer herbivory exerted a strong influence on the species composition and height distributions of tree regeneration across a range of gap sizes (Figure 2.1). In control plots, small stems (≤ 1 m) were abundant and only a few species such as sugar maple, ironwood, balsam fir and black ash were able to attain heights >4 m. In exclosure plots, additional species were observed at heights >4 m, including yellow birch, American basswood, eastern hemlock, and black cherry. Within small gaps, few individual stems attained heights >4 m and stems ≤ 1 m were the most abundant of any gap size class (Figure 2.1).

Regeneration abundances in exclosures differed from control plots for each of the three height classes in our analysis (GLMM, $p(>\chi^2) \leq 0.005$, Table 2.3). Overall, seedlings (≤ 1 m) were more abundant in control plots, and saplings (>1 m) were generally more abundant in exclosures for larger gap sizes (Table 2.4). When abundances were compared within each gap size class, small sapling (>1 to ≤ 4 m) abundance differed between exclosure treatment only in medium and large gaps ($p \leq 0.043$, Table 2.4) and large saplings (>4 m) only in medium gaps ($p = 0.011$, Table 2.4). The grouping of browse sensitive species revealed the strongest differences between exclosure treatments (GLMM, $p(>\chi^2) \leq 0.001$, Table 2.5). In larger gaps sizes, browse sensitive seedlings were more abundant in control plots ($p \leq 0.029$, Table 2.6) but all saplings were more abundant in exclosure plots ($p \leq 0.034$, Table 2.6). Browse tolerant species abundances were generally similar between exclosure treatments across stem heights and gap sizes, only seedlings in small gaps were more abundant in control plots ($p = 0.046$, Table 2.6) and small saplings in medium gaps were more abundant in exclosure plots ($p = 0.036$, Table 2.6).

2.3.2 Composition

The NMS ordination resulted in a 3-dimensional solution with a final stress of 16.15 and an instability of <0.0001 after 57 iterations. Axis 1 ($r^2 = 0.25$) and axis 2 ($r^2 = 0.27$) explained a higher value of variability than axis 3 ($r^2 = 0.12$). Overall, the ordination explained 64.3% of the variation in composition. In the ordination space, exclosure plots

moved away from control plots although some overlap did occur (Figure 2.2). Tall stems (>4 m) of eastern hemlock, American basswood, black ash, and balsam fir were located in ordination space associated with exclosure plots, whereas smaller stems (≤ 4 m) of ironwood, black cherry, and yellow birch associated more with regions exclusive to control plots (Figure 2.2). Correlation coefficients revealed a negative relationship between gap area and axis 1 ($r = -0.32$, $r^2 = 0.1$), and a positive correlation with axis 2 ($r = 0.51$, $r^2 = 0.24$) (Figure 2.2, 2.3). Plots of all three gap sizes tended to occupy different portions of the ordination space with some overlap in the center of the plot (Figure 2.3). Tall stems (>4m) of most species tended to associate with medium and large gap sizes (Figure 2.3). Large saplings (>8m) of yellow birch and eastern hemlock were associated with regions of the ordination spaces dominated by large gaps, whereas ironwood was the only species for which all stem heights occurred within the ordination space associated with the small gap size (Figure 2.3).

Compositional differences of regeneration between exclosure treatments at the study level (all gaps) were strongly divergent (MRPP, $A = 0.016$, $p = 0.012$). Our comparison of composition between gap size classes revealed an even greater difference between treatment groups ($A = 0.037$, $p < 0.001$). Pairwise comparisons indicated the greatest difference existed between small and large gaps ($p = 0.001$), medium gaps were also compositionally distinct from small and large gaps ($p \leq 0.022$). After isolating exclosure treatments into separate analyses, only the control treatment generated significant differences between gap size classes ($A = 0.044$, $p = 0.023$). Within control plots, pairwise comparisons highlighted differences only between small and large gaps ($p = 0.027$) and medium and large gaps ($p = 0.03$).

2.3.3 Indicator Species

The indicator species analysis revealed significant trends between exclosure treatments for two species. At taller stem heights, eastern hemlock (small saplings) and yellow birch (large saplings) were significant indicators of exclosure treatments (ISA, $p \leq 0.024$, Table 2.7). Conversely, eastern hemlock and yellow birch seedlings were strong indicators of the control treatment, but nearly absent at equal heights in exclosure plots ($p \leq 0.042$, Table 2.7). After isolating exclosure and control treatment groups to compare

gap size treatments, the majority of indicating species for gap sizes occurred in control plots. Within control plots, sugar maple seedlings in small gaps (ISA, $p = 0.001$, Table 2.8), sugar maple large saplings in large gaps ($p = 0.042$, Table 2.8), and American basswood seedlings in large gaps ($p = 0.008$, Table 2.8) were the main drivers of compositional differences between gap sizes. Within exclosure plots, only sugar maple seedlings in small gaps ($p = 0.028$, Table 2.8) were significant indicators of the gap size treatment.

2.3.4 Browse

The total proportion of stems with recent evidence of browse in control plots was $61.4 \pm 44.2\%$. Stem heights ranging from 0.51 to 2 m were observed with high instances of recent browse ($90.4 \pm 25.4\%$). Smaller stems (<0.5 m) were seldom browsed ($33.7 \pm 39.2\%$) and taller stems (>2 to ≤ 8 m) often showed evidence of browse on lower lateral branches ($60.7 \pm 47.6\%$). Species with the greatest proportion of stems with browse were yellow birch ($83.9 \pm 36.1\%$), American basswood ($77.1 \pm 41.6\%$), eastern hemlock ($76.2 \pm 41.5\%$), followed by sugar maple ($66.5 \pm 40.8\%$), red maple ($50.2 \pm 44.3\%$) and northern white cedar ($50 \pm 57.7\%$). The smallest proportion of browsed stems were observed on black cherry ($12.5 \pm 35\%$), preceded by white spruce, balsam fir, and ironwood ($<40\%$).

Table 2.3. Generalized linear mixed-effects models with negative binomial distributions of regeneration abundance in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Fixed effects were exclosure and gap size treatments, the random effect was gap ID. Sample size (n) = 139 for all treatments. Asterisks (*) denote statistical significance $p < 0.05$.

Seedlings (≤ 1 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	13.573	$<0.001^*$
Gap size	2	12.471	0.002^*
Exclosure x gap size	2	0.05	0.977
Small saplings (>1 to ≤ 4 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	12.38	$<0.001^*$
Gap size	2	0.86	0.651
Exclosure x gap size	2	0.694	0.707
Large saplings (>4 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	8.065	0.005^*
Gap size	2	4.051	0.132
Exclosure x gap size	2	1.73	0.421

Table 2.4. Regeneration abundance (mean stems $100 \text{ m}^{-2} \pm 1 \text{ SD}$) in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Mean plot values are summarized by height class, gap size, and a deer exclosure treatment effect. Generalized linear mixed effects models (see Table 2.3) and post-hoc Tukey pairwise comparisons generated *p*-values between exclosure and control groups. Asterisks (*) denote differences of statistical significance ($p < 0.05$) between treatments. Stem height classes are seedlings ($\leq 1 \text{ m}$), small saplings ($>1 \text{ to } \leq 4 \text{ m}$), large saplings ($>4 \text{ m}$).

Height Class	Small gaps			Medium gaps			Large gaps		
	Exclosure	Control	<i>p</i> -value	Exclosure	Control	<i>p</i> -value	Exclosure	Control	<i>p</i> -value
$\leq 1 \text{ m}$	748 ± 512	1125 ± 579	$p = 0.04^*$	374 ± 247	623 ± 475	$p = 0.032^*$	255 ± 166	367 ± 168	$p = 0.033^*$
$>1 \text{ to } \leq 4 \text{ m}$	142 ± 149	94 ± 84	$p = 0.167$	147 ± 75	70 ± 62	$p = 0.01^*$	152 ± 60	93 ± 44	$p = 0.043^*$
$>4 \text{ m}$	8 ± 12	8 ± 11	$p = 0.746$	49 ± 59	15 ± 29	$p = 0.011^*$	49 ± 42	35 ± 43	$p = 0.11$

Table 2.5. Generalized linear mixed-effects models with negative binomial distributions of regeneration abundance in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Species were grouped as either browse sensitive or tolerant (see Table 2.2) Fixed effects were exclosure and gap size treatments, the random effect was gap ID. Sample size (n) = 139 for all treatments. Asterisks (*) denote statistical significance $p < 0.05$.

Browse sensitive species			
Seedlings (≤ 1 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	10.577	0.001*
Gap size	2	0.853	0.653
Exclosure x gap size	2	0.561	0.755
Small saplings (>1 to ≤ 4 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	13.477	$<0.001^*$
Gap size	2	0.609	0.738
Exclosure x gap size	2	3.687	0.158
Large saplings (>4 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	10.212	0.001*
Gap size	2	0.06	0.97
Exclosure x gap size	2	0.079	0.961
Browse tolerant species			
Seedlings (≤ 1 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	10.392	0.001*
Gap size	2	13.342	0.001
Exclosure x gap size	2	0.119	0.942
Small saplings (>1 to ≤ 4 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	8.105	0.004*
Gap size	2	0.664	0.717
Exclosure x gap size	2	0.402	0.818
Large saplings (>4 m)	Df	χ^2	$p > \chi^2$
Exclosure treatment	1	2.537	0.111
Gap size	2	2.658	0.265
Exclosure x gap size	2	0.626	0.731

Table 2.6. Browse group regeneration abundance (mean stems $100 \text{ m}^{-2} \pm 1 \text{ SD}$) in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Mean plot values are summarized by browse groupings (see Table 2.2), height class, gap size, and a deer exclosure treatment effect. Generalized linear mixed effects models (see Table 2.5) and post-hoc Tukey pairwise comparisons generated *p*-values between exclosure and control groups. Asterisks (*) represent differences of statistical significance ($p < 0.05$) between treatments. Stem height classes are seedlings ($\leq 1 \text{ m}$), small saplings ($>1 \text{ to } \leq 4 \text{ m}$), large saplings ($>4 \text{ m}$).

	Height class	Small gaps			Medium gaps			Large gaps		
		Exclosure	Control	<i>p</i> -value	Exclosure	Control	<i>p</i> -value	Exclosure	Control	<i>p</i> -value
6	Browse sensitive species									
	≤1 m	16 ± 21	29 ± 35	p = 0.29	18 ± 22	64 ± 91	p = 0.029*	12 ± 13	37 ± 27	p = 0.025*
	>1 to ≤4 m	7 ± 13	4 ± 5	p = 0.505	21 ± 21	0 ± 0	p = 0.019*	26 ± 30	3 ± 4	p < 0.001*
	>4 m	0 ± 0	0 ± 0	p = 1	13 ± 14	0 ± 0	p = 0.034*	12 ± 6	0 ± 0	p = 0.018*
	Browse tolerant species									
	≤1 m	732 ± 522	1096 ± 577	p = 0.046*	356 ± 236	559 ± 393	p = 0.062	243 ± 157	330 ± 158	p = 0.088
	>1 to ≤4 m	135 ± 150	90 ± 79	p = 0.192	126 ± 71	70 ± 62	p = 0.036*	126 ± 60	90 ± 50	p = 0.136
	>4 m	8 ± 12	8 ± 11	p = 0.746	36 ± 62	15 ± 29	p = 0.124	38 ± 41	35 ± 43	p = 0.416

Table 2.7. Regeneration abundance (mean stems $100 \text{ m}^{-2} \pm 1 \text{ SD}$) and indicator species values in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Mean plot values are summarized by species, height class and a deer exclosure treatment effect. Indicator values (IV) were calculated in an indicator species analysis that combines metrics of species frequency and abundance. Comparisons of exclosure and control maximum IV for each species height class subset were performed with Monte Carlo tests. Asterisks (*) denote differences of statistical significance ($p < 0.05$). Five species subsets with no observations were removed from the analysis. Stem height classes are seedlings ($\leq 1 \text{ m}$), small saplings ($>1 \text{ to } \leq 4 \text{ m}$), large saplings ($>4 \text{ m}$). Species symbols refer to species names listed in Table 2.2.

Species	Height class	Density		Indicator value		
		Exclosure	Control	Exclosure	Control	<i>p</i> -value
ACESAC	≤1 m	359 ± 385	471 ± 389	43	57	0.370
	>1≤4 m	92 ± 63	62 ± 57	60	34	0.059
	>4 m	22 ± 45	14 ± 29	28	12	0.384
ACERUB	≤1 m	84 ± 134	191 ± 318	17	56	0.084
	>1≤4 m	30 ± 70	10 ± 25	26	6	0.278
	>4 m	1 ± 4	0	10	0	0.483
TSUCAN	≤1 m	7 ± 12	17 ± 20	9	49	0.026*
	>1≤4 m	7 ± 12	0	30	0	0.018*
	>4 m	0.5 ± 2	0	5	0	1
BETALL	≤1 m	3 ± 7	16 ± 43	3	42	0.042*
	>1≤4 m	9 ± 18	2 ± 4	20	6	0.515
	>4 m	6 ± 10	0	30	0	0.024*
TILAME	≤1 m	3 ± 7	9 ± 14	3	31	0.068
	>1≤4 m	2 ± 6	0	15	0	0.227
	>4 m	2 ± 5	0	15	0	0.236
ABIBAL	≤1 m	5 ± 12	4 ± 9	11	9	0.860
	>1≤4 m	4 ± 8	6 ± 16	8	12	0.782
	>4 m	1 ± 4	1 ± 4	5	8	0.934
OSTVIR	≤1 m	0	1 ± 3	0	20	0.105
	>1≤4 m	1 ± 4	3 ± 6	3	25	0.094
	>4 m	1 ± 4	3 ± 7	1	20	0.159
FRANIG	≤1 m	4 ± 18	6 ± 17	4	15	0.483
	>1≤4 m	1 ± 4	0.5 ± 2	3	2	1.000
	>4 m	1 ± 4	0.5 ± 1	4	1	1
PRUSER	≤1 m	0	4 ± 14	0	15	0.236
	>1≤4 m	1 ± 2	1 ± 4	2	7	0.745
	>4 m	1 ± 2	0	5	0	1
THUOCC	<1 m	2 ± 8	2 ± 4	6	8	1
PICGLA	<1 m	2 ± 7	1 ± 5	3	2	1
	>1≤4 m	0	1 ± 3	0	10	0.478
POPGRA	>1≤4 m	1 ± 4	0	5	0	1

Table 2.8. Indicator species values in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. To isolate gap size treatment effects by exclosure treatment, two separate indicator species analyses were performed. Indicator values (IVs) were calculated for each gap size grouping separately for exclosure and control plots. IVs were computed in an indicator species analysis that combines metrics of species frequency and abundance. Comparisons between gap size group maximum IV for each species height class subset were performed with Monte Carlo tests. Asterisks (*) denote differences of statistical significance ($p < 0.05$). Five species subsets with no observations were removed from the analysis. Rows without values describe a species height class subset with no observations in any exclosure or control sampling plot. Stem height classes are seedlings (≤ 1 m), small saplings (>1 to ≤ 4 m), large saplings (>4 m). Gap sizes are small (Sm), medium (Med), and large (Lg). Species symbols refer to species names listed in Table 2.2.

Species	Height class	Exclosure treatment				Control treatment			
		Gap size				Gap size			
		Sm	Med	Lg	<i>p</i> -value	Sm	Med	Lg	<i>p</i> -value
ACESAC	≤1 m	60	20	19	0.028*	61	19	20	0.001*
	>1≤4 m	32	30	39	0.696	23	20	45	0.234
	>4 m	1	11	53	0.082	0	7	51	0.042*
ACERUB	≤1 m	15	38	7	0.333	30	44	6	0.459
	>1≤4 m	7	24	3	0.596	16	19	0	0.609
	>4 m	6	9	0	0.770				
TSUCAN	≤1 m	3	37	2	0.126	18	41	12	0.321
	>1≤4 m	0	35	13	0.159				
	>4 m	0	0	17	0.299				
BETALL	≤1 m	3	3	19	0.417	10	26	10	0.837
	>1≤4 m	1	10	19	0.584	25	0	21	0.402
	>4 m	0	27	18	0.391				
TILAME	≤1 m	9	0	13	0.579	2	3	65	0.008*
	>1≤4 m	18	0	6	0.735				
	>4 m	0	5	21	0.431				
ABIBAL	≤1 m	0	20	10	0.525	2	22	2	0.369
	>1≤4 m	0	3	41	0.061	3	20	2	0.647
	>4 m	0	9	6	1	6	16	0	0.671
OSTVIR	≤1 m					4	4	14	0.814
	>1≤4 m	9	6	0	0.78	39	6	2	0.096
	>4 m	14	0	0	1	28	10	0	0.269
FRANIG	≤1 m	13	0	2	1	18	0	19	0.677
	>1≤4 m	14	0	0	1	14	0	0	1.000
	>4 m	0	14	0	1	0	0	17	0.294
PRUSER	≤1 m					12	5	0	0.772
	>1≤4 m	0	0	17	0.296	6	0	10	0.527
	>4 m	0	14	0	1				
THUOCC	<1 m	10	5	0	0.779	5	29	0	0.248
PICGLA	<1 m	0	14	0	1	0	14	0	1
	>1≤4 m					8	6	0	0.782
POPGRA	>1≤4 m	0	14	0	1				

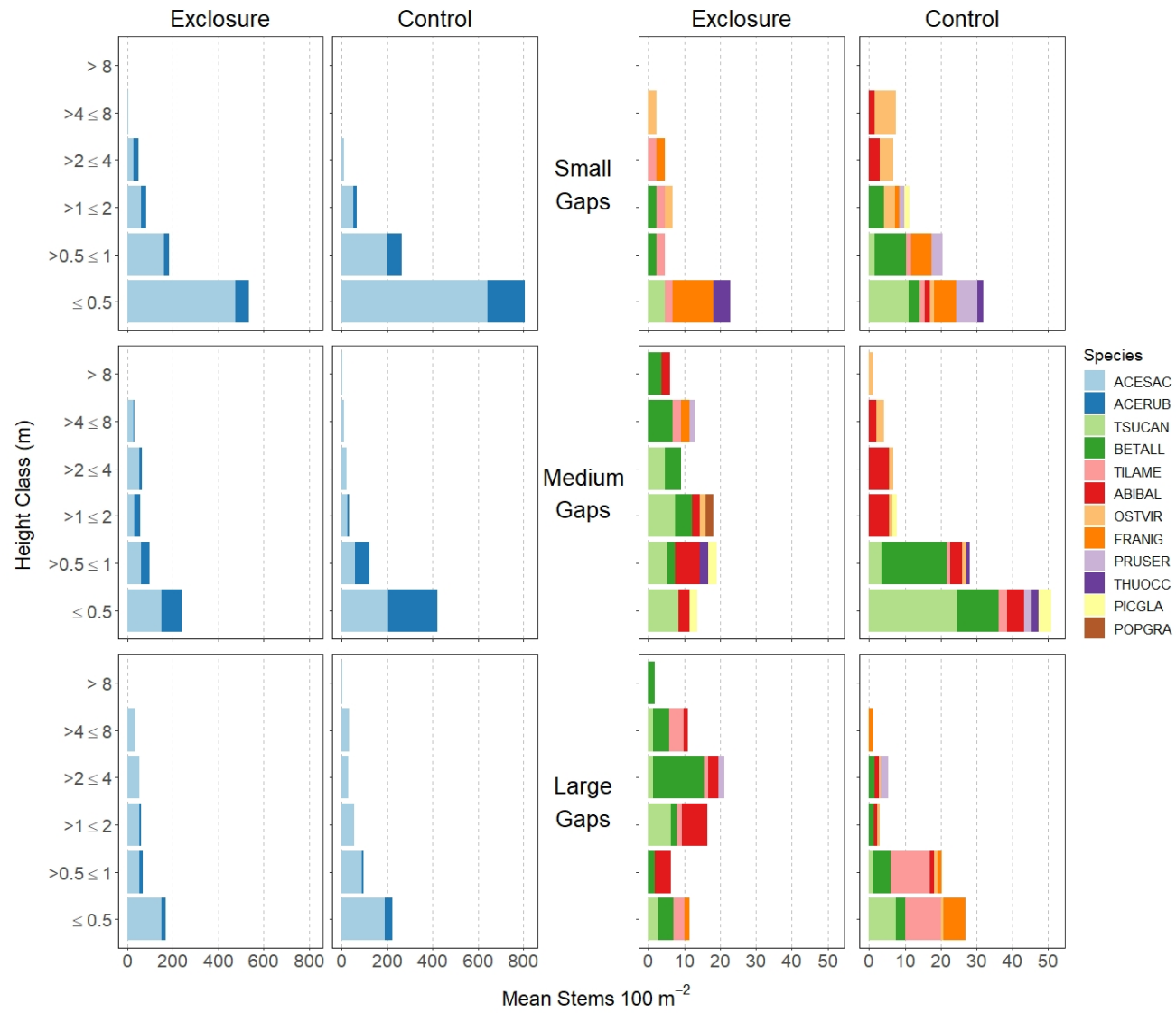


Figure 2.1. Stacked bar plot of mean tree regeneration abundance (stems 100 m⁻²) in hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Species abundance values are summarized by exclosure treatment, gap size treatment, species and height class. Stacked bar plot panes are split into two groups: maples on the left-hand side of figure (*Acer saccharum* Marsh. and *Acer rubrum* L.) and all other species on the right-hand side of figure. Note difference in scale between the two species groupings. Species symbols refer to species names listed in Table 2.2.

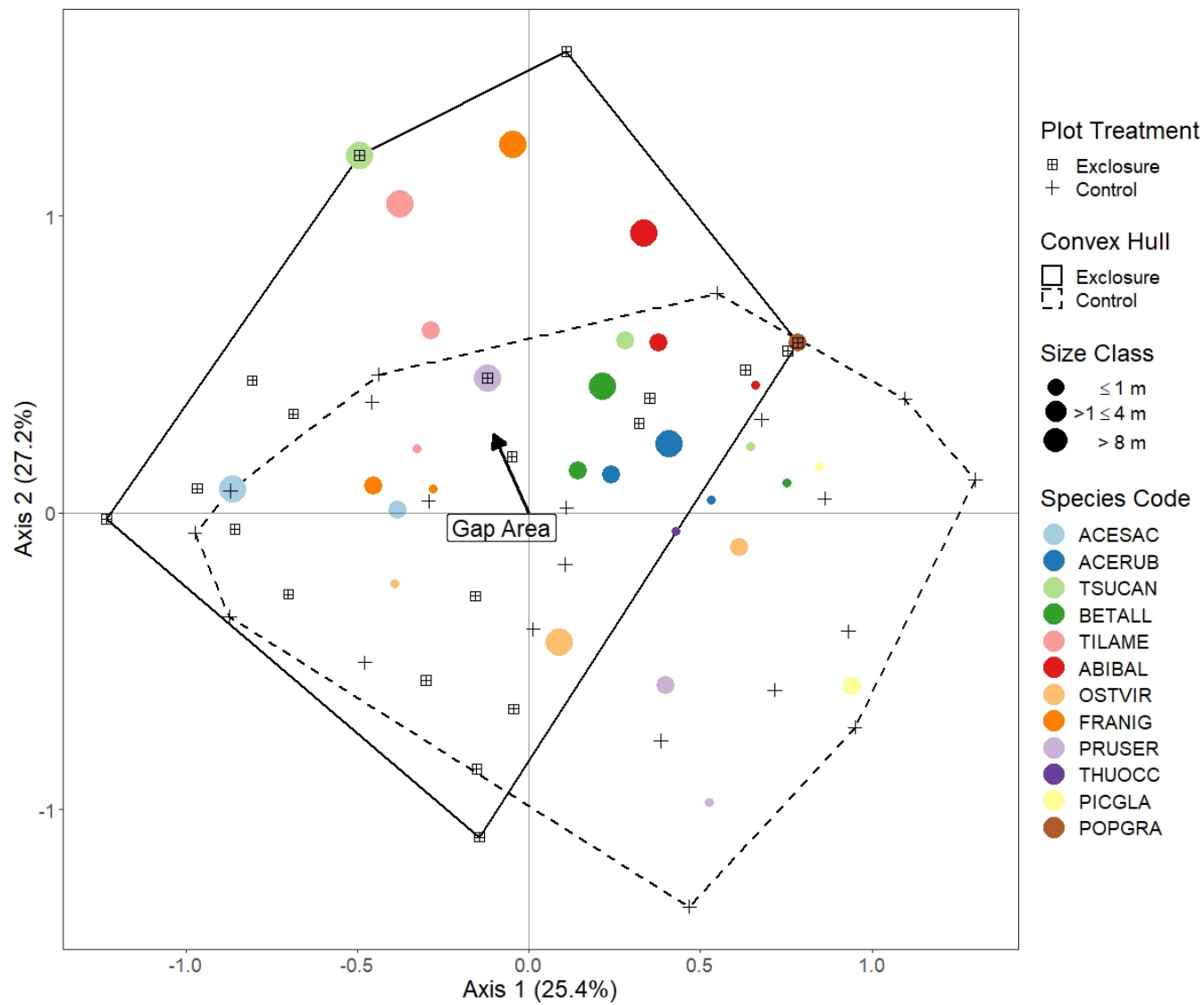


Figure 2.2. Nonmetric multidimensional scaling ordination joint-axis plot of tree regeneration in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Plots are characterized by deer exclosure treatment and convex hull polygons indicate the bounding area for exclosure treatment type. Filled circles represent species of varying height class subgroups (represented by circle size) and colors distinguish each species. The environmental variable of gap area is represented as a vector corresponding to the Kendall and Pearson correlation coefficients for each axis of the joint plot. Axes labels include R^2 values corresponding to axis in parenthesis. In the legend, species are ordered by frequency, species symbols refer to species names listed in Table 2.2.

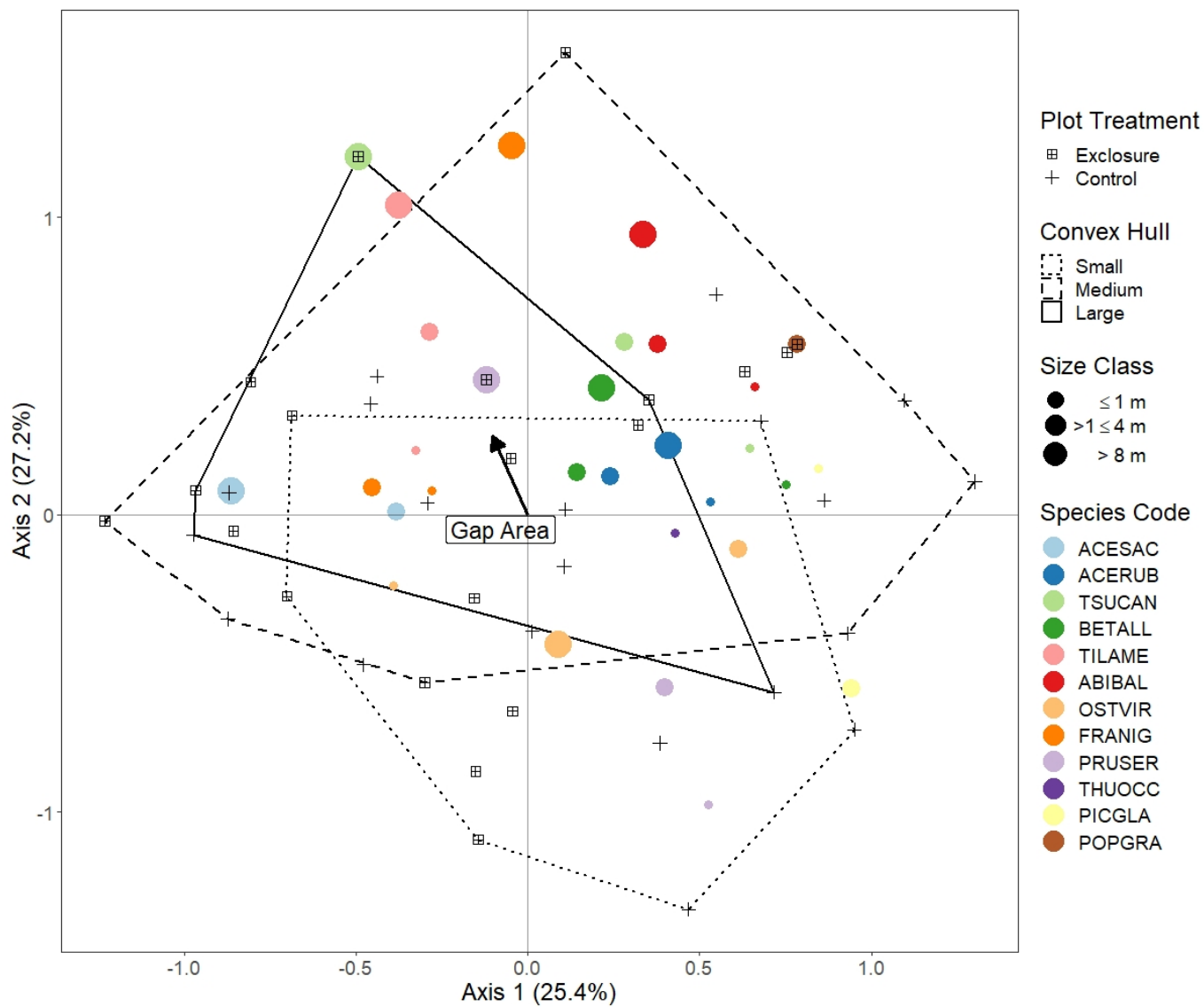


Figure 2.3. Nonmetric multidimensional scaling ordination joint-axis plot of tree regeneration in a hemlock canopy gap study in a northern hardwood forest 18 years after harvest near Alberta, Michigan, USA. Plots are characterized by deer exclosure treatment and convex hull polygons indicate the bounding area for gap size treatment types. Filled circles represent species of varying height class subgroups (represented by circle size) and colors distinguish each species. The environmental variable of gap area is represented as a vector corresponding to the Kendall and Pearson correlation coefficients for each axis of the joint plot. Axes labels include R^2 values corresponding to axis in parenthesis. In the legend, species are ordered by frequency, species symbols refer to species names listed in Table 2.2.

2.4 Discussion

In this study, we revisited hemlock canopy openings 18 years post-harvest to test our hypothesis that the combined effects of deer herbivory and microsite limitation would prevent the successful regeneration of browse sensitive species. However, our results indicate that deer herbivory is a major bottleneck to the recruitment of browse sensitive species into heights above 1 m. Many species such as eastern hemlock and yellow birch were unable to overcome herbivory and advance into taller height classes. Herbivory was associated with compositional changes between gap sizes. The browse tolerant sugar maple was the dominant tree species across all treatments and ironwood stems were frequently the tallest stems in small gaps. When sheltered from browse in exclosures, yellow birch saplings often co-dominated the tallest layers of regenerating stems and were well-positioned for gap capture.

Deer herbivory exerted a strong filtering effect on tree regeneration at our study site. Although we expected a largely homogeneous response due to overriding limitations, the deer exclosure treatment altered regeneration composition. Exclosures were associated with taller stems and consisted of greater proportions of browse sensitive species. For northern hardwood forests across northern Wisconsin, Bradshaw and Waller (2016) highlight the impact of deer herbivory to long-term regional declines and even regeneration failure of highly palatable species such as eastern hemlock. At year 5 post-harvest, Holmes and Webster (2010) reported an overwhelming dominance of sugar maple regeneration at heights above 1 m even in exclosure plots while browse sensitive species remained in the seedling layer (≤ 1 m). Therefore, we expected a similar trend of sugar maple dominated sapling response at year 18 post-harvest. However, our results indicate that the installation of deer exclosures, even at year 2 post-harvest, may still provide opportunities for tree regeneration of browse sensitive species. In another study, Sabo et al. (2017) reported exclosures to promote abundance and richness of regeneration, especially for less shade-tolerant saplings at 7 years after gap harvest. Other studies indicate an increased growth response for some species of tree regeneration within exclosures, especially in heavier harvest treatments (Kern et al. 2012; Walters et

al. 2016; Parker et al. 2020). Furthermore, the recruitment of browse sensitive, small-seeded species also implies these species were able to overcome microsite limitations.

Eastern hemlock and yellow birch were the primary drivers of compositional differences between deer exclosure treatments, indicating for exclosure plots as saplings (>1 m) and for control plots as seedlings (≤ 1 m). Both species are susceptible to herbivory but also sensitive to recruitment failure when a specific suite of seedbed and resource requirements are not available (Caspersen and Saprunoff 2005). Eastern hemlock seedling establishment is negatively impacted by hardwood litter layers and is highly dependent on prolonged moisture availability, preferring decaying wood substrates (e.g. hemlock nurse logs) (Rooney and Waller 1998; Marx and Walters 2008). Yellow birch seedlings have nearly identical requirements for establishment, but also germinate well on bare mineral soil that may only be available after heavy disturbances and/or soil scarification (Tubbs et al. 1977; Prévost et al. 2010; Marx and Walters 2008). Yet, without additional site preparations at this hemlock gap study, seedbed and microsite limitation did not eliminate seedling establishment of species often prone to diminished recruitment capacity in northern hardwood systems. Moreover, lower abundances of seedlings inside exclosures may also describe a faster transition to the stem exclusion stage of regeneration (Oliver and Larson 1996) while herbivory delays overall recruitment in many control plots and nearly eliminates saplings of browse sensitive species. Eastern hemlock is particularly vulnerable to herbivory in northern hardwood stands, as stems protruding above snow pack are often heavily browsed in winter resulting in severely limited recruitment (Alverson et al. 1988; Witt and Webster 2010). As for yellow birch, herbivory is reported to impact survival and reduce growth (Godman and Krefting 1960; Elie et al. 2009; Kern et al. 2012), though disturbance type, soil substrate quality, and light availability are often cited as the primary factors limiting successful recruitment (Bolton and D'Amato 2011; Shabaga et al. 2019; Hupperts et al. 2018, 2020). However, yellow birch was the species with the highest occurrence of browse on stems at our study site.

Interacting gradients of deer use and resource availability may drive differences in the regeneration response between gap sizes at our study site. Although herbivory can

homogenize plant communities along environmental gradients such as gap size (Rooney et al. 2004; Holmes and Webster 2011; Frerker et al. 2014), we hypothesized that differing levels of deer use between gap sizes may help sort out regeneration heights 18 years post-harvest. Indeed, we found compositional change between gap sizes primarily driven by plots exposed to deer herbivory. This was largely due to a high abundance of suppressed sugar maple stem heights (≤ 1 m) in small gaps. In earlier research at our study site, Tahtinen et al. (2014) found deer use highest in small gaps and decreased with increasing gap size. Smaller gaps with accessible forage may provide easier access to deer as they usually contain less standing biomass (Webster and Lorimer 2002) and in winter, coniferous hemlock canopies intercept snow and therefore may decrease snow depths in smaller gap sizes (Morrison et al. 2003). However, gradients of light may also promote taller sugar maple stems in large gaps or suppress release in smaller gap sizes (Canham 1985, 1985; Beaudet and Messier 1998; Webster and Lorimer 2002). In exclosure plots, sugar maple seedlings indicated for small gaps and were rare in large gaps, yet this may indicate limited growth in small gaps and/or stem exclusion conditions in large gap sizes (Oliver and Larson 1996). Surprisingly, seedlings of American basswood in control plots were strong indicators for large gaps. Although basswood often regenerates by vigorous vegetative basal sprouts (Woods 1984; Evans and Morris 2016), seedling establishment and sapling recruitment were relatively common in deer exclosures. Larger gap sizes may promote some aspect of seedling establishment for this midtolerant species, yet under herbivory it is unlikely any will recruit into taller heights.

Considering the future recruitment of gap regeneration into the overstory, the influence of herbivory led to the success of a few species and the near elimination of many species. Maple species largely dominated the regeneration response at all heights and across all treatments. Although red maple was common in smaller gap sizes, sugar maple was particularly well-suited for regeneration at our study site. This highly shade-tolerant species can persist for many years under forest canopy as advance regeneration well-positioned and well-adapted for rapid release after a disturbance event (McClure et al. 2000; Moreau et al. 2019; Reuling et al. 2019). Furthermore, previous research by Holmes and Webster (2010) at our study site emphasized stem-layering as mechanism for

sugar maple persistence under repeated herbivory events and can further enhance release after canopy disturbance. In small gaps, ironwood and balsam fir often outgrew sugar maple when exposed to herbivory. Very high deer use in small gaps may permit the success of only the least palatable shade-tolerant tree species (Matonis et al. 2011; Tahtinen et al. 2014; Bradshaw and Waller 2016). The replacement of sugar maple regeneration with less valuable ironwood in managed northern hardwood stands is of growing concern to forest managers but may be remedied by targeting ironwood removal during harvest, increasing harvest opening size and deer management (Miller 2004; Donovan 2005; Matonis et al. 2011). Although herbivory strongly selected for browse tolerant species at any height above winter snowpack ($>1\text{m}$), the installation of deer exclosures enabled the recruitment of browse sensitive species. For example, yellow birch capitalized on deer exclosures in larger gap sizes, often well-represented in the tallest height class of regenerating stems.

Eastern hemlock and yellow birch appear to be particularly sensitive to deer herbivory in this forest system. This study suggests that herbivory may be a greater impediment to their recruitment than microsite limitations. Relatively small ($\sim 3.5\%$ of total gap area) and inexpensive deer exclosures enabled the recruitment of regionally underrepresented eastern hemlock and yellow birch into the upper strata of regeneration cohorts in larger gap sizes. Although sugar maple remained the most common tree species at all heights and in all treatments, exclosures created opportunities for species prone to diminished recruitment capacity to co-dominate cohorts most likely to capture gaps. Therefore, the exclusion of deer from a group-selection harvest of sufficient size in areas containing adequate microsites and nearby seed trees may encourage the successful recruitment of browse sensitive species. Overall, our findings suggest that the installation of a few, relatively small deer exclosures within canopy gaps may help promote the recruitment of some underrepresented species in northern hardwood forests.

3 Spatial patterning of low-density tree regeneration in experimental canopy gaps 15-24 years post-harvest

3.1 Introduction

Successful forest regeneration hinges on factors operating at many spatial scales. The influences of disturbance regimes, biological legacies and competing vegetation can shape spatial patterns of forest regeneration (Carlton and Bazzaz 1998; Dovciak et al. 2003; Shive et al. 2018). Worldwide, the capacity of natural forest regeneration is threatened by changes in climate, land-use, disturbance regime, herbivory, and the introduction of invasive species (Hansen et al. 2018; Miller and McGill 2019; Dey et al. 2019; Löf et al. 2019; Petersson et al. 2019). An issue common to eastern North American forests is the formation of recalcitrant shrub layers following disturbance which can interfere with tree regeneration and lead to large areas of delayed recruitment (Royo and Carson 2006).

Due to local and/or landscape factors, aggressive understory vegetation has sometimes contributed to limited tree regeneration following disturbance. In eastern North American forests, regional increases in deer abundance and herbivory can lead to forest understories dominated by fern layers that can limit seedling establishment (Cretaz and Kelty 2002; Engelman and Nyland 2006). In northern hardwood forests, the combined effects of local forest management and herbivory may lead to dense sedge mats associated with low-density regeneration (Powers and Nagel 2009). Similarly, following heavy harvests or gap disturbances, aggressive ruderal species such as *Rubus* spp. have been found to associate with areas satisfying conditions of regeneration failure for 10+ years (Metzger and Tubbs 1971; Kern et al. 2012; Widen et al. 2018; Knapp et al. 2021). Furthermore, the homogenization of northern hardwood forests in recent decades (Schulte et al. 2007) may also limit spatial distributions of seed trees and available microsites critical for the regeneration of some species (Caspersen and Saprundoff 2005; Willis et al. 2016).

Silvicultural strategies including canopy gap creation and the retention of biological legacies may remedy some of these challenges by increasing stand structure and resource

heterogeneity. Foresters have sought alternative harvest methods as declining trends in species diversity may be due in part to widespread use of single-tree selection systems (Angers et al. 2005; Schulte et al. 2007; Neuendorff et al. 2007). Gap-based silviculture models natural windthrow disturbances and gap size can be modified in attempts to recruit species within certain ranges of shade-tolerance (Coates and Burton 1997; Leak et al. 2014; Kern et al. 2017). In many forest systems, the retention of living trees (hereafter, ‘legacy-tree retention’) after harvest may introduce further structural and resource complexity as well as increase seed availability for the recruitment of desired species (Gustafsson et al. 2010; Mitchell and Beese 2011; Fedrowitz et al. 2014). However, the relative success of these strategies in northern hardwood forests is still under debate due to mixed experimental results and few long-term studies (Shields et al. 2007; Poznanovic et al. 2013; D’Amato et al. 2015; Kern et al. 2017; Knapp et al. 2019a, 2021).

The spatial patterns of forest regeneration can offer valuable insights into the mechanisms driving or limiting forest regeneration at specific spatial scales. Canopy gap disturbances introduce spatial gradients of light and soil microclimates into the regeneration environment (Raymond et al. 2006). The Gap Partitioning Hypothesis suggests these resource gradients can pattern tree regeneration according to species-specific life-history traits (Ricklefs 1977; Denslow 1980). Moreover, height distributions of tree regeneration may also follow these resource gradients, where certain regions of gaps may be more favorable for recruitment (Brown 1996; Powers et al. 2008). At northern latitudes, north-south resource gradients also can sort out tree regeneration. In some forest systems, more direct solar radiation and drier soils in northern portions of gap can introduce a trade-off of reduced seedling establishment and/or increased growth rates (Gray and Spies 1996, 1997; Wright et al. 1998). After germination, seedling establishment of many tree species can be very sensitive to high temperatures, drier soils, and competing vegetation (Montgomery et al. 2010; Arx et al. 2013; Andrus et al. 2018; Grossnickle 2018). Furthermore, the establishment of understory vegetation after canopy disturbance can also pattern along resource gradients (Gálhidy et al. 2006; Fahey and Puettmann 2007) and filter spatial patterns in tree regeneration (Royo and Carson 2006; Gilliam 2014). Light-demanding species, such as *Rubus* spp., may favor gap areas with

more light and tolerate drier soils, thus developing shrub layers in those areas that further limit seeding establishment (Ricard and Messier 1996; Kern et al. 2013; Knapp et al. 2021). Therefore, at the gap scale, the spatial organization of tree regeneration and thus areas of low-density regeneration may match the spatial patterns of resource gradients. The degree to which low-density regeneration patterns along resource gradients and changes with increasing gap size may offer further insight on the factors influencing regeneration patterns 10+ years after gap creation.

In this study, our objective was to investigate spatial patterns of low-density regeneration in canopy gaps. We mapped areas (patches) within gaps that met criteria of low-density regeneration at two study sites, 15 and 24 years post-harvest. Each study included a range of gap sizes, and one included a mature legacy tree positioned at gap center. We hypothesized that patches of low-density regeneration would pattern along spatial resource gradients most limiting to seedling establishment. Therefore, we predicted patches to be more common in northern regions of gaps, a result of more solar radiation and drier soils limiting seedling limitation. In larger gap sizes with higher overall light levels, we expected patches to occupy higher percentages of gap area with larger individual patch sizes. For gaps with legacy-tree retention, we hypothesized that patches would also wrap around legacy-tree canopies, resulting in patches nearer to gap edges and with more complex patch shapes.

3.2 Materials and Methods

We examined the spatial patterns of low-density regeneration at two long-term experimental trials of canopy gaps in northern hardwood forests of the upper Great Lakes region, USA. Both studies included a range of gap sizes, and one study retained a legacy tree at the center of each gap. Since the experiments were established approximately a decade apart, our data reflect conditions at 15 and 24 years post-harvest, respectively. Experimental design and study attributes are described below.

3.2.1 Study sites

3.2.1.1 Divide Canopy Gap Study

The Divide Canopy Gap Study (DCGS) was established in 1994 and is located within the Chequamegon-Nicolet National Forest in northern Wisconsin, USA (N 45°56', W88°59'). The study resides within a 136 ha second-growth northern hardwood forest. Mean annual temperature ranges from -8.7 °C to 18.8 °C and mean annual precipitation is 75.3 cm (Arguez et al. 2010). Regionally, the natural disturbance regime has been characterized predominately by windthrow and fire (Frelich and Lorimer 1991; Hupperts et al. 2018). Historical disturbances at the DCGS include exploitive timber harvesting during the 1870s-1890s that targeted eastern white pine (*Pinus strobus* L.) and a commercial hardwood clearcut in the 1930s (Rhemtulla et al. 2009), after which the site was unmanaged until 1994. At the time of study establishment, the forest was estimated to be 60 years old and in the stem exclusion stage of stand development (Kern et al. 2013). Sugar maple (*Acer saccharum* Marsh.) dominates the forest canopy at this site, and the primary habitat type observed is Acer-Tsuga/Dryopteris (ATD) (Burger and Kotar 2003; Cohen et al. 2014; Knapp et al. 2019b). Soil types are generally described as sandy loam to glacial outwash, consisting largely of a well-drained and deep Padus soil type with lesser components of Pence and Tipler (Soil Survey Staff 2007). Topographical features at the stand scale are best described by glacial kame and kettle patterns with small scale pit and mound topography from tree blowdowns. Aspect is often flat with smaller areas of variable directions and slope.

Gap size treatments at the DCGS were designed in randomized complete blocks. Three replicates of six treatments were randomly assigned a spatial location within four blocks (n = 56). Treatments were as follows: 0 m (reference), 3 m, 5 m, 10 m, 15 m, and 23 m radius circular canopy gaps. Gaps were cut during the winters of 1994 (2 blocks) and 1995 (2 blocks). All stems over 2.5 cm diameter at breast height (dbh) were cut, and commercial timber trees (>11.4 cm dbh) were removed from gaps. In the forest matrix adjacent to gaps, a concurrent “improvement cut” thinning operation (Erdmann 1986) reduced forest basal area to 23 m² ha⁻¹.

3.2.1.2 Yellow Birch Legacy-Tree Project

The Yellow Birch Legacy-Tree Project (YBLP) was established in 2003 at Michigan Technological University's Ford Center and Forest in Michigan's Upper Peninsula, USA (N 46°37', W 88°29'). This study is located within a 235 ha mature northern hardwood forest. Mean annual temperature ranges from -9.2 °C to 17.7 °C, and annual precipitation is 84.0 cm (Arguez et al. 2010). Historical disturbances include a substantial eastern white pine harvest in the 1890s and a harvest removing nearly 70% of merchantable timber (mainly hardwoods) in the 1930s. Forest management since the 1960s has used a single-tree selection system in which iterative harvests (10-15 year cycle) maintain a set residual basal area of 16.1-20.7 m² ha⁻¹ (Neuendorff et al. 2007). Sugar maple and red maple (*Acer rubrum* L.) dominate the forest canopy with minor inclusions of eastern hemlock (*Tsuga canadensis* L.) and yellow birch (*Betula alleghaniensis* Britton) (Shields et al. 2007). Primary habitat type of the site is ATD (Burger and Kotar 2003; Poznanovic et al. 2014). Soil types consist mainly of Champion cobbly silt loam with lesser components of Champion-Net complex, Witbeck muck and Alstad silt loam (Soil Survey Staff 2007). Topography is generally characterized as level to hilly upland moraines, with scattered pits and mounds from tree blowdowns. Aspect is variable but most commonly west- to north-facing and paired with gradual slopes.

Gap size treatments at the YBLP follow a complete randomized design. Three gap treatment radii of 11 m ($n = 16$), 16.5 m ($n = 17$), and 22 m ($n = 16$) were centered on mature yellow birch retained as legacy trees (Shields et al 2007). Twenty reference sites were established at the same time around mature yellow birch in the surrounding forest matrix. Spatial locations of each gap and reference site were randomly selected from a map of potential legacy trees such that a minimum buffer distance of 60 m was maintained between gap edges and/or reference sites. All stems over 10 cm dbh were cut inside gaps and were harvested in the winter of 2003 as part of a commercial timber sale. A concurrent single-tree selection harvest was performed in the surrounding forest matrix.

3.2.2 Data collection

We mapped the spatial extents of low-density regeneration at the YBLP in the summer of 2018 and the DCGS in the spring of 2019. These areas, or patches, consisted of no more than one sapling at or above 1.37 m per 10 m². Minimum patch area for mapping was based on the patch measuring ≥ 3 m across at the narrowest axis. Areas adjoining two patches needed to be ≥ 3 m wide to count as a single patch. Patch boundaries were truncated by driplines of border trees if necessary. All gaps at both studies were inspected for patch occurrence. However, due to lateral canopy closure from bordering trees, gaps with small initial areas (3 m and 5 m gap treatment radii at the DCGS) as well as reference sites did not contain patches that met our mapping criteria. In total, we sampled patches from 35 and 49 gaps at the DCGS and YBLP, respectively. Patch perimeters were mapped with a submeter Trimble GeoXH 6000 receiver. Global Positioning System (GPS) data were subsequently corrected with values obtained from the nearest Continually Operating Reference Station (CORS). Average horizontal precision error values for data recorded were slightly more accurate at the YBLP (mean 0.79 m, standard error [SE] ± 0.09) than those collected at the DCGS (mean 1.34 m, SE ± 0.14). Gap areas were calculated as eight-sided polygons determined from field-measured gap center to gap edge radii measured in the first or second year after gap creation (see Knapp et al. 2019b).

3.2.3 Data analyses

To test the distribution of patches along a north-south resource gradient, we compared data by two methods of gap area subdivisions: halves and quadrants. The first method compared percentage of gap area occupied by patches in the northern half of each gap to the southern half. Any patch polygon that occupied area intersecting the west-east axis of gaps were split into north and south patch portions. Areas of gap subdivisions were calculated as polygons consisting of the subset of gap radii that matched the subdivision. The second method compared percentages between quadrants subdivisions of gap areas (each quadrant centered on bearings of 0, 90, 180, 270). Similar to the procedure above, patch polygons were split and area summed according to their spatial intersection with gap quadrant then divided by quadrant specific gap area to generate a percentage value.

To compare the patch response between subdivisions of gap area, we used linear mixed-effects models in R version 4.0.3. (R Core Team 2020) using the *nlme* package v 3.1-149 (Pinheiro et al. 2020). A separate model was created for each study with gap subdivision and gap treatment radius as fixed effects. Models at the DCGS included a random effect of gap identification (ID) nested within block ID, and models at the YBLP included gap ID as a random effect. After model validation, post-hoc pairwise comparisons of estimated marginal means using the Tukey method were performed within each gap treatment radii between halves and quadrants with the *emmeans* package v. 1.5.4 (Lenth 2021). An arcsine transformation was performed on the proportional dependent variable to improve the normality of residual distributions and improve model fit (Gotelli 2004; Zuur et al. 2009).

To examine the distributions of patch distances from gap edges, we calculated the percentage distance from gap edge for all patch areas. Patch polygons were converted to a raster of cell size 0.25 m, which was determined by an iterative method to minimize transformation error adapted from Congalton (1997) and resulted in no less than 95% accuracy in area comparison between the two data types. Gap edges were defined for each gap as straight lines connecting neighboring gap radii. Then, distances were measured from each raster cell center (representing 0.0625 m² of patch area) to nearest gap edge. In order to compare distances between gap treatment radii, percentage distance from edge was calculated for each patch cell as near distance to edge divided by the average gap radii distance for the corresponding gap. Negative values were attributed to patch areas outside of straight lines of gap edges. We included these data in our analyses as we attribute these values to some gap edges that expanded in distance from center since creation (Klingsporn et al. 2012) and variations related to the horizontal precision error of the GPS unit as reported above. Linear mixed-effects models were generated for each study in R version 4.0.3 (R Core Team 2020) using the *nlme* package v. 3.1-149 (Pinheiro et al. 2020). Gap treatment radius was defined as the fixed effect and a hierarchical structure of patch ID nested within gap ID were defined as random effects (the DCGS included block ID at the highest nested level). To compare percentage distance distributions between gap treatment radii, pairwise comparisons of marginal

means (Tukey method) were generated for each gap treatment radii within studies with the *emmeans* package v. 1.5.4 (Lenth 2021).

To compare individual patch congruency across gap treatment radii, patch shapes and dimensions were analyzed with the software FRAGSTATS (McGarigal et al. 2012). First, patch polygons were converted to a raster (cell size 0.5 m) using a similar method as stated above but we chose a larger cell size to minimize discontinuous patch fragments. Any patch fragments with an area less than 0.5 m² were removed from the analysis (n = 7). Any gap areas without occupying patches were specified as internal background and areas outside of gap edges were specified as external background. We chose two metrics to assess patch shapes and dimensions across gap treatment radii. Shape index quantifies the irregularity of patch shape and is calculated by patch perimeter divided by the square root of patch area adjusted by a square standard constant of 0.25 (McGarigal et al. 2012). A square patch will have an index of 1, and the index increases indefinitely with patch irregularity. Core area index is defined as the patch area inside of a specified patch edge depth divided by total patch area (units are a percentage) (McGarigal et al. 2012). We chose this metric as an approach to compare areas of most persistent resistance to tree regeneration and a relative measure of individual patch size. At the lower limit (0%), core area index describes a patch that consists entirely within the patch edge depth, whereas a patch approaching the upper limit (100%) has higher proportions of core area inside the edge depth. We specified the patch edge depth to 1.5 m as it was half the minimum value of patch diameter. Linear mixed-effects models were generated for each metric and each study in R version 4.0.3 (R Core Team 2020) using the *nlme* package v. 3.1-149 (Pinheiro et al. 2020). The fixed effect was defined as gap treatment radius and random effects were gap ID (YBLP) or gap ID nested within block ID (DCGS). Differences between gap treatment radii were analyzed by post-hoc pairwise comparisons (Tukey method) with the *emmeans* package v. 1.5.4 (Lenth 2021).

The relationship between percentage of gap area occupied by patches and gap areas were examined with linear models in R version 4.0.3 (R Core Team 2020). Our dependent variable was proportional patch area, defined as the sum of patch areas divided by gap area. Separate models were created for each study: DCGS, linear mixed-effects;

YBLP, simple linear model. At the DCGS, models were created with the *nlme* package v. 3.1-149 (Pinheiro et al. 2020); the fixed effect was gap area and random effect was block ID. The model for the YBLP was created with the R core package *STATS* (R Core Team 2020) and also included gap area as the fixed effect. For the YBLP, we also performed a sensitivity analysis to examine the influence of legacy tree mortality on patch attributes (4 legacy trees died prior to sampling by Klingsporn et al. [2012] 8-years post-harvest). To accomplish this, we created a second linear model that excluded the 4 gaps that experienced legacy-tree mortality. Validation of model assumptions were assessed visually, and an arcsine transformation was performed on the proportional dependent variable to improve the normality of residual distributions and improve model fit (Gotelli 2004; Zuur et al. 2009).

3.3 Results

3.3.1 Spatial patterns of low-density regeneration

At the DCGS, patches of low-density regeneration ($n = 27$) were observed in 23 of the 53 gaps inspected (Table 3.1). At the YBLP, patches ($n = 44$) were observed in 29 of the 49 gaps inspected (Table 3.1). Patches were not preferentially found in the northern or southern halves of gaps (DCGS: $P = 0.487$, YBLP: $P = 0.192$; Table 3.2, Figure 3.1, 3.2), nor were greater patch areas found in quadrants corresponding to cardinal directions within gaps (DCGS: $P = 0.521$, YBLP: $P = 0.177$; Table 3.2, Figure 3.1, 3.2). Our area-based approach to compare patch distance from gap edge revealed similar trends within studies and across gap treatment radii (Figure 3.3). There were no differences between patch distance from gap edge in any of the gap treatment radii (DCGS: $F_{2, 17} = 2.317$, $P \geq 0.129$; YBLP: $F_{2, 26} = 0.315$, $P \geq 0.732$; Table 3.3). Mean \pm SE percentage patch distance from edge at the DCGS were $42.1 \pm 0.5\%$ in the 10 m, $41.4 \pm 0.6\%$ in the 15 m, and $41.4 \pm 0.5\%$ in the 23 m radius gaps. Mean values at the YBLP were $31.4 \pm 0.6\%$ in the 11 m, $29.5 \pm 0.6\%$ in the 16.5 m, and $32.7 \pm 0.4\%$ in the 22 m radius gaps. Although we did not directly compare study sites in our analysis because of differences in experimental design, distributions of proportional distance to gap edge at the YBLP were more variable and closer to gap edges than distributions at the DCGS. Coefficients of variation

(standard deviation divided by mean) averaged 0.52 ± 0.1 at the DCGS and 0.67 ± 0.02 at the YBLP.

Shape indices remained regular at the YBLP even as gap treatment radii increased ($F_{2, 26} = 2.178$, $P = 0.133$; Table 3.4, Figure 3.4). However, although there were no overall trends at the DCGS ($F_{2, 10} = 3.208$, $P = 0.084$, Table 3.4) patch shape indices were slightly more regular (or less complex) in 23 m compared to 15 m gaps ($p = 0.07$, Table 3.4). While core area index maintained very similar values for all gap treatment radii at the YBLP ($F_{2, 26} = 0.171$, $P = 0.845$, Table 3.4), the DCGS core area index model ($F_{2, 10} = 3.898$, $P = 0.056$, Table 3.4) indicated an increase in individual patch extents in the largest gaps compared to patches in the smallest gap treatment radius ($p = 0.046$, Table 3.4, Figure 3.4).

3.3.2 Influence of gap area on low-density regeneration

At the DCGS, the total percentage of gap area occupied by patches was 17.3% and averaged $3.9 \pm 1.7\%$ in the 10 m, $16.2 \pm 4.9\%$ in the 15 m, and $18.8 \pm 4.9\%$ in the 23 m radius gaps. Variation in percentage gap area occupied exhibited a strong and positive relationship with gap area ($p = 0.012$; Table 3.5, Figure 3.5). At the YBLP, the total gap area occupied by patches was 4.8% and averaged $3.8 \pm 1.8\%$ in the 11 m, $6.7 \pm 2.4\%$ in the 16.5 m, and $3.8 \pm 1.5\%$ in the 22 m radius gaps. Variation in percentage gap area occupied did not reveal a relationship with gap area ($p = 0.513$; Table 3.5, Figure 3.5). In total, 4 legacy trees died before year 8 post-harvest. A sensitivity analysis revealed that these observations did not have high leverage as the relationship remained non-significant when they were omitted from the model ($p = 0.167$, Table 3.5).

Table 3.1. Summary of gap and low-density regeneration patch attributes at two experimental gap studies in northern hardwood forests of the upper Great Lakes states, USA. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Mean patch frequency was calculated as mean number of patches that occurred in each gap replicate, summarized by gap treatment radius. For patch size, values represent mean for all patches sampled, summarized by gap treatment radius. \pm denote standard errors, m = meters.

Study	Legacy-tree retention	Years post-harvest	Gap treatment radius (m)	No. of replicates	Mean gap size (m ²)	No. of replicates with patches	Mean patch Frequency	Mean Patch Size (m ²)
DCGS	No	24	10	11	249.78 \pm 28.27	4	0.36 \pm 0.15	30.34 \pm 3.27
			15	12	699.27 \pm 26.81	9	0.83 \pm 0.17	135.57 \pm 35.59
			23	12	1729.03 \pm 54.14	10	1.41 \pm 0.26	236.76 \pm 64.81
YBLP	Yes	15	11	16	321.23 \pm 15.78	5	0.31 \pm 0.12	29.77 \pm 6.62
			16.5	17	697.46 \pm 21.17	12	1.12 \pm 0.26	42.66 \pm 9.62
			22	16	1238.81 \pm 36.36	12	1.25 \pm 0.28	39.69 \pm 7.77

Table 3.2. Comparisons of mean \pm SE percentage gap area occupied by patches between subdivisions of gap area and gap treatment radii. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Linear mixed-effects models were created for half and quadrant comparisons separately by study. Random effects were gap ID (YBLP) or gap ID (nested) within block ID (DCGS). Pairwise comparisons were generated from differences between estimated marginal means of subdivision and gap treatment radii. *p*-values represent the lowest value of pairwise comparisons between subdivision directions (D) and between directions within each gap treatment radius group (D x TR). For *p*-values below 0.1, the pairwise comparison was listed below value.

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DCGS Halves ($F_{1, 32} = 0.494, P = 0.487$)					YBLP Halves ($F_{1, 46} = 1.755, P = 0.192$)				
	10m	15m	23m	p -value (D)		11m	16.5m	22m	p -value (D)
North	3.35 ± 2.24	20.15 ± 6.68	21.44 ± 5.85	0.476	North	4.11 ± 2.42	8.8 ± 3.5	4.93 ± 2.3	0.195
South	5.72 ± 3.17	19.08 ± 6.46	23.2 ± 6.03		South	2.47 ± 2.07	4.88 ± 2.08	2.69 ± 1.15	
p -value (D x TR)	0.438	0.955	0.616		p -value (D x TR)	0.502	0.315	0.555	
DCGS Quadrants ($F_{3, 96} = 0.757, P = 0.521$)					YBLP Quadrants ($F_{3, 138} = 1.664, P = 0.177$)				
	10m	15m	23m	p -value (D)		11m	16.5m	22m	p -value (D)
North	3.24 ± 2.59	18.54 ± 6.74	23.16 ± 6.66	≥0.486	North	5.18 ± 3.12	10.82 ± 4.22	5.36 ± 2.96	≥0.133
East	3.5 ± 2.35	14.9 ± 5.84	20.42 ± 4.49		East	0.44 ± 0.31	6.95 ± 3.74	4.94 ± 1.82	
South	6.02 ± 4.26	17.69 ± 6.37	24.93 ± 8.08		South	3.79 ± 2.95	7.52 ± 2.97	3.29 ± 1.92	
West	4.48 ± 2.93	26.8 ± 10.04	21.73 ± 6.92		West	2.37 ± 1.53	2.37 ± 1.42	1.83 ± 0.68	
p -value (D x TR)	≥0.965	≥0.16	≥0.856		p -value (D x TR)	≥0.512	≥0.054 (N vs W)	≥0.882	

Table 3.3. Comparisons of patch mean \pm SE percentage distance from edge between gap treatment radii. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Linear mixed-effects models were created for each study. Random effects were patch ID (nested) within gap ID (YBLP), or patch ID within gap ID within block ID (DCGS). Pairwise comparisons were generated from differences between estimated marginal means of gap treatment radii. *p*-values represent the lowest value of pairwise comparisons.

DCGS ($F_{2, 17} = 2.317, P = 0.129$)				YBLP ($F_{2, 26} = 0.315, P = 0.732$)			
10m	15m	23m	<i>p</i> -value	11m	16.5m	22m	<i>p</i> -value
42.05 \pm 0.47	41.14 \pm 0.16	41.4 \pm 0.08	≥ 0.11	31.4 \pm 0.52	29.5 \pm 0.19	32.75 \pm 0.16	≥ 0.765

Table 3.4. Comparisons of patch mean \pm SE shape indices and core area indices between gap treatment radii. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Linear mixed-effects models were created for each metric at both studies. Random effects were gap ID (YBLP), or gap ID (nested) in block ID (DCGS). Pairwise comparisons were generated from differences between estimated marginal means of gap treatment radii. *p*-values represent the lowest value of pairwise comparisons. Asterisks (*) denote statistically significant differences (>0.05) and the pairwise comparison that generated the lowest value (when under 0.1) is listed below the *p*-value.

DCGS Shape Index ($F_{2, 10} = 3.208$, $P = 0.084$)				YBLP Shape Index ($F_{2, 26} = 2.178$, $P = 0.133$)			
10m	15m	23m	<i>p</i> -value	11m	16.5m	22m	<i>p</i> -value
1.61 \pm 0.13	1.77 \pm 0.1	1.49 \pm 0.05	≥ 0.071 (15m - 23m)	1.56 \pm 0.19	1.57 \pm 0.06	1.4 \pm 0.05	≥ 0.129
DCGS Core Area Index ($F_{2, 10} = 3.898$, $P = 0.056$)				YBLP Core Area Index ($F_{2, 26} = 0.171$, $P = 0.845$)			
10m	15m	23m	<i>p</i> -value	11m	16.5m	22m	<i>p</i> -value
7.34 \pm 3.58	36.27 \pm 6.68	39.85 \pm 5.85	$\geq 0.046^*$ (10m - 23m)	12.53 \pm 4.55	12.18 \pm 2.99	15.2 \pm 3.34	≥ 0.833

Table 3.5. Linear mixed-effects model (DCGS) and linear models (YBLP) for percent gap area occupied by patches predicted by gap area. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². The DCGS includes Block ID as a random effect to account for hierarchy of study design. The second model at the YBLP is a sensitivity analysis in which 4 gaps that experienced legacy-tree mortality at or before year 8 post-harvest were removed from the model.

	Fixed Effect	Estimate	Standard Error	df	t-Value	Pr(> t)	Random Effect	Std Dev of Intercept	Std Dev of Residual
	DCGS								
	Gap Area	1.74E-04	6.46E-05	30	2.688	0.012*	Block ID	6.76E-06	0.241

	Fixed Effect	Estimate	Standard Error	df	t-Value	Pr(> t)	F-statistic	Residual standard error	
	YBLP (<i>all gaps</i>)								
	Gap Area	4.14E-05	6.28E-05	47	0.66	0.513	0.436	0.169	
	YBLP (<i>only gaps with living legacy trees after year 8</i>)								
	Gap Area	7.46E-05	5.29E-05	43	1.41	0.166	1.989	0.14	

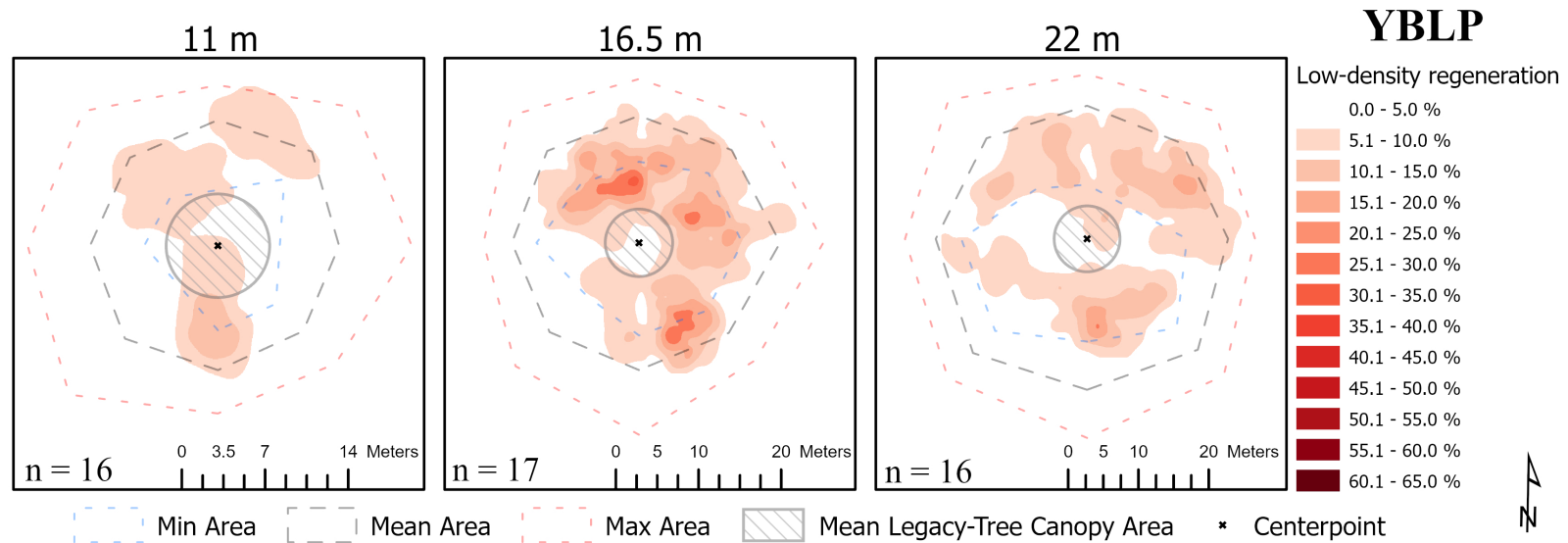
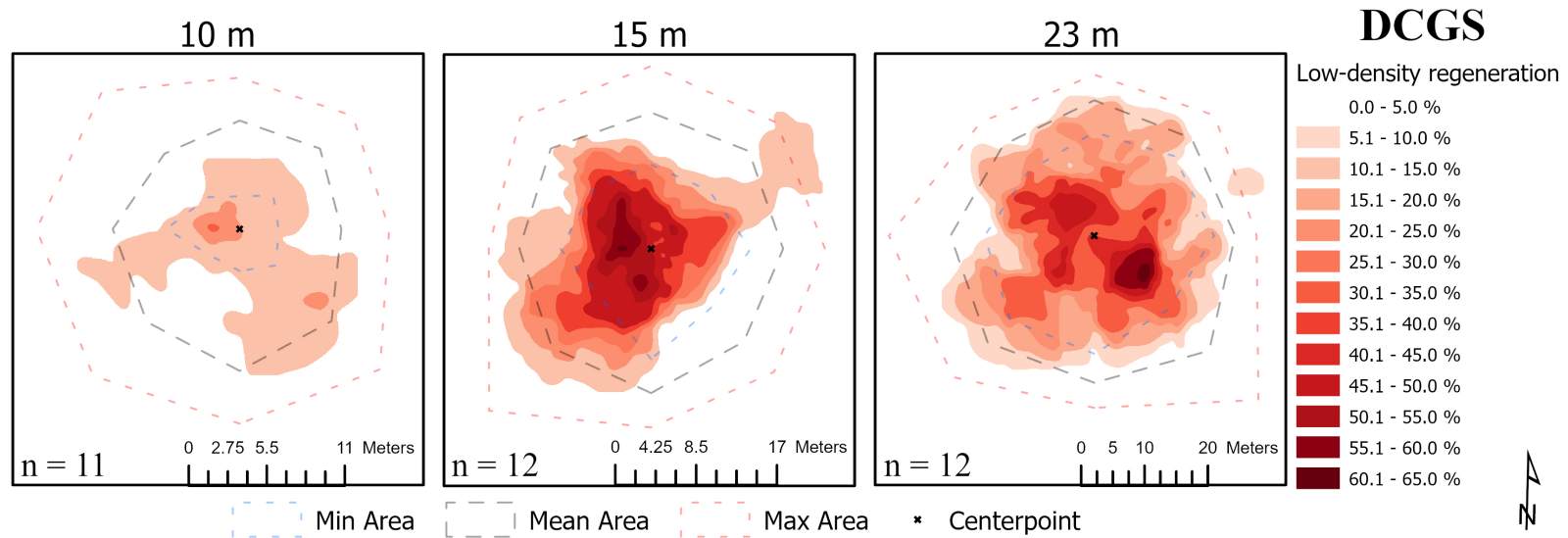


Figure 3.1. Heat map of patches of low-density regeneration at two experimental gap studies in northern hardwood forests of the upper Great Lakes states, USA. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Kernel density maps were generated by translocating patches into a common gap centerpoint from gap replicates that share study and gap treatment radius categories. Percentage low-density regeneration for each gap grouping was calculated as the number of gap replicates with patches present at each spatial location divided by total number of replicates. Mean, minimum, and maximum gap areas, also mean legacy tree canopy areas and gap centerpoints included for reference. Note difference in scale for each map inset.

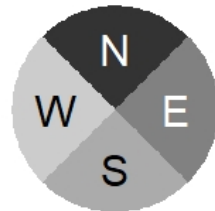
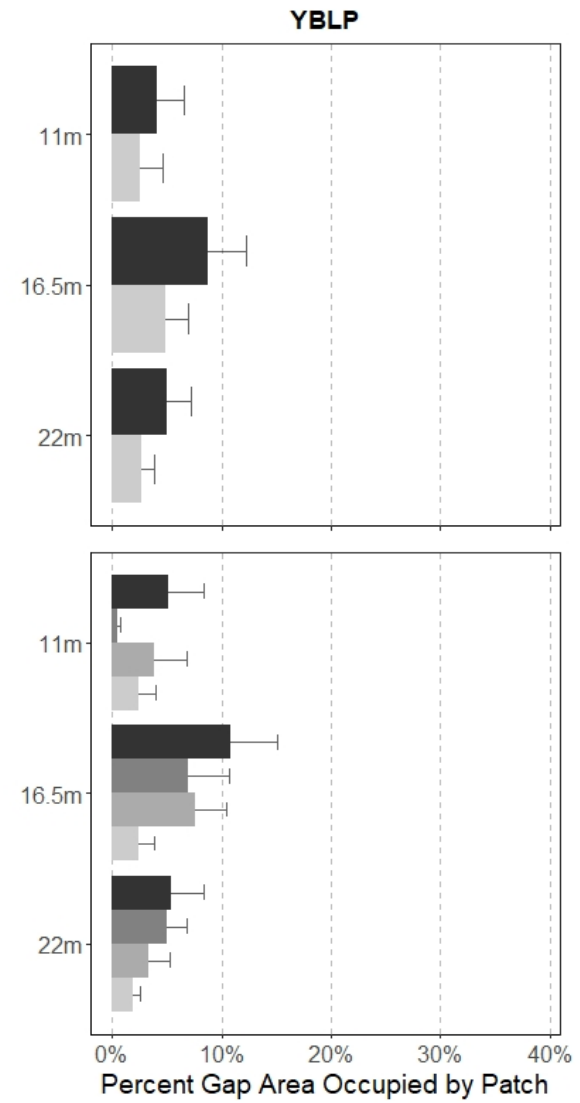
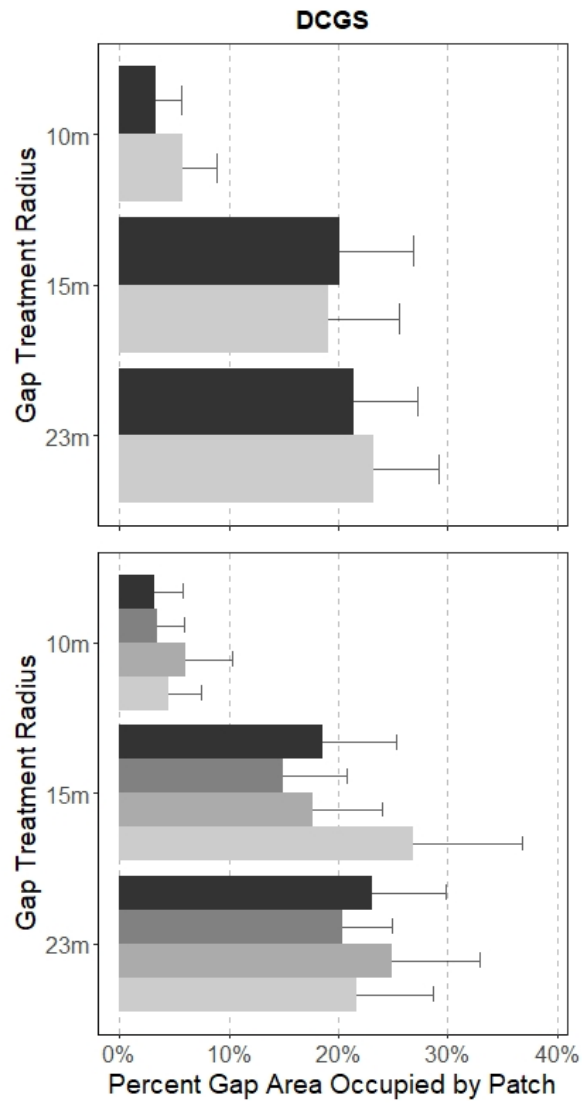


Figure 3.2. Bar graphs of percent gap area occupied by patches for subdivisions of gap area in halves and quadrants summarized by study and gap treatment radius category. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Bar lengths represent mean percent gap area occupied by patches for each subdivision, error bars represent standard errors of mean. Pie chart legends represent subdivisions of gap area locations within gaps. No differences ($p \geq 0.178$) between any subdivisions of gap area were detected.

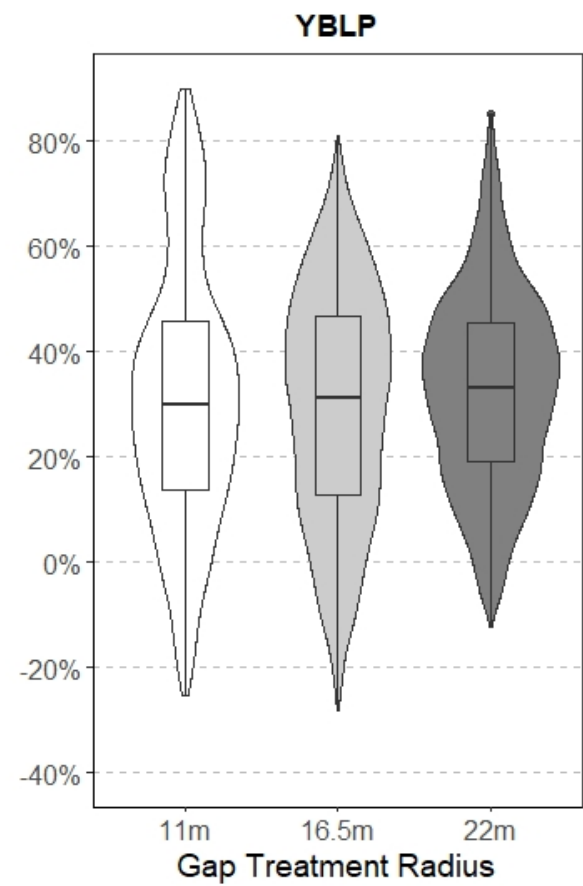
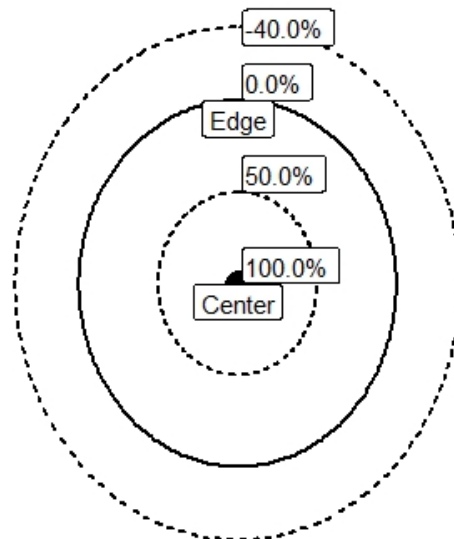
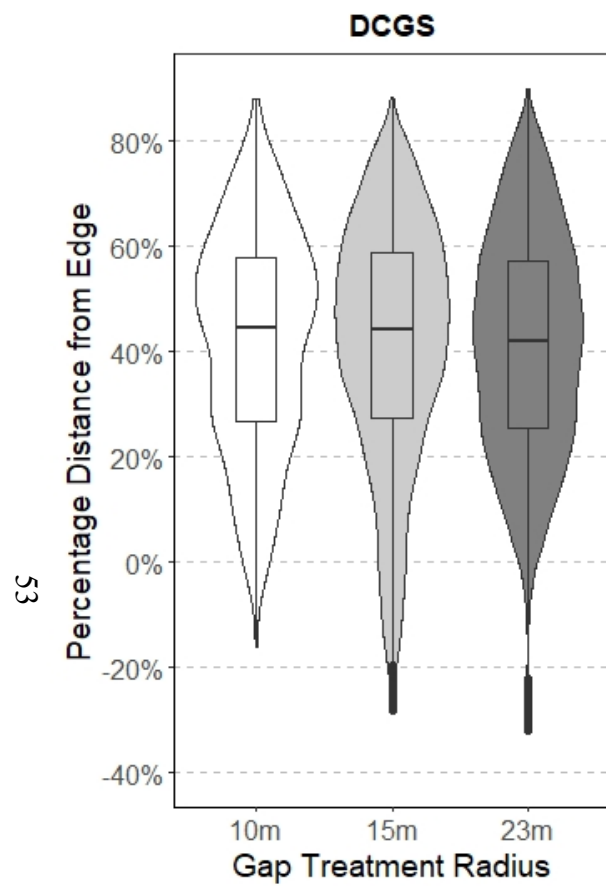


Figure 3.3. Violin box plot distributions of low-density regeneration percentage distance from edge summarized by study and gap treatment radius category. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Violin plots are a mirrored density estimate of distribution scaled to a uniform maximum of 1. Area of violin plots are not representative of patch area. Nested box plot center horizontal line represents median, box edges are first and third quartiles, bold dots or lines at edge of distribution represent outliers. Key in center indicates spatial location of percentage thresholds from gap edge. No significant differences ($p \geq 0.128$) between any gap treatment radii were detected.

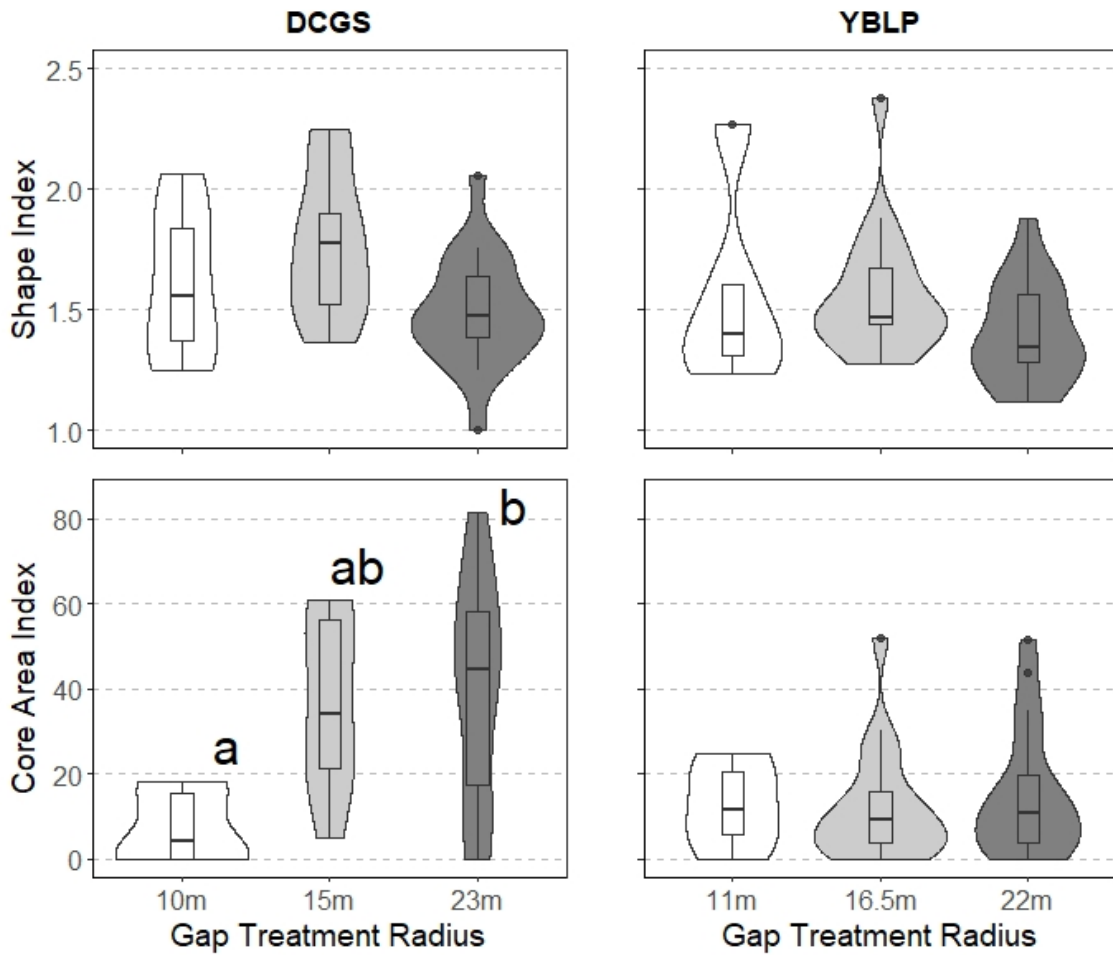


Figure 3.4. Violin box plot distributions of FRAGSTATS metrics of patch shape index and patch core area index summarized by study and gap treatment radius. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Violin plots are a mirrored density estimate of distribution scaled to a uniform maximum of 1. Nested box plot center horizontal line represents median, box edges are first and third quartiles, bold dots or lines at edge of distribution represent outliers. Letters denote statistically significant difference in distributions within DCGS for core area index (10 vs 23 m, $p = 0.046$; Table 3.4).

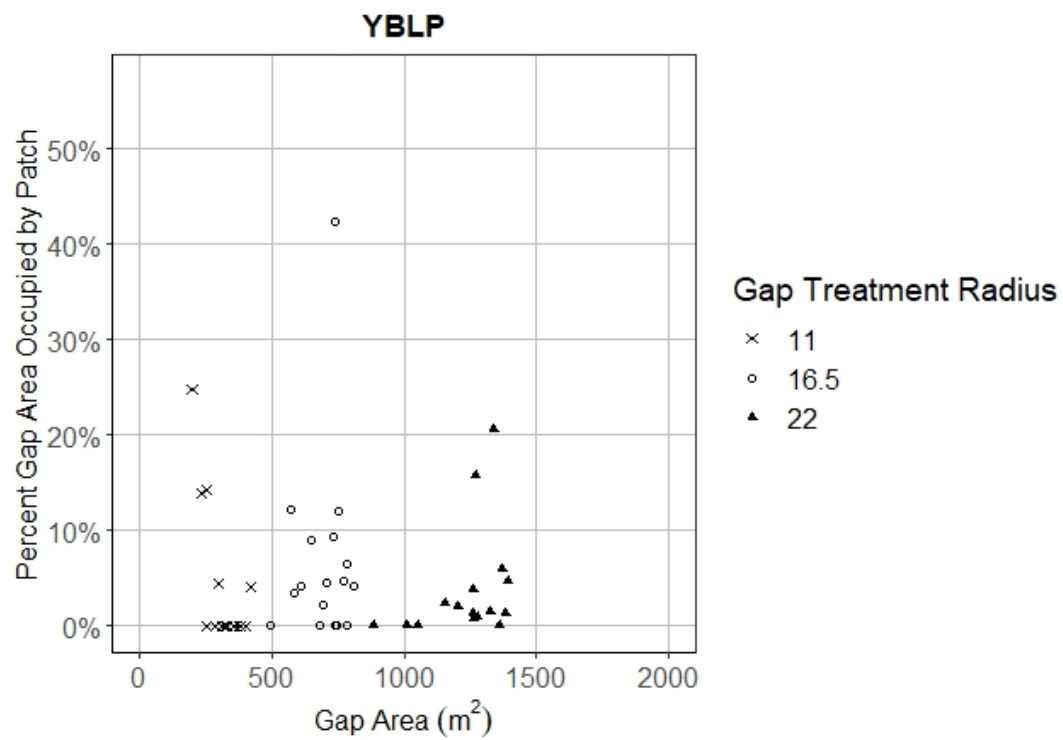
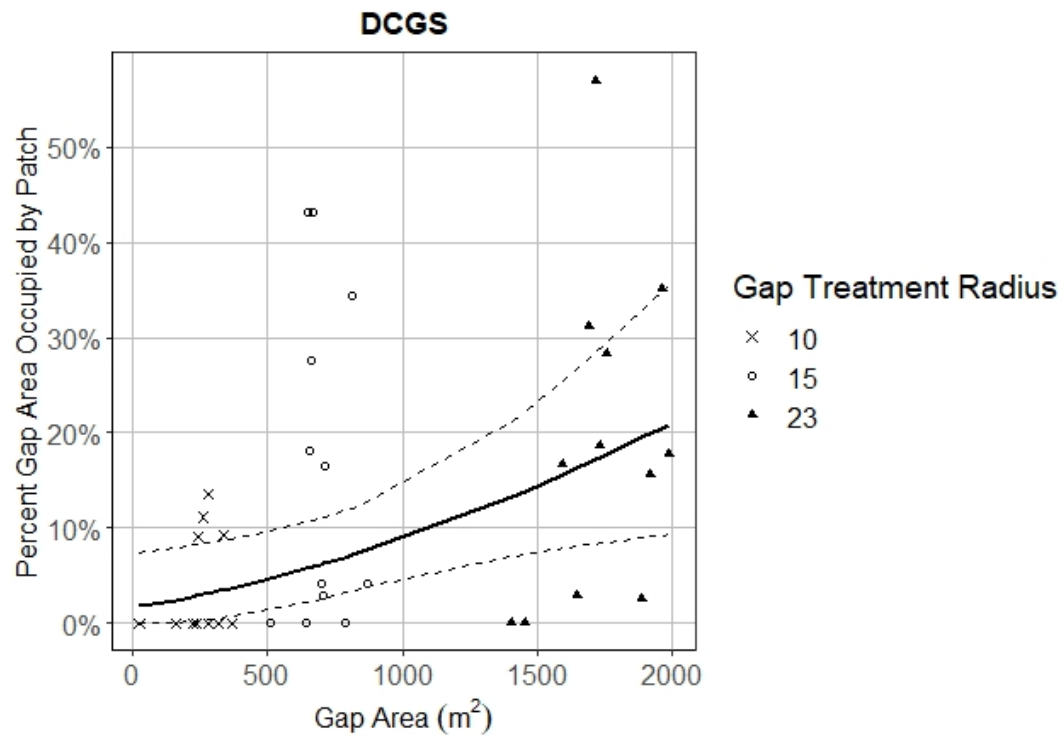


Figure 3.5. Scatterplots of percent gap area occupied by patches and gap area for YBLP and DCGS. Patches were defined as areas consisting of no more than one sapling at or above 1.37 m per 10 m². Values for each gap are organized by gap treatment radius and represented by their corresponding shape. Solid line represents predictions of a linear mixed-effect model (DCGS) indicating a positive linear relationship with the predictor of gap area (see Table 3.5), dashed lines indicate intervals of 95% confidence.

3.4 Discussion

Collectively our results suggest that spatial patterns of low-density regeneration are likely determined by factors disentangled from within-gap spatial resource gradients. At the gap scale, patches did not associate with northern regions of gaps. Larger gap sizes were more susceptible to areas of low-density regeneration at one study site, but legacy-tree retention appeared to moderate patch extents. Patches tended to occupy areas nearer to gap edges in gaps that retained legacy trees, but patch shape complexity remained similar throughout all gaps. Our findings suggest that randomly arranged patterns of advance regeneration may have determined spatial areas of low-density regeneration. However, patterns may also be influenced by other constraints such as competing vegetation, deer herbivory, and/or microsite limitation. Furthermore, legacy-tree retention may be a complimentary strategy to abate areas of low-density regeneration in gaps. In addition to the creation of canopy gaps and legacy-tree retention, further considerations and/or modifications to the regeneration environment may be needed to achieve timely recruitment goals in northern hardwoods.

Spatial distributions of low-density regeneration did not sort out as hypothesized along spatial resource gradients at the gap scale. Canopy disturbances modify resource availability in the forest understory and can pattern tree regeneration along resource gradients (Denslow 1980; Canham et al. 1990; Barik et al. 1992). At northern latitudes, northern portions of large canopy gaps receive more direct sunlight resulting in drier soil conditions (Raymond et al. 2006), which may limit tree seedling establishment and favor ruderal species. For example, in western coniferous forest gaps, Gray and Spies (1996) found that conditions in northern regions of canopy gaps tended to limit seedling establishment even if they were beneficial to growth. Similar patterns of establishment versus growth have been observed in northern hardwood forests gaps for tree species particularly sensitive to moisture stress as seedlings (Poznanovic et al. 2014). On the other hand, both establishment and growth of many ruderal species are favored by high-resource availability and can quickly dominate post-disturbance environments (Gálhidy et al. 2006; Fahey and Puettmann 2007). This layer can have a strong filtering effect on spatial patterns in tree regeneration (Royo and Carson 2006; Gilliam 2014).

Consequently, it is notable that patterns of low-density regeneration within gaps at the two study sites we examined did not map closely along resource gradients. Instead, patches tended to be more uniformly distributed within gaps and did not increase in prevalence in more illuminated zones relative to other gap regions. There was however a general tendency for patches of low-density regeneration to increase in prevalence with gap size when legacy trees were not retained. This suggests that although patches did not sort along resource gradients in gaps, changes such as total light availability in larger gaps may be related to the magnitude of patch extent.

Gap size has been linked previously to overall abundance of some species of competing vegetation, such as *Rubus* spp. (Shields et al. 2007; Kern et al. 2013). *Rubus* spp. are among a larger group of species that can form recalcitrant vegetation layers and severely limit seedling establishment (Royo and Carson 2006). In previous research at the DCGS, Kern et al. (2013) found higher densities of *Rubus* spp. in larger gap sizes at year 12 post-harvest. Similarly, at the YBLP, Shields and Webster (2007) reported increasing cover of *Rubus* spp. that tracked with increasing opening size at year 2 and Widen et al. 2018 found a similar relationship at year 13 post-harvest. Other highly competitive species of sedge and fern may also compete with trees for growing sites in large gaps (George and Bazzaz 1999; Cretaz and Kelty 2002; Engelman and Nyland 2006; Shields et al. 2007; Powers and Nagel 2009). Nevertheless, the occurrence of competing vegetation in larger gaps soon after harvest has not proven to be a strong predictor of future regeneration patterns. For example, Donoso and Nyland (2006) suggest that in eastern forests, regenerating stems generally overtop *Rubus* shrubs within 5-7 years of disturbance. Similarly, at the DCGS and YBLP, while surprisingly persistent at the gap scale, abundance of *Rubus* spp. on sample plots soon after harvest has been a poor predictor of future tree sapling density 15-20 years post-harvest (Widen et al. 2018; Knapp et al. 2021). The best long-term overall predictor of tree recruitment into the gap cohort at these studies has been the abundance of advance regeneration present after harvest (Widen et al. 2018; Knapp et al. 2021). While the risk of low-density regeneration may increase with gap size, patches of competing vegetation may be a

consequence rather than a cause of low-density regeneration at the study sites we examined.

Overall abundance and underlying spatial distributions of advance regeneration may help to explain the patterning of low-density regeneration. Established seedlings of shade-tolerant species can persist for many years in the understory before a canopy disturbance and subsequent release (McClure et al. 2000; Wright et al. 2000). In temperate hardwood forests, the removal of advance regeneration after harvest can promote the recruitment of midtolerant species (Gauthier et al. 2016) or result in large areas of delayed recruitment (Metzger and Tubbs 1971; Kern et al. 2013; Knapp et al. 2021). Sugar maple comprised the majority of advanced regeneration before harvest at our study sites (Knapp et al. 2019b). In a northern hardwood forest, Messaoud and Houle (2006) found seedling establishment of sugar maple to be largely uncoupled from spatial variation in soil nitrogen, moisture, litter depth, and light. Other studies confirm that even after disturbance, sugar maple does not partition along resource gradients (Sipe and Bazzaz 1995; McClure and Lee 2011). Therefore, areas of low-density regeneration may pattern after spatially random distributions of advance regeneration at the gap scale.

Furthermore, patches shared simple, congruent shapes across all gaps. We predicted that more complex patterns of resource heterogeneity in gaps at the study site with legacy-tree retention would result in patch shapes of greater complexity. While there may have been a slight decrease in shape complexity in the largest gaps at the DCGS, our results overall may indicate the presence of some common spatial constraints on areas of low-density regeneration. We assumed patch sizes would be large enough to wrap around legacy-trees, but our findings suggest that small, discontinuous patches collectively wrap around legacy trees. However, our criteria for patch delineation and conversion to shape index may have over generalized differences in patch shapes across gaps at our study sites.

The retention of legacy-trees at one study site may help explain variations in the patch response between the two study sites. Contrary to our prediction, the proportion of area occupied by low-density regeneration remained similar for all gap sizes at the YBLP. Moreover, legacy-tree retention seemed to regulate patch core areas and resulted in patch

locations closer to gap edges. Tree retention can limit light levels and slow regeneration growth, but may also increase densities of regenerating stems (Urgenson et al. 2013; Wike et al. 2019). In other studies, the retention of reserve trees (or multiple legacy trees) alleviated some negative consequences of heavy harvests by increasing seed availability (Freitas and Pinard 2008) and enriching resource heterogeneity (Gustafsson et al. 2010; Fedrowitz et al. 2014). Thus, retention may be valuable as a strategy to meet recruitment goals of greater diversity in northern hardwood forests (D'Amato et al. 2015; Knapp et al. 2019a). However, considerable differences in the amount of advance regeneration retained at each study site may strongly influence differences in patch patterns (Widen et al. 2018; Knapp et al. 2021). Moreover, differences in historical land-use, management history, harvest methods, rates of deer herbivory, soil type, and others may all contribute to contrasting patch response between study sites (Knapp et al. 2019b). Nevertheless, our results are encouraging and clearly suggest further investigation related to legacy trees may help inform management practices aimed at increasing resiliency and species diversity.

Areas of low-density regeneration were common at two canopy gap studies 15 and 24 years post-harvest. At the gap scale, spatial patterns of low-density regeneration did not follow expected patterns in resource gradients. Spatial distributions may rather be organized according to randomly arranged patterns of advance regeneration or other constraints such as competing vegetation and deer herbivory. Larger gaps revealed a higher risk of low-density regeneration only at the study site without legacy-tree retention. Although legacy-tree retention seemed to moderate the spatial extent of low-density regeneration, further research is needed to clarify the mechanisms of legacy trees in this forest system.

4 Conclusion

Although there can be many obstacles that prevent a robust and diverse regeneration response after disturbance in northern hardwood forests, there are also opportunities to overcome these challenges. This research focused on results from well-replicated, long-term, gap-based silviculture experiments 15-24 years post-harvest. Our results reiterate the need for further modifications to the regeneration environment beyond simply varying gap sizes. The limitations interfering with successful recruitment may be complex, but our findings suggest there may be simple solutions that may help practitioners achieve recruitment goals.

The exclusion of deer in hemlock canopy gaps may promote the recruitment of underrepresented, browse sensitive species such as yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock (*Tsuga canadensis* L.) (Chapter 2). Although sugar maple (*Acer saccharum* Marsh.) tended to dominate cohort composition across height classes, gap sizes, and exclosure treatments, browse sensitive species recruited into the tallest layers of regenerating stems only within deer exclosures and larger gap sizes (>150 m²). Moreover, browse sensitive seedlings were abundant outside exclosures at heights below average winter snowpack, which indicates these species were able to overcome microsite limitations, but unable to overcome herbivory and advance into taller height classes.

Spatial patterns of low-density regeneration at two experimental gap studies are plausibly driven by factors disentangled from resource gradients at the gap scale (Chapter 3). Although increasing gap size was associated with larger percentages of gap areas occupied by low-density regeneration at one study site, spatial distributions did not reflect the north-south gradient of light and soil resource gradients likely present in these gaps. In context of previous research at these study sites (Kern et al. 2013; Widen et al. 2018; Knapp et al. 2021), our results may also provide some support to the conclusion that a lack of advance regeneration may be a primary driver of low-density regeneration. Furthermore, the study site with legacy-tree retention appeared to moderate areas of low-density regeneration and push these areas closer to gap edges.

Therefore, our results suggest that strategies such as the installation of deer exclosures and gap placement in areas of sufficient and desirable advance regeneration

may accelerate gap capture and enhance tree species diversity. The deer exclosures installed at the hemlock canopy gap study were simply constructed, economical, and enclosed a very small percentage (~3.5%) of gap area. Similarly, in forests with areas of sufficient biological and material legacies (e.g. advance regeneration, seed trees, coarse woody debris), adjustments of gap placement and the protection of these legacies during harvest should be prioritized. Depending on stand/site conditions, more extensive measures such as vegetation control (Man et al. 2009), soil scarification (Willis et al. 2015), artificial plantings (Owings et al. 2017), or other novel techniques and/or combinations may be needed to overcome limitations. Many managed northern hardwood stands struggle to regenerate naturally after a harvest treatment (Kern et al. 2017; Henry et al. 2021). However, robust and diverse recruitment goals may be achieved with silvicultural methods well-suited for stand-specific regeneration limitations (Webster et al. 2018; Kenefic et al. 2021).

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