

Initial effects of structural complexity restoration treatments and deer browsing on  
ground-layer community composition and tree regeneration in northern hardwood forests

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## **Abstract**

As researchers realize the value of old-growth forests and their unique attributes and dynamics, managers have begun developing management regimes aimed at restoring old-growth characteristics in forests managed for wood products. However, changes in these forests since European settlement, especially increased population of white-tailed deer (*Odocoileus virginianus* Zimmerman) may have important implications for forest composition and regeneration. The objective of this research was to determine the initial (three- and four-year) effects of several old-growth structural restoration treatments and browsing by white-tailed deer on tree regeneration and understory community composition in northern hardwood forests in northern Wisconsin, USA. Community composition and tree regeneration were measured in stands with six different silvicultural treatments replicated across three large study areas (> 50 ha). Treatments consisted of a combination of two levels of coarse woody debris and three overstory gap treatments designed to emulate patterns of natural gap and mesoscale canopy disturbance: small gaps (10.7m diameter), large gaps (18.3 and 24.4m diameter), and a mesoscale wind disturbance treatment consisting of 0.4 and 1.2 ha shelterwoods. All treatments included multiple small deer exclosures to examine the impact of deer herbivory.

Assessment of cover by herbaceous plants and seedlings indicated that overstory treatments had a larger effect on understory community composition than browsing by deer, whereas there was no effect of coarse wood levels. Species richness was highest in the small gap treatment and lowest in the control stands, possibly reflecting the increased

dominance by a few ruderal and exotic species in treatments with increased canopy openness. Richness was also significantly lower inside exclosures than outside in some treatments, although browse-sensitive *Trillium* spp. were largely restricted to exclosures. Post-harvest seedling density increased with increasing overstory removal, with the mesoscale wind disturbance treatment containing the highest seedling density after three years. While browse protection generally did not have a significant effect on overall density of regeneration, several species, especially *Betula alleghaniensis* benefitted from protection from deer browse. These initial results underscore the utility of natural disturbance-based treatments at increasing the complexity of second-growth communities and the importance of accounting for herbivory impacts on treatment responses.

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## **Chapter 1 : Introduction**

This thesis examines the effects of silvicultural treatments designed to increase structural and compositional complexity as well as the impacts of browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman) on tree regeneration and ground-layer community composition in second-growth northern hardwoods forests located in northern Wisconsin, USA. Concerns over structural and compositional homogenization of these forests through past land use, including the long-term application of single-tree selection, have led to an increased interest in management regimes that increase structural heterogeneity and compositional diversity while allowing for the removal of wood products (Bauhus et al., 2009). Additionally, white-tailed deer populations in this region are significantly higher than they were historically and may, through selective and pervasive browsing, affect the understory community as much or more than intentional manipulation with harvesting (Goetsch et al., 2011; Horsley et al., 2003; Kain et al., 2011; Kern et al., 2012; Rooney, 2001). In this study, harvests were implemented at the landscape level and were designed to emulate effects of natural gap-scale and mesoscale disturbances on the overstory as well as manipulate coarse woody debris volume and forest floor conditions. Small deer exclosures were installed around a fraction of sampled plots to evaluate the impacts of deer browsing on both herbaceous and woody species in the understory.

The second chapter of this thesis examines the effects of a range of harvest-created canopy gap sizes as well as microsite preparation on regeneration of woody species. Density and diversity of woody species in seedling and sapling size classes were

analyzed. We found that although densities of shade-intolerant and midtolerant species increased with larger canopy openings, all treatments mostly served to release advance regeneration of shade-tolerant species. Microsite preparation through scarification was successful in reducing regeneration of shade-tolerant species and provided a slight benefit to new establishment of *Betula alleghaniensis* (yellow birch), but did not greatly benefit regeneration of other tree species.

The third chapter of this thesis looks at the effects of the abovementioned treatments, overstory and microsite manipulation, on ground layer community composition and diversity. We used multivariate measures to compare composition of the ground layer as a whole in addition to examining cover by specific species and functional groups. While diversity measures were generally higher in harvested stands than unharvested controls, we saw the highest ground-layer diversity in the overstory treatment that caused the least canopy disturbance. Treatments with the largest canopy openings caused increases in ruderal and exotic species and treatments manipulating regeneration microsites had little effect on the ground layer community in this study.

The fourth chapter of this thesis considers the role of browsing by white tailed deer in affecting both ground-layer composition and regeneration response of tree species in the context of the above treatments. Understory communities in plots inside and outside of small deer exclosures were compared. Results indicated that browsing by deer can affect cover of specific ground-layer species, even though it did not have a strong effect on species richness or diversity. Overall density of tree regeneration was not

affected by deer browsing, but negative effects on regeneration were seen for specific tree species, including *B. alleghaniensis*.

The fifth and final chapter of this thesis offers conclusions based on this research. Implications of the results of this work for designing management strategies to promote structural heterogeneity and compositional diversity are discussed, particularly in the context of elevated levels of deer herbivory. Lastly, the potential limitations of this study and recommendations for future research are presented.

## **Chapter 2 : Initial tree regeneration response to structural complexity restoration in second-growth northern hardwood forests**

### **Introduction**

Old-growth, northern hardwood forests once made up a significant portion of the upper Great Lakes region of North America (Frelich, 1995; Rhemtulla et al., 2007). Due in large part to the heavy logging of the late 1800s and early 1900s, very little old-growth forest remains in this region (Frelich, 1995; Rhemtulla et al., 2007). Researchers have come to realize that old-growth forests have unique attributes and dynamics and are important to many species of plants and animals (e. g. Humphrey, 2005). In response, forest managers have begun exploring management regimes aimed at restoring and sustaining old-growth characteristics in forests managed for wood products (Bauhus et al., 2009).

Several major structural and compositional differences have been identified between old-growth and second-growth northern hardwood forests. Major differences exist in tree diameter distributions (Hale et al., 1999), the number and size of cavity trees (Goodburn and Lorimer, 1998), the amount and decay class distribution of coarse woody debris (Crow et al., 2002; Goodburn and Lorimer, 1998; Hale et al., 1999), and the size and distribution of canopy gaps (Dahir and Lorimer, 1996). The last two attributes are especially important for tree regeneration as, respectively, they influence microsite conditions for seedling establishment (Gray and Spies, 1997) and gradients of available light (Canham et al., 1990) at the understory level.

Downed, decaying logs are important in creating microsite conditions that favor the regeneration of several historically important species in old-growth northern hardwood forests, especially *Betula alleghaniensis* (yellow birch) and *Tsuga canadensis* (eastern hemlock) (Bolton and D'Amato, 2011; Marx and Walters, 2008; Scheller and Mladenoff, 2002). Old-growth northern hardwood stands have significantly higher volumes of coarse woody debris relative to second-growth systems (Crow et al., 2002; Goodburn and Lorimer, 1998). In addition, old-growth stands tend to have more large downed logs, which are more important as microsites for seedling establishment compared to small logs (Goodburn and Lorimer, 1998).

Variation in canopy structure creates variable light conditions on the forest floor, which favor the regeneration or expansion of different canopy tree species (Denslow, 1980). When compared to both pole-size and mature second-growth northern hardwood stands, old-growth stands tend to have a larger mean canopy gap area, but also a larger range in sizes of gaps (Dahir and Lorimer, 1996). Although second-growth forests have a higher average number of gaps per stand, most of these gaps tend to be small (less than 30 m<sup>2</sup>) due in part to the smaller crown dimensions of overstory trees in younger forests (Dahir and Lorimer, 1996). In contrast, gaps in old-growth stands are more evenly distributed among size classes, ranging from 50 to >200 m<sup>2</sup> (Dahir and Lorimer, 1996; Tyrell and Crow, 1994). This range of gap sizes provides opportunities for species with different reproductive strategies and different levels of shade tolerance to coexist within the same stand (Dahir and Lorimer, 1996; Richards and Hart, 2011; Vepakomma et al., 2011; Webster and Lorimer, 2005, 2002). Smaller gaps are typically captured by shade-



tolerant species with advance regeneration in the understory (Canham, 1988), whereas species with lower shade tolerance may require larger gaps in order to reproduce, and if provided enough sunlight may be at a competitive advantage over slower-growing shade-tolerant species (Dahir and Lorimer, 1996; McClure et al., 2000). The lack of larger gaps and lower heterogeneity in gap size in second-growth forests may reduce the diversity of tree species that are able to regenerate (Richards and Hart, 2011) and has been suggested as a possible factor contributing to the loss of species of lower shade tolerance in various forest systems (Nuttle et al., 2013).

Northern hardwood stands in the upper Great Lakes are often managed using single-tree selection, which creates small canopy gaps and generally favors the regeneration of very shade-tolerant species, especially *Acer saccharum* (sugar maple). The loss of midtolerant species and subsequent increase in shade-tolerant species with this type of management has been well documented in long-term studies (Jenkins and Parker, 2001; Johnson, 1984; Leak and Filip, 1977; Leak and Sendak, 2002; Schuler, 2004; Tubbs, 1977). Partially in response to these research findings, silviculture based on natural disturbance patterns that creates a greater range and diversity of gap sizes has been proposed as a way to maintain or increase diversity of shade tolerance classes in tree regeneration, particularly midtolerant species, as well as accelerate the development of old-growth characteristics (Bauhus et al., 2009; Hanson and Lorimer, 2007; Keeton, 2006).

One focus of a natural disturbance-based approach for northern hardwood management includes greater use of larger canopy gaps than single tree selection

generally accommodates. A rationale for this, stemming from the gap partitioning hypothesis, is that larger gaps will have increased diversity of regeneration due to microclimate differences within individual gaps (Denslow, 1980). Light and moisture conditions are more variable in large gaps than small gaps and increased resource heterogeneity may increase species diversity as well (Canham et al., 1990; Denslow, 1980). Several studies in northern hardwood systems have indicated that creating larger canopy gaps, similar in size to those found in older forests, may increase the diversity of tree regeneration and allow trees of lower shade tolerance to regenerate (Leak and Filip, 1977; Leak, 1999; Nuttle et al., 2013; Olson and Wagner, 2011; Shields et al., 2007). However, in cases where advance regeneration of shade-tolerant species is abundant or a well-developed shrub layer exists, canopy gaps may only serve to release species already present and accelerate succession to a forest with increased dominance of shade-tolerant species (Abrams and Scott, 1989; Beckage et al., 2000; Webb and Scanga, 2001).

While smaller-scale tree fall gaps are the most common disturbance in northern hardwood forests, mesoscale disturbances, especially wind disturbance, also occur on the landscape. Historically, the rotation period for disturbance that removed 30-60% of the canopy in patches ranging from 10 to 5000 m<sup>2</sup> was 300-390 years in hardwood forests of upper Michigan (Frelich and Lorimer, 1991a; Hanson and Lorimer, 2007). Most natural disturbance-based approaches focus only on emulating tree fall gaps and do not account for these larger-scale wind disturbances. However, these larger disturbances, which may on average occur one time during the lifespan of a cohort, can have important consequences for forest composition and structure through larger canopy openings,

increased solar radiation on the forest floor, and increased heterogeneity in solar radiation when compared to typical uneven-aged harvests (Hanson and Lorimer, 2007), all potentially increasing regeneration opportunities for midtolerant tree species.

The creation of favorable microsites in canopy gaps is also important for the regeneration of several northern hardwoods and associated species. Species such as *B. alleghaniensis* and *T. canadensis* require decaying wood or exposed mineral soil seedbeds often associated with uprooted trees, while *A. saccharum* seedlings are unlikely to be associated with decaying wood (Bolton and D'Amato, 2011; Erdmann, 1990; Marx and Walters, 2008; Shields et al., 2007). Site scarification and removal of advance regeneration have been suggested as ways to increase regeneration of *B. alleghaniensis* and other midtolerant species (Godman and Krefting, 1960; Hatcher, 1966; Raymond et al., 2003), particularly on more nutrient-rich sites where dense understory layers of *A. saccharum* seedlings have developed.

This study examines silvicultural treatments aimed at increasing structural complexity and compositional diversity of second-growth northern hardwood stands by emulating the full gradient of historical disturbance severities, rather than only small tree-fall gaps. Harvesting and experimental treatments designed to create a range of canopy gap sizes, augment coarse woody debris levels, and provide a diversity of regeneration microsites were implemented at operational scales across three sites in northern Wisconsin. We examined the initial (three-year) response of tree seedlings and saplings to address the following questions: (i) how does overstory treatment affect composition and diversity of trees in the seedling and sapling layer, and (ii) does microsite preparation

within gaps increase the representation of midtolerant and intolerant tree species and/or have an effect on diversity?

## **Methods**

### *Study Sites*

This large-scale study was replicated across three sites in northern Wisconsin in a randomized complete block design. Sites were located at the Flambeau River State Forest (Flambeau or FLMB), the Northern Highland-American Legion State Forest (Northern Highland or NHAL) and the Argonne Experimental Forest within the Chequamegon-Nicolet National Forest (Argonne or AGRN). Four hardwood stands ranging in size from 46 to 55 hectares each were chosen at each site with selection criteria that stands be 70-90 years old and have no management in the previous 10 years. Mean summer (June, July, August) temperatures range from 17 to 18° C, and mean winter (December, January, February) temperatures range from -10 to -12° C for this region. Mean annual precipitation is between 80 and 84 cm, with 15-20% falling as snow (1971-2000, Midwest Regional Climate Center, <http://mcc.sws.uiuc.edu>). Additional site characteristics by treatment area are shown in Table 2.1.

### *Silvicultural Treatments*

Three overstory treatments and two coarse woody debris treatments were implemented at each site in the winter of 2007-2008 in a split plot design (with the exception of the large gaps/ambient CWD treatment [see description below] at ARGN,

which was implemented one year later in winter 2008-2009). Each stand (whole plot) was divided into two approximately 25 hectare half-stands (split plot), with the entire stand receiving one overstory treatment and each half-stand receiving a different coarse woody debris treatment. Each site also had an approximately 50 hectare uncut control stand, which did not receive any harvest treatment.

The overstory treatments were as follows: (i) small gaps (10.7 m diameter), (ii) large gaps (18.3 m and 24.4 m diameter); and (iii) a treatment designed to emulate a mesoscale wind disturbance based on the patterns of disturbance documented by Hanson and Lorimer (2007). The three overstory treatments were defined by the size of canopy gaps, number of gaps created per hectare, and additional thinning done to the matrix surrounding gap treatment areas. For the small gap treatment, approximately ten gaps with a 10.7 m diameter were created per hectare and the rest of the stand was thinned to a residual basal area of 18.3-20.7 m<sup>2</sup>/ha. Additionally, these gaps were cleaned of all saplings greater than 2.54 cm diameter at breast height (dbh), a practice that is widely implemented in the region to encourage the development of quality hardwood regeneration.

The large gap treatment involved creating one 18.3 m or one 24.4 m diameter gap per 0.4 ha. Areas between gaps were thinned to achieve a residual basal area of 18.3-20.7 m<sup>2</sup>/ha. Within the large gap treatment, a nested gap-level site preparation treatment was implemented with one of three treatments randomly assigned to each gap: (i) no cleaning (hereafter referred to as “not cleaned”) in which only poorly formed saplings were removed, (ii) cleaning (hereafter referred to as “cleaned”) in which all saplings greater

than 2.54 cm dbh were removed, and (iii) cleaned and scarified gaps, (hereafter referred to as “scarified”) in which gaps were cleaned of all saplings greater than 2.54 cm dbh and then scarified with a Salmon blade to expose 70-90% mineral soil. Scarification was performed in September following harvest using a Salmon blade on a crawler bulldozer.

The mesoscale wind treatment included four small-scale shelterwood harvests, a heavily thinned matrix area, and a lightly thinned matrix area in each split plot (half stand). Of the four shelterwoods, two were 0.4 ha and two were 1.2 ha in size. Each shelterwood was cut to leave 60-65% residual basal area. The lightly thinned area covered approximately 25% of the stand and remaining portion of the stand was heavily thinned (approximately 65% of the stand). The lightly- and heavily thinned areas were reduced to 20.7-23.0 m<sup>2</sup>/ha and 18.3-20.7 m<sup>2</sup>/ha residual basal area, respectively. A second harvest entry is planned in these stands for six to ten years after the initial harvest. At this time, shelterwoods will be reduced to about 10% crown closure and the heavily thinned area will be reduced to approximately 17.2 m<sup>2</sup>/ha residual basal area. See Fig. 2.1 for aerial photographs of treatment stands.

Coarse woody debris (CWD) treatments were identified as ambient and high. In stands receiving the ambient CWD treatment, no additional CWD was deliberately created. In the stands receiving the high CWD treatment, the number of snags and amount of downed wood were deliberately increased during harvest to approximately 65% of the density and volume found in old-growth northern hardwood stands in the Sylvania Wilderness in Upper Michigan (Goodburn and Lorimer, 1998), the nearest

similar old-growth forests in the region. Snags were created by double-girdling live trees and downed logs were created by felling poorer formed canopy trees.

### *Field Methods*

#### *Plot selection*

A series of 25 m<sup>2</sup> plots were established at each stand one year prior to treatment implementation for measuring tree regeneration. All regeneration plots were 5 m by 5 m except mid-distance quads in 24.4 m diameter gaps, which were 7.19 m by 3.48 m in order to sample a larger portion of the variation from gap edge to gap center (Fig. 2.2). In treatment stands, regeneration plots were located within harvest gaps and shelterwoods, as described below. Sampling was also done in the thinned matrix of all harvest stands, but this study focuses only on plots from the gaps and shelterwoods.

Small gaps (10.7 m diameter) each contained one sampled regeneration plot randomly selected from one of five possible locations (Fig. 2.2a). Each small gap was treated as a separate unit of analysis. Thirty-six small gaps were sampled at each stand for a total of 108 small gaps sampled across the study. Large gaps (18.3 m and 24.4 m diameter) contained three or four sampled plots in nine possible locations in order to sample areas with different light levels within each gap (Fig. 2.2b and c). The center plot was sampled in all gaps and two or three additional plots were randomly selected to be sampled. Measurements from the 25 m<sup>2</sup> regeneration plots were averaged within each gap and each gap was treated as an individual unit of analysis. In each stand, 24 gaps were sampled for each gap-level cleaning treatment (twelve 18.3 m diameter gaps and

twelve 24.4 m diameter gaps) for a total of 72 large gaps sampled in each stand and 216 large gaps sampled across the study, divided equally across each gap-level cleaning treatment (not cleaned, cleaned, scarified). Shelterwoods in the mesoscale wind treatment contained one (0.4 ha shelterwoods) or two (1.2 ha shelterwoods) square 32 m by 32 m macro-plots with a sampled 5 m by 5 m regeneration plot located at three or four corners of the larger macro-plot (Fig. 2.2d). Measurements were averaged to the shelterwood level and shelterwoods were treated as individual units of analysis. Twenty-four total shelterwoods were sampled in this study, eight in each stand. The control stands contained 27 (Flambeau), 29 (Northern Highland), or 33 (Argonne) macro-plots arranged in a grid pattern across the stand. Exact number of macro-plots depended on the shape of the stand as well as presence of wet areas and vernal ponds, which were not sampled. Similar to the sampling scheme for the mesoscale wind treatment, sampled 5 m by 5 m meter regeneration plots were located randomly at one or two corners of each larger macro-plot in the control stands (Fig. 2.2d). Measurements from regeneration plots were averaged for each macro-plot and macro-plots were treated as individual units of analysis. A total of 89 control stand macro-plots were sampled across the study.

### *Regeneration sampling*

During the summer of 2007, the growing season prior to harvest, stem counts of regeneration in three size classes: small seedlings (0.1 m to < 0.5 m tall), large seedlings (0.5 m tall to < 2 cm dbh), and saplings (2 cm dbh to < 10 cm dbh) were tallied by species. Small seedlings were sampled in two 0.5 m by 1 m subplots within each regeneration



plot. These subplots were located directly east and west or north and south and 1.5 m from plot center. Large seedlings were counted in a circular subplot centered in each regeneration plot with a 1.5 m radius (total area=7 m<sup>2</sup>). Saplings were sampled in the entire 25 m<sup>2</sup> regeneration plot. Regeneration in these subplots was again measured three years post-treatment in June-August 2011, except the large gaps/ambient CWD treatment at ARGN, which had been harvested one year after the other stands, and so was sampled in June-August 2012.

### *Statistical analyses*

For all analyses, response variables were averaged to the gap, shelterwood, or macro-plot level and each gap (small gap and large gap treatments), shelterwood (mesoscale wind treatment) or macro-plot (controls) was treated as an individual unit of analysis, despite the fact that overstory treatments were applied at the stand level. The significant distance between these plots (>15 m in small and large gaps treatments and >50 m in mesoscale wind treatment and controls) and the large scale of the treatment stands (~50 ha) allowed us to consider each gap, shelterwood, and control stand macro-plot as an independent observation.

Mixed model analysis of variance (ANOVA) was used to determine effects of overstory treatments and gap-cleaning treatments on species richness (number of species per plot), Shannon-Wiener index (Shannon and Weaver, 1949), and evenness (Pielou, 1969) of tree regeneration. Mixed model analysis of covariance (ANCOVA) was used to determine effects of overstory treatment and gap-cleaning treatment on post-treatment

densities of seedlings and saplings. ANOVAs and ANCOVAs were performed using SAS statistical software (SAS Institute, 2010). Overstory treatment or gap-cleaning treatment was treated as a fixed variable and site was treated as a random variable. For ANCOVAs, pretreatment stem densities for the same size class were used as the covariate. When comparing overstory treatment effects on regeneration, only the “cleaned” gaps were used for the large gap treatment, since the other within-gap treatments were not applied to the smaller gaps or shelterwoods. When assumptions of normality and constant variance were not met, data were transformed using a square root transformation or aligned rank transformation (Mansouri, 1999). When significant main effects of fixed variables were found, Tukey’s HSD was used to determine pairwise differences between treatments with  $p < 0.1$  considered significant. Coarse woody debris treatment was not a significant factor in any of our analyses, thus these results are not presented.

## **Results**

### *Overstory treatments*

Overstory treatments generally increased the density of small and large tree seedlings relative to the unharvested controls (Fig. 2.3a-c). Density of small seedlings was significantly higher in the shelterwoods of the mesoscale wind treatment than all other treatments (Fig. 2.3a). Large seedling densities were highest in the mesoscale wind treatment and large gaps, but all three overstory treatments had significantly higher densities than the controls (Fig. 2.3b). Sapling densities were significantly lower in the

small and large gaps than the controls, but no other differences were significant (Fig. 2.3c).

Overstory treatments also affected the abundance of species of different shade tolerance classes and life form. Densities of shade-tolerant regeneration in the two smaller size classes were highest in the mesoscale wind (small and large seedlings) and the large gap (large seedlings) treatments, whereas the density of shade-tolerant saplings was highest in the control stands (Fig. 2.3d-f). This group included mostly *A. saccharum*, with a significant component of *Ostrya virginiana* and smaller proportions of *Tilia americana* and *Acer rubrum*. Small midtolerant seedlings were at significantly higher densities in the large gaps than the controls, but no other differences were significant (Fig. 2.3d). Large midtolerant seedlings in the small gaps and mesoscale wind treatment were at higher densities than the controls, and the density of midtolerant saplings was higher in the mesoscale wind treatment than any other treatment or the controls (Fig. 2.3e and f). This group was largely composed of *Fraxinus* spp. as well as some *B. alleghaniensis*, *Quercus rubra*, and *Ulmus* spp. The most common shade-intolerant seedlings and saplings were *Prunus serotina*, but *Carya cordiformis*, *Populus tremuloides*, and *Betula papyrifera* were also present. These seedlings and saplings were at their highest densities in the small and large gaps and were at very low densities in the mesoscale wind treatment and the controls, however, densities of shade-intolerant regeneration were low overall, making assessment of treatment effects difficult (Fig. 2.3d-f).

Small and large *A. saccharum* seedlings had highest density in the mesoscale wind treatment, and among the overstory treatments, seedling densities generally increased with increasing canopy opening size (Fig. 2.4a and b). *A. saccharum* sapling densities were higher in the controls than the large gaps, but no other differences were significant (Fig. 2.4c). *Fraxinus* spp. regeneration was also high in the mesoscale wind treatment, with large seedling and sapling densities significantly higher than in all other treatments (Fig. 2.4b and c). Treatment had little effect on small *Fraxinus* seedlings, with only densities in large gaps significantly higher than those in the controls (Fig. 2.4a). *O. virginiana* seedlings and saplings were also common in the understory. Densities of large *O. virginiana* seedlings were higher in all treatment stands than in the controls, while densities of small seedlings and saplings of this species were not significantly affected by overstory treatment (Fig. 2.4). *B. alleghaniensis* was found in very low densities in all stands. There were no large *B. alleghaniensis* seedlings in the small gaps or control treatments, while the large gaps had a mean of 43 stems/ha and the mesoscale wind treatment shelterwoods had a mean density of 20 stems/ha (Fig. 2.4b). *Rubus* spp. of all sizes were at much higher densities in the mesoscale wind and large gap treatments than the other stands. The control stands had very little *Rubus* and no *Rubus* stems taller than 0.5 meters (Fig. 2.4a and b).

Overstory treatments only affected plot-level diversity measures in the large seedling and sapling size classes (Table 2.2). Species richness and evenness for large seedlings were significantly higher in the treatments than in the controls, with no difference between treatments (Table 2.2). Shannon index for large seedlings was

significantly higher in the small and large gaps than the controls (Table 2.2). In the sapling size class, diversity measures were highest in the controls; species richness was significantly higher in the controls than in any overstory treatment, while diversity and evenness in the controls were only significantly higher than in the large gaps (Table 2.2).

#### *Gap-level cleaning treatments*

Overall, scarification reduced regeneration of most tree species, but had less effect on seedlings in the smallest size class (Fig. 2.5). In the sapling size class, stem densities were generally highest in the gaps that had not been cleaned, likely because many of the saplings measured three years post treatment were also present prior to treatment, but were not removed as they were in the cleaned and scarified gaps (Fig. 2.5c). However, densities of shade-intolerant saplings were actually highest in the cleaned gaps (Fig. 2.5f).

The only species that did not have the lowest regeneration densities in the scarified gaps were *Rubus* spp., *B. alleghaniensis*, *O. virginiana*, and *A. rubrum* (Fig. 2.6). Neither small nor large *A. rubrum* seedlings were affected by gap-cleaning treatments (Fig. 2.6a and b). Large seedling-sized *Rubus* spp. had higher regeneration densities in the highly disturbed scarified and cleaned gaps relative to gaps that had not been cleaned and the same pattern was true for small *O. virginiana* seedlings (Fig. 2.6a and b). Regeneration of *B. alleghaniensis* was very low in all treatments, but no *B. alleghaniensis* of any size was present in the gaps that had not been cleaned. Small *B. alleghaniensis* seedlings were at higher densities in scarified gaps than cleaned gaps, but

there was no difference in densities of large seedlings between gaps that were cleaned and gaps that were scarified (Fig. 2.6a and b). Scarification had a significant negative impact on densities of *A. saccharum* in all size classes (Fig. 2.6).

Scarification had a significantly negative effect on species richness of large seedlings and saplings (Table 2.3). Shannon index of diversity was also significantly lower for large seedlings in scarified gaps than gaps that had been only cleaned or not cleaned (Table 2.3). Diversity of small seedlings was not affected by gap cleaning or scarification (Table 2.3).

## **Discussion**

Our findings suggest that restoring diversity of tree regeneration in second-growth northern hardwoods using silvicultural techniques aimed at increasing structural and compositional complexity may prove challenging under contemporary forest conditions. While the creation of canopy gaps and shelterwoods did increase the density of tree regeneration, overstory treatment had only a small effect on species diversity and generally served to release advance regeneration of shade-tolerant species. Only species richness for saplings was lower in the small gaps than the large gaps, otherwise no differences in diversity were detected between the three overstory treatments. Mean densities of shade-tolerant *A. saccharum* were at least 1.5 times higher and sometimes more than six times higher than mean densities of the next most common species (*Fraxinus* spp. or *O. virginiana*) in all size classes. Microsite preparation through scarification was successful in reducing regeneration of shade-tolerant species and

provided a slight benefit to new establishment of *B. alleghaniensis*, but did not greatly benefit regeneration of other species. Scarification also had a small, but slightly negative effect on diversity of regeneration.

Larger gaps allow more light to reach the forest floor, and this increase in resources can increase the density of tree regeneration (Bolton and D'Amato, 2011; Schumann et al., 2003; Webster and Lorimer, 2002). This study found higher densities of small and large seedlings in large-sized canopy gaps and mesoscale wind treatment, but fewer saplings in the large gaps than controls. Saplings present prior to treatments were likely damaged or intentionally removed during harvest and it is probable that seedlings will grow into larger size classes causing sapling densities in treatment stands to increase for a number of years. However, the effect of significantly higher densities of *Rubus* spp. found in the large gaps and mesoscale wind treatment on this dynamic is unclear. The work of Donoso and Nyland (2006) suggests that northern hardwood tree seedlings can grow through *Rubus* patches and form a closed canopy above the shrub layer within 15 years, but only when advance regeneration is present. In contrast, higher shrub densities, especially *Rubus* spp., were still inhibiting regeneration 13 years after group selection harvests in northern Wisconsin (Kern et al., 2013a). The stands studied by Kern et al. (2013a) were slightly younger than those examined in our research and had little advance regeneration prior to harvest, but it is possible that the *Rubus* patches we documented could impede growth of seedlings into larger size classes in the large gaps and mesoscale wind treatment, particularly when coupled with high levels of deer herbivory (Chapter 4).

The gap partitioning hypothesis suggests that larger gaps will also have increased diversity of regeneration, as they have a wider range of light and moisture conditions than small gaps (Denslow, 1980). Shade-tolerant species may be more successful on the edges of these larger gaps, while the center or northern portion of the gap receives higher light and may support species less tolerant of shade (Canham et al., 1990; Denslow, 1980). Midtolerant and even some shade-intolerant tree species may receive enough light in larger gaps to outgrow advance regeneration of shade-tolerant species. In northern hardwoods, several studies have found *B. alleghaniensis* to have higher growth rates than *A. saccharum* in more open conditions (Gasser et al., 2010; Hill, 1987; McClure et al., 2000). Similarly, the creation of canopy gaps in hardwood systems has often been associated with increases in tree species diversity (Kraft et al., 2004; Olson and Wagner, 2011; Shields et al., 2007; Webster and Lorimer, 2002) and/or the presence of species less tolerant of shade (Dale et al., 1995; Leak and Filip, 1977; Leak, 1999; Webster and Lorimer, 2002). In contrast, other studies have found that gaps had little effect on or decreased diversity, especially in the presence of high densities of advance regeneration or dense shrub layers (Bolton and D'Amato, 2011; Jenkins and Parker, 2001; Kraft et al., 2004; Shure et al., 2006; Webb and Scanga, 2001). We found that gaps did increase regeneration diversity, with diversity of large seedlings higher in gaps and shelterwoods than controls, but saw no additional effect of increasing gap size. Sapling diversity was the same or lower in the treatments compared to the controls, which may reflect the limited timeframe of this study (3 years post-harvest).



Consistent with several other studies, larger gap sizes led to higher numbers of midtolerant and shade-intolerant seedlings and saplings (Clebsch and Busing, 1989; Dale et al., 1995; Denslow, 1980; Gasser et al., 2010; McClure and Lee, 1993). In particular, large seedling- and sapling-sized midtolerant regeneration was highest in the mesoscale wind treatment, in accord with the hypothesis proposed by Hanson and Lorimer (2007) that moderate severity wind storms are the mechanism by which midtolerant tree species, such as *B. alleghaniensis* historically established in *A. saccharum*-dominated northern hardwood stands. Shade-intolerant regeneration favored large gaps where it may benefit from the higher light conditions found in the center and northern portions of these gaps (Gálhidy et al., 2006). It is important to note that despite these patterns, midtolerant and shade-intolerant species were only a small component of the regeneration in all treatments which were dominated by shade-intolerant species, especially *A. saccharum*.

Advance regeneration is an important strategy for many shade-tolerant tree species. *A. saccharum* is very tolerant of shade and can remain in the understory for many years before being released by a canopy opening event (McClure et al., 2000; Poulson and Platt, 1996). The majority of dominant *A. saccharum* that establish in gaps are from advance regeneration, while most dominant *B. alleghaniensis* establish after gap creation (Albert and Barnes, 1987; McClure et al., 2000; Webster and Lorimer, 2005, 2002). Since *A. saccharum* advance regeneration responds well even to low light levels (Canham, 1988), single-tree and group selection often leads to release of *A. saccharum* seedlings and saplings and has little effect on other, less shade-tolerant species (Abrams and Scott, 1989; Barden, 1981; Bolton and D'Amato, 2011; Jenkins and Parker, 2001;

Leak and Sendak, 2002; Shure et al., 2006; Tubbs, 1977). In this study all overstory treatments released *A. saccharum* regeneration and it was the most abundant species in all treatments and across all size classes.

Others have suggested that the removal or reduction of advance regeneration would allow for more diversity of regeneration in gaps (Kelty et al., 2003; Tubbs and Metzger, 1969). In this study, scarification was successful in reducing densities of *A. saccharum* and other shade-tolerant species, consistent with the findings of Raymond et al. (2003). However, neither cleaning nor the combination of cleaning and scarifying in large gaps had a positive effect on species richness or diversity. Scarification decreased species diversity and had a negative impact on all species except *Rubus* spp., *B. alleghaniensis*, and *O. virginiana*. Effects of cleaning and scarification on new establishment are likely short-lived, as scarification had less effect on small seedlings than other size classes and did not reduce overall density of small seedlings. Other work has also found that effects of scarification on establishing plants are not significant after just a few years (Duguid et al., 2013; Raymond et al., 2003).

While gap size and light availability are significant factors affecting *B. alleghaniensis* germination and establishment, it is likely that favorable microsite conditions are even more important (Bolton and D'Amato, 2011; Shields et al., 2007). Several studies have noted the importance of scarification and exposed mineral soil for the establishment of *B. alleghaniensis* (Godman and Krefting, 1960; Hatcher, 1966; Raymond et al., 2003). While we saw very little regeneration of *B. alleghaniensis* in any stands or treatments, no large *B. alleghaniensis* seedlings were present in the controls or

small gaps. This is consistent with the findings of Webster and Lorimer (2005) who suggested a minimum gap opening size of 0.02 to 0.1 ha, a range in which the large gaps in this study fall, and Shields et al. (2007) who found an increase in *B. alleghaniensis* regeneration in openings from 267-1192 m<sup>2</sup>. In large gaps, *B. alleghaniensis* was present in gaps that had been cleaned and those that had received a combination of cleaning and scarification. Scarification may have provided a microsite for new *B. alleghaniensis* seedlings to establish, but some advance regeneration of *B. alleghaniensis* may have already been present at the time of harvest with cleaning alone serving to release those seedlings from competition (Shields et al., 2007). Although it is only midtolerant of shade, *B. alleghaniensis* seedlings establishing a few years before gap creation can survive in the understory and become dominant or codominant overstory trees after release (McClure et al., 2000).

Regardless of treatment, *B. alleghaniensis* densities and overall occurrence were very low, likely not high enough to sustain the 3-6% of basal area of dominant *B. alleghaniensis* currently found in these stands. Additional factors including drought, substrate height and browsing by white-tailed deer may have negatively impacted regeneration. During dry years, seedbed conditions in open, exposed microsites can be volatile, reducing germination and survival of *B. alleghaniensis* seedlings (Tubbs, 1969). During the growing seasons following harvest (April-September 2008-2011), 58% of months had negative Palmer Drought Severity Index (PDSI) values, with values less than -2 (drought conditions) for 19% of growing season months (NOAA, 2013). Additionally, substrate height may influence *B. alleghaniensis* survival; after a natural disturbance, *B.*

*alleghaniensis* seedlings often establish on tip-up mounds or downed wood, giving them a distinct height advantage over existing advance regeneration not afforded by mechanical scarification after harvest (Erdmann, 1990; Gilbert, 1965; Marx and Walters, 2008; Winget et al., 1965). Finally, browsing by white-tailed deer can reduce regeneration success of sensitive species including *B. alleghaniensis* (Godman and Krefting, 1960; Horsley et al., 2003; Kern et al., 2012). Effects of white-tailed deer at these sites are discussed in Chapter 4.

In addition to its importance to *B. alleghaniensis*, downed and decaying wood has also been shown to be important for germination of *Tsuga canadensis* (Marx and Walters, 2008). However, in this study we did not see any significant effect of increased CWD on regeneration. These data were collected only three years after treatments were applied, and most trees that were cut and left as CWD had not reached higher decay classes (personal observation). It is possible that the effect of CWD treatment will become significant in the future after harvested trees are able to reach higher decay classes. These microsites will be particularly important in matrix areas where future gap harvests will likely coincide with areas containing well-decayed coarse wood substrates.

In addition to microsite characteristics and light availability, habitat type characteristics such as nutrient availability and soil moisture can influence composition and diversity of regeneration (Matonis et al., 2011). Most of the stands in this study were *Acer-Tsuga-Dryopteris* (ATD) habitat type, as well as some *Acer/Osmorhiza-Caulophyllum* (AOCa) and *Acer/Hydrophyllum* (AH), all of which are medium to very nutrient rich (Kotar et al., 2002). Other species might compete better with *A. saccharum*

on less productive sites, such as the *Acer-Tsuga/Maianthemum* (ATM) habitat type, which is not as nutrient rich (Kotar et al., 2002; Matonis et al., 2011; Shields et al., 2007; Webster and Lorimer, 2005). Matonis et al. (2011) found that mean seed production of species other than *A. saccharum* and *O. virginiana* were 80% higher on ATM than on more nutrient-rich AOCa sites. ATD sites are often heavily dominated by *A. saccharum* in all successional stages (Kotar et al., 2002). Had this study been performed on slightly less productive sites, it is possible that *B. alleghaniensis* and other hardwood species would have had stronger recruitment and competition with *A. saccharum*. These findings further underscore the value of integrating information on habitat types with silvicultural prescriptions to better anticipate treatment responses and identify commonalities across a particular region or forest type.

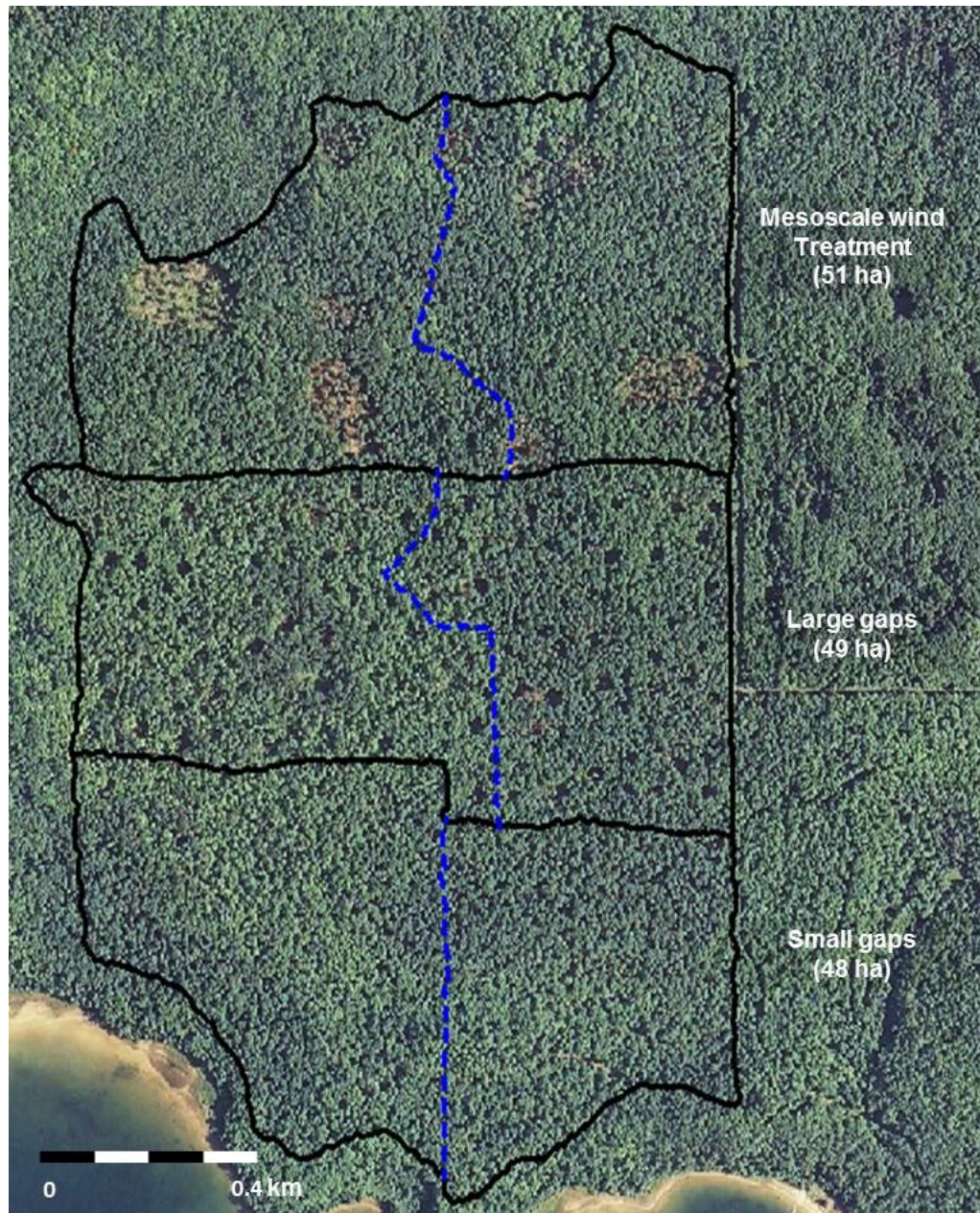
#### *Management implications*

Creating small canopy gaps did increase the diversity of large seedlings, but tree regeneration diversity did not increase further at larger gaps sizes (>10.7 m), although overall density of tree seedlings did increase and was highest in the mesoscale wind treatment. Densities of large midtolerant seedlings and saplings were also highest in the mesoscale wind treatment; however, all treatments primarily released advance regeneration of *A. saccharum*, which may not be desirable when attempting to increase compositional diversity of a stand. In most plots, the second most common taxum of seedlings and saplings was *Fraxinus* spp., which is threatened by the spread of the introduced emerald ash borer (*Agrilus planipennis*) in this region. *B. alleghaniensis*

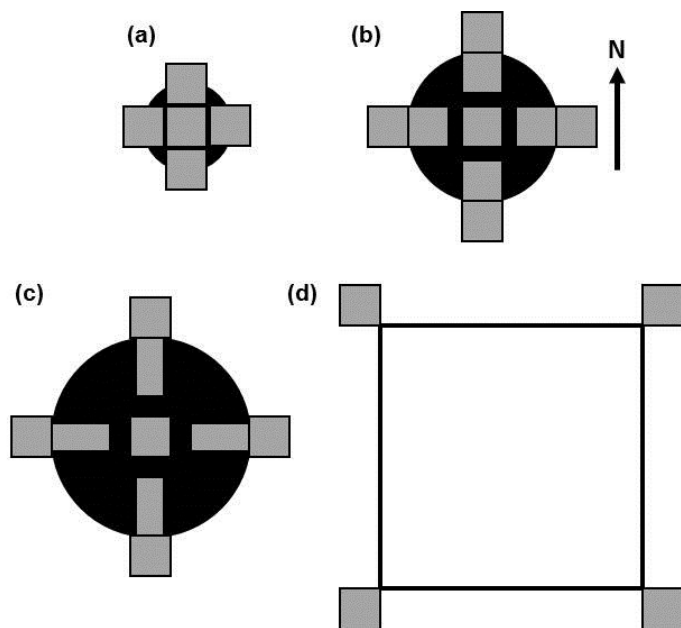
seedlings were only found in large gaps and mesoscale wind treatment shelterwoods, as has been suggested by other studies, this midtolerant species is unlikely to regenerate in small gaps (Webster and Lorimer, 2005, 2002). Despite being present in low numbers in all stands, established *B. alleghaniensis* seedlings seemed to benefit from release from competition in cleaning treatments and scarification slightly increased densities of small *B. alleghaniensis* seedlings. These treatments may have been more effective at increasing the abundance of this species if more deliberate measures, such as scarification near mature *B. alleghaniensis*, retention of within-gap seed sources (Poznanovic et al., 2013), and gap-cleaning and release treatments around established seedlings were applied.

The operational-scale of this study reflects a common situation in the field where there is little seed source of desired species, making the goal of increasing diversity of regeneration very challenging. Given these findings, the use of more targeted restoration through planting or seeding may be needed to increase the representation of less common species, however this recommendation would be dependent on several factors including advance regeneration already present, coarse wood and microsite availability, pressure from herbivory (see Chapter 4), and habitat type.

## Figures

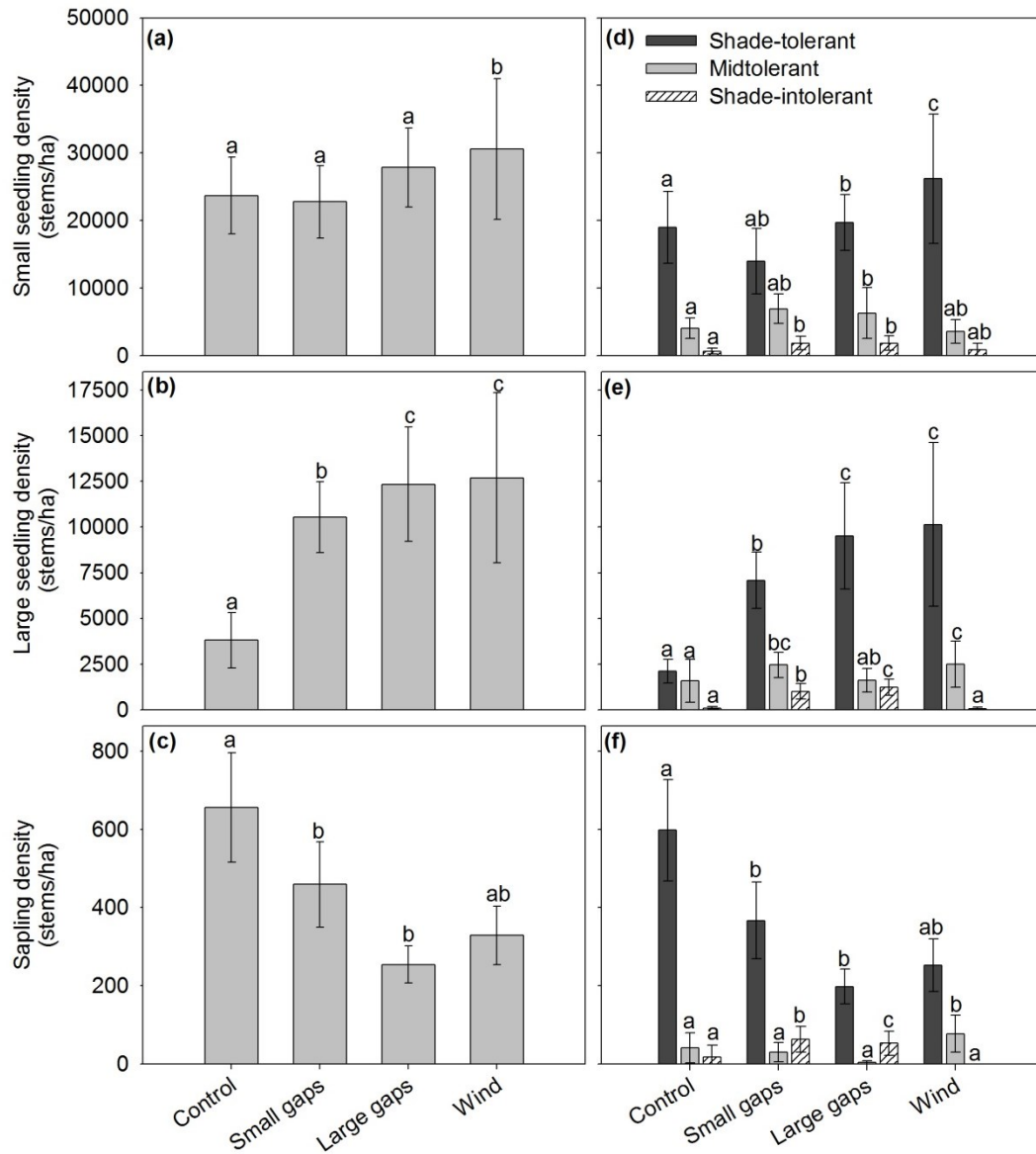


**Fig. 2.1.** Aerial photos of mesoscale wind treatment, large gap treatment, and small gap treatment stands at the Northern Highland site. Solid lines represent overstory treatment boundaries; dashed lines indicate split plot divisions for ambient and high coarse woody debris (CWD) treatments.

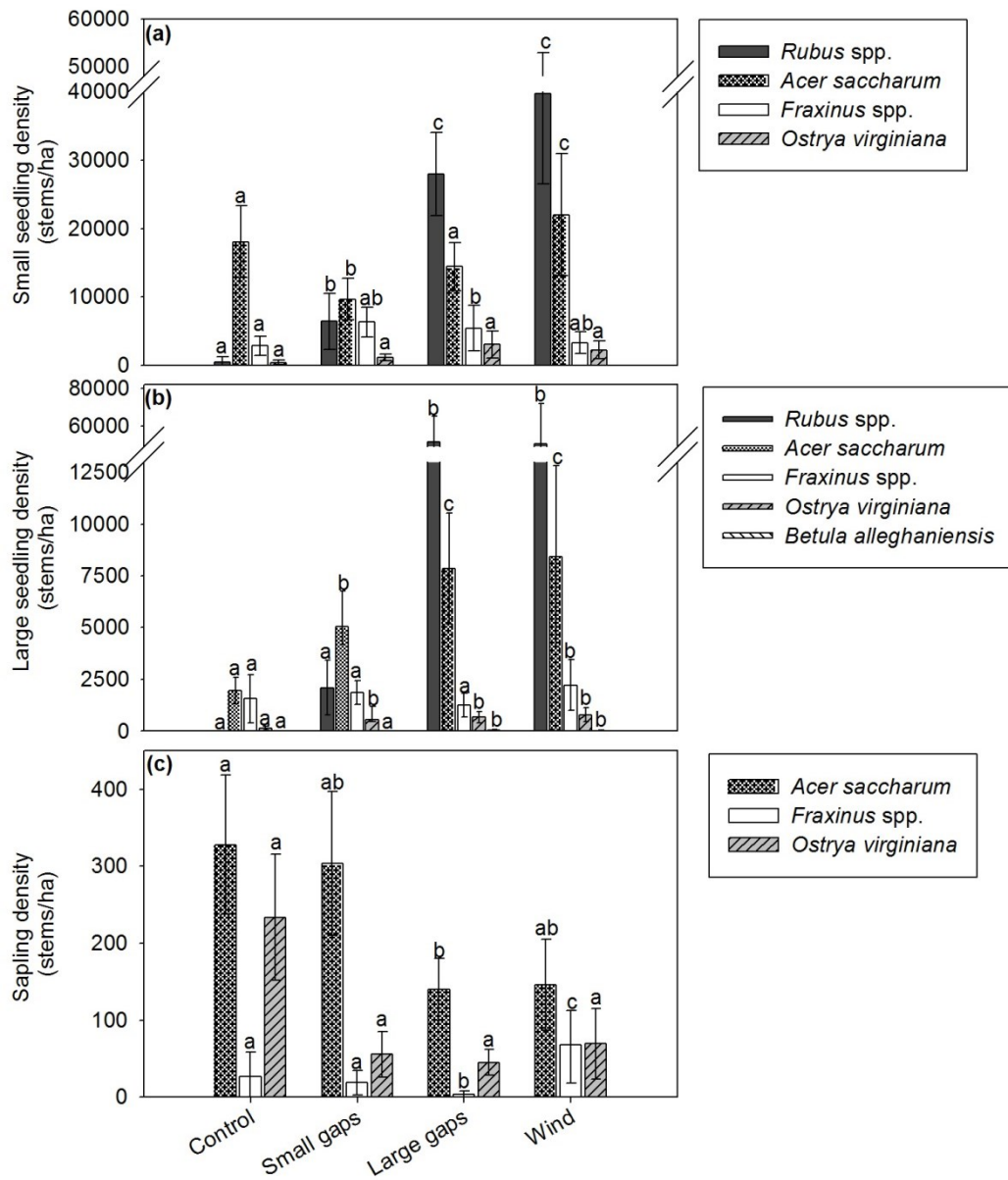


**Fig. 2.2.** Locations of 25 m<sup>2</sup> regeneration plots in (a) 10.7 m diameter small gaps, (b) 18.3 m diameter large gaps, (c) 24.4 m diameter large gaps, and (d) mesoscale wind treatment and control stand macro-plots. Black circles indicate canopy gaps; gray boxes indicate possible locations of regeneration plots within gaps and macro-plots. All locations were not sampled at each gap or macro-plot. In 10.7 m gaps only one of the five regeneration plot locations was sampled, in each 18.3 m and 24.4 m gap three or four of the nine plot locations were sampled, in mesoscale wind treatment macro-plots three or all four plot locations were sampled, and in control macro-plots one or two of the four plot locations were sampled. Small shelterwoods (0.4 ha) in the mesoscale wind treatment contained one macro-plot and large shelterwoods (1.2 ha) contained two.

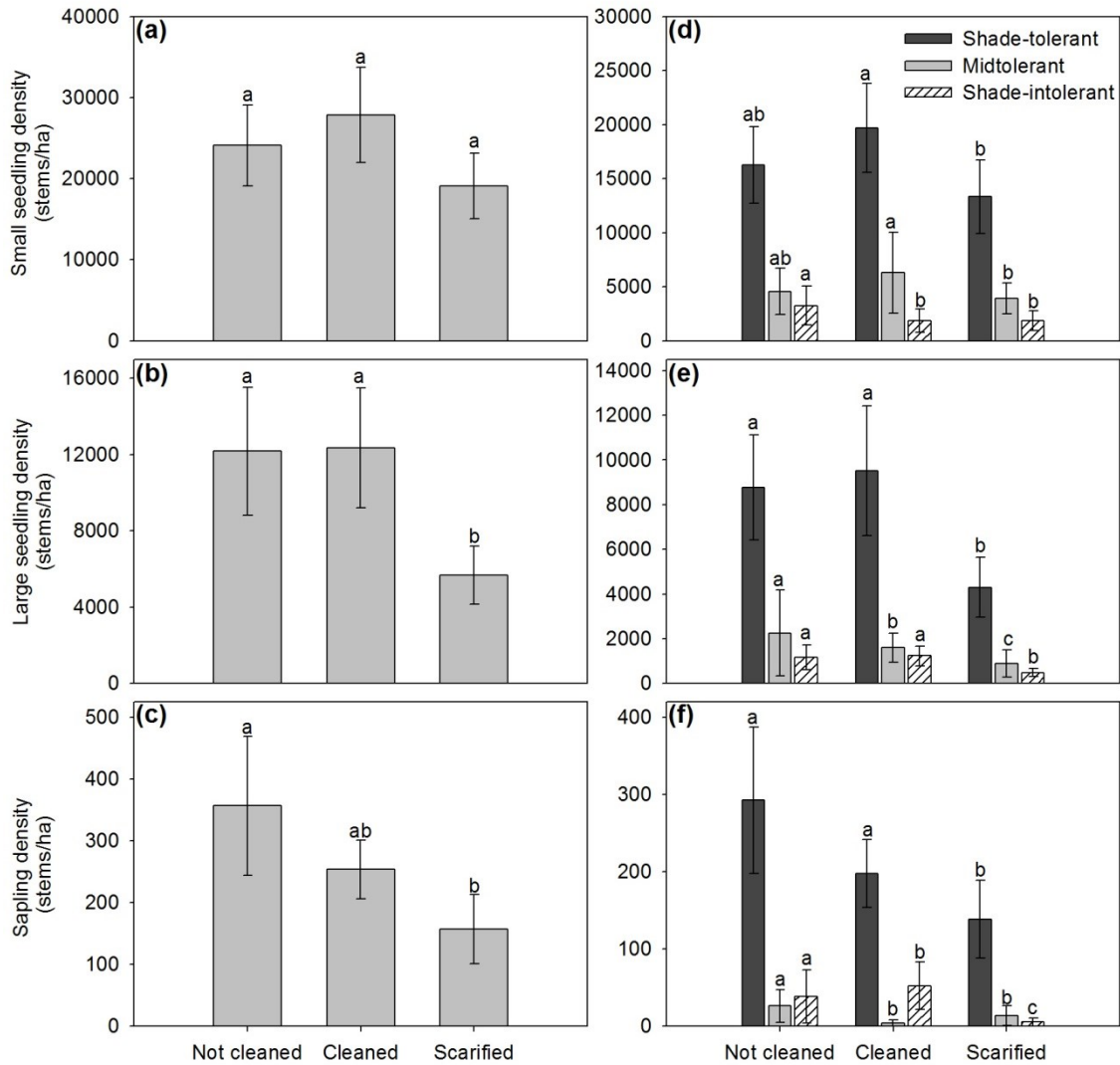




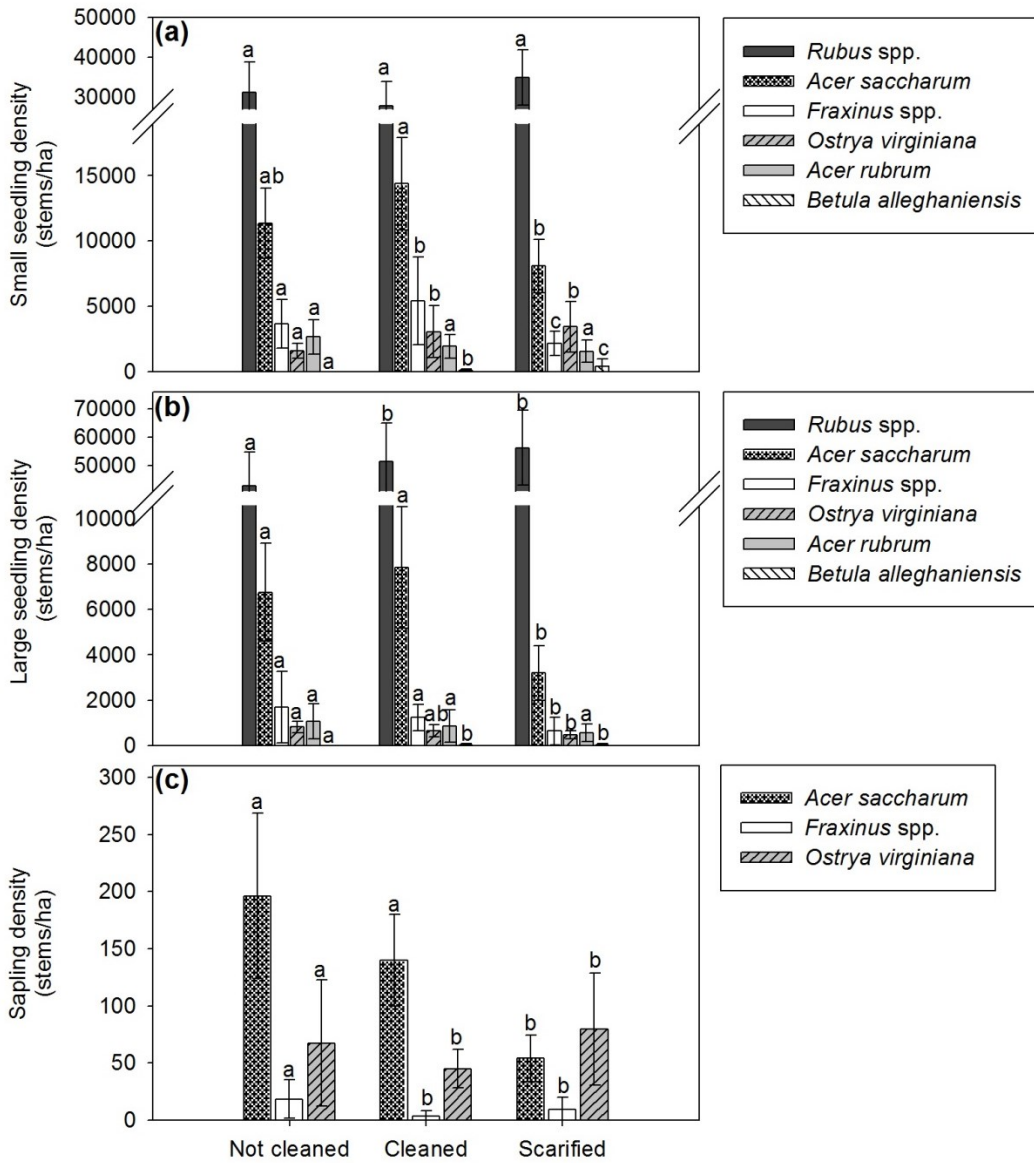
**Fig. 2.3.** Mean density (stems/ha) of all tree species in three size classes: (a) small seedlings (0.1 m to <0.5 m tall), (b) large seedlings (0.5m tall to <2 cm dbh), and (c) saplings (2 cm dbh to <10 cm dbh). Mean density of trees by shade tolerance class in three size classes: (d) small seedlings, (e) large seedlings, and (f) saplings. Error bars represent 90% confidence intervals; values for a given species group with different letters are significantly different at  $p < 0.1$  with ANCOVA and Tukey's HSD.



**Fig. 2.4.** Mean densities of (a) small seedlings, (b) large seedlings, and (c) saplings for common species in each overstory treatment. Error bars represent 90% confidence intervals; values for a given species with different letters are significantly different at  $p < 0.1$  with ANCOVA and Tukey's HSD. See Fig. 2.3 for size class definitions.



**Fig. 2.5.** Mean density (stems/ha) of all tree species in three size classes: (a) small seedlings, (b) large seedlings, and (c) saplings by gap-cleaning treatment. Mean density of trees by shade tolerance class in three size classes: (d) small seedlings, (e) large seedlings, and (f) saplings by gap-cleaning treatment. Error bars represent 90% confidence intervals; values for a given species group with different letters are significantly different at  $p < 0.1$  with ANCOVA and Tukey's HSD. See Fig. 2.3 for size class definitions.



**Fig. 2.6.** Mean densities of (a) small seedlings, (b) large seedlings, and (c) saplings for common species by gap-cleaning treatment. Error bars represent 90% confidence intervals; values for a given species with different letters are significantly different at  $p < 0.1$  with ANCOVA and Tukey's HSD. See Fig. 2.3 for size class definitions.

## Tables

**Table 2.1.** General site-level characteristics of the three study sites. FLMB=Flambeau River State Forest, NHAL=Northern Highland-American Legion State Forest, and ARGN=Argonne Experimental Forest. Stand age is the age range of dominant canopy trees. Habitat type is defined by Kotar et al. (2002). Overstory composition is based on basal area of trees greater than 10 cm diameter at breast height (dbh).

Site	Stand age (years)	Habitat type	Soils	Percent overstory composition by basal area of dominant trees					
				<i>Acer saccharum</i>	<i>Tilia americana</i>	<i>Fraxinus</i> spp.	<i>Tsuga canadensis</i>	<i>Acer rubrum</i>	<i>Betula alleghaniensis</i>
<b>FLMB</b>	75-83	AH/ATD	silt loam over sandy loam	40.2	13.7	12.1	6.8	11.4	5.8
<b>NHAL</b>	89-91	ATD	sandy loam	70.0	12.3	0.7	2.9	1.3	4.5
<b>ARGN</b>	79-92	AOCa/ATD	sandy loam	71.6	6.0	4.4	7.3	4.0	3.1

**Table 2.2.** Mean species richness (number of species per plot), evenness (Pielou, 1969), and Shannon-Wiener diversity index (Shannon and Weaver, 1949) in 2m<sup>2</sup> plots for all woody species by size class and overstory treatment. Values in parentheses are 90% confidence intervals; for control n=89, small gaps n=108, large gaps n=72, and mesoscale wind n=24. Different letters indicate significant differences between overstory treatments within a size class at p<0.1 using Tukey’s HSD. See Fig. 2.3 for size class definitions.

	Species richness		Species evenness		Shannon index	
	Mean	CI (90%)	Mean	CI (90%)	Mean	CI (90%)
<b>Small seedlings</b>						
Control	0.9	(0.7, 1.1) <sup>a</sup>	0.22	(0.16, 0.29) <sup>a</sup>	0.17	(0.12, 0.23) <sup>a</sup>
Small gaps	1.1	(0.9, 1.3) <sup>a</sup>	0.27	(0.20, 0.34) <sup>a</sup>	0.23	(0.17, 0.30) <sup>a</sup>
Large gaps	1.1	(0.9, 1.2) <sup>a</sup>	0.23	(0.18, 0.29) <sup>a</sup>	0.20	(0.15, 0.26) <sup>a</sup>
Wind	1.1	(0.9, 1.3) <sup>a</sup>	0.29	(0.21, 0.38) <sup>a</sup>	0.23	(0.16, 0.30) <sup>a</sup>
<b>Large seedlings</b>						
Control	0.7	(0.6, 0.9) <sup>a</sup>	0.13	(0.08, 0.18) <sup>a</sup>	0.10	(0.06, 0.14) <sup>a</sup>
Small gaps	1.7	(1.5, 2.0) <sup>b</sup>	0.38	(0.31, 0.44) <sup>b</sup>	0.40	(0.33, 0.48) <sup>b</sup>
Large gaps	1.6	(1.3, 1.8) <sup>b</sup>	0.34	(0.28, 0.40) <sup>b</sup>	0.35	(0.28, 0.42) <sup>b</sup>
Wind	1.4	(1.1, 1.7) <sup>b</sup>	0.31	(0.23, 0.38) <sup>b</sup>	0.26	(0.19, 0.32) <sup>ab</sup>
<b>Saplings</b>						
Control	0.8	(0.7, 1.0) <sup>a</sup>	0.15	(0.09, 0.21) <sup>a</sup>	0.11	(0.07, 0.16) <sup>a</sup>
Small gaps	0.6	(0.5, 0.7) <sup>b</sup>	0.11	(0.06, 0.16) <sup>ab</sup>	0.09	(0.05, 0.13) <sup>ab</sup>
Large gaps	0.4	(0.3, 0.4) <sup>c</sup>	0.04	(0.02, 0.06) <sup>b</sup>	0.03	(0.01, 0.04) <sup>b</sup>
Wind	0.5	(0.4, 0.5) <sup>bc</sup>	0.06	(0.02, 0.10) <sup>ab</sup>	0.04	(0.01, 0.08) <sup>ab</sup>

**Table 2.3.** Mean species richness (number of species per plot), evenness (Pielou, 1969), and Shannon-Wiener index of diversity (Shannon and Weaver, 1949) in 2m<sup>2</sup> plots for all woody species in large gaps by size class and gap-cleaning treatment. Values in parentheses are 90% confidence intervals; n=48 for each gap-cleaning treatment. Different letters indicate significant differences between gap-cleaning treatments within a size class at p<0.1 using Tukey's HSD. See Fig. 2.3 for size class definitions.

	Species richness		Species evenness		Shannon index	
<b>Small seedlings</b>						
Not cleaned	1.1	(0.9, 1.2) <sup>a</sup>	0.25	(0.20, 0.31) <sup>a</sup>	0.22	(0.17, 0.28) <sup>a</sup>
Cleaned	1.1	(0.9, 1.2) <sup>a</sup>	0.23	(0.18, 0.29) <sup>a</sup>	0.20	(0.15, 0.26) <sup>a</sup>
Scarified	0.9	(0.8, 1.1) <sup>a</sup>	0.22	(0.16, 0.27) <sup>a</sup>	0.18	(0.13, 0.23) <sup>a</sup>
<b>Large seedlings</b>						
Not cleaned	1.5	(1.2, 1.8) <sup>a</sup>	0.33	(0.27, 0.39) <sup>a</sup>	0.32	(0.26, 0.39) <sup>a</sup>
Cleaned	1.6	(1.3, 1.8) <sup>a</sup>	0.34	(0.28, 0.40) <sup>a</sup>	0.35	(0.28, 0.42) <sup>a</sup>
Scarified	1.0	(0.9, 1.2) <sup>b</sup>	0.25	(0.19, 0.31) <sup>a</sup>	0.22	(0.17, 0.28) <sup>b</sup>
<b>Saplings</b>						
Not cleaned	0.4	(0.3, 0.4) <sup>a</sup>	0.06	(0.03, 0.09) <sup>a</sup>	0.05	(0.02, 0.07) <sup>a</sup>
Cleaned	0.4	(0.3, 0.4) <sup>a</sup>	0.04	(0.02, 0.06) <sup>a</sup>	0.03	(0.01, 0.04) <sup>a</sup>
Scarified	0.2	(0.2, 0.3) <sup>b</sup>	0.03	(0.01, 0.05) <sup>a</sup>	0.02	(0.01, 0.03) <sup>a</sup>

## **Chapter 3 : Ground-layer plant community response to structural complexity restoration in second-growth northern hardwood forests**

### **Introduction**

In most forest types, the ground layer has the greatest number of plant species and contributes most to plant diversity in the ecosystem (Thomas et al., 1999). This layer plays several important roles in forest ecosystem functioning including providing forage and cover for animals (Carey and Johnson, 1995; Coppeto and Kelt, 2006) and significantly affecting nutrient cycling (MacLean and Wein, 1977; Moore et al., 2007; Roberts and Gilliam, 1995; Zak et al., 1990). Many ground layer plants grow and/or reproduce slowly and may be sensitive to disturbances in the forest canopy layer (Meier et al., 1995); however, disturbance processes also may increase environmental heterogeneity and create microsites for plants with different environmental and seedbed requirements to establish, thus increasing species diversity (Elliott and Knoepp, 2005; Vellend et al., 2000).

There is concern that current forest management practices such as single-tree selection, which is commonly used in forests dominated by shade-tolerant species, lead to homogenization of species composition and structural characteristics (Crow et al., 2002; Johnson, 1984; Leak and Sendak, 2002; Meier et al., 1995; Royo and Carson, 2006; Scheller and Mladenoff, 2002). The small canopy gaps created by this practice generally favor ground layer species that are shade-tolerant (Denslow, 1980; Fahey and Puettmann, 2007; Kern et al., 2013b). In addition, the ground layer of second-growth and managed



stands may be more compositionally homogeneous than old-growth stands, due in part to a lower degree of microhabitat heterogeneity including less downed, decaying wood as a germination substrate in these systems (Duffy and Meier, 1992; Goodburn and Lorimer, 1998; Hale et al., 1999; Scheller and Mladenoff, 2002).

Concerns over the homogenization of structural and compositional conditions by traditional forest management approaches have led to an increased emphasis on using ecological forestry and natural disturbance-based silviculture to enhance structural complexity and heterogeneity, as well as species diversity, while still harvesting timber products (Franklin et al., 2007; Seymour and Hunter, 1999; Smith et al., 2008). In natural disturbance-based silviculture, harvests are designed to emulate the frequency and intensity of natural disturbances (such as insect outbreaks, wind, and fire) that occur on the landscape (Bauhus et al., 2009; Franklin et al., 2007). In northern hardwood forests natural disturbance-based systems have focused primarily on small scale tree-fall disturbances by creating canopy gaps up to 2000 m<sup>2</sup>, but often significantly smaller (Arseneault et al., 2011; Bolton and D'Amato, 2011; Keeton, 2006; Seymour, 2005). However mesoscale disturbances, especially from wind events, are also important in determining stand structure and composition in these systems, but are often ignored in natural disturbance-based management (Franklin et al., 2007; Frelich and Lorimer, 1991a, 1991b; Hanson and Lorimer, 2007). These mesoscale canopy disturbances historically occurred approximately once during the lifespan of a cohort of trees in northern hardwood forests of the upper Great Lakes region and had important consequences for forest compositional and structural development by generating larger

canopy openings, increased solar radiation on the forest floor, and increased heterogeneity in solar radiation when compared to typical uneven-aged harvests (Frelich and Lorimer, 1991a; Hanson and Lorimer, 2007).

Although natural disturbance-based approaches often emulate natural patterns of disturbance severity through removal of canopy trees, inherent differences still exist between these approaches and the natural processes they aim to emulate (Franklin et al., 2007). In particular, degree of soil disturbance may be greater following timber harvest, depending on season of operation and degree of site preparation, and the use of harvest equipment increases the probability of transportation of exotic invasive species in to an area (Buckley et al., 2003; Crow et al., 2002; Haeussler and Kneeshaw, 2003).

Collectively, these factors can significantly impact ground layer composition in managed forests (Buckley et al., 2003; Duffy and Meier, 1992; Small and McCarthy, 2002); however, some work has indicated that these are transient initial impacts that become negligible over time (Albert and Barnes, 1987; Duguid et al., 2013; Kern et al., 2006; Metzger and Schultz, 1984). Despite increasing emphasis on applying ecological forestry to restore and sustain elements of forest biodiversity, including the ground layer, there is little operational-scale research that examines the effectiveness of these approaches in achieving this objective.

This study examines ground layer community response to silvicultural treatments developed to increase structural complexity and heterogeneity and compositional diversity of second-growth northern hardwood stands by emulating the effects of small- and mesoscale disturbances. Harvesting treatments designed to manipulate canopy gaps,

coarse woody debris, and microsite conditions were implemented at three replicate landscapes in northern Wisconsin. We examined ground layer community composition to address the following questions: (i) how do overstory treatments based on emulation of a range of natural disturbances, from single tree-fall gaps to mesoscale wind disturbances, affect ground layer composition and diversity, and (ii) how does microsite preparation within gaps affect the ground layer?

## **Methods**

### *Study sites*

The study system is second-growth northern hardwood forests in northern Wisconsin. This study took place in the Flambeau River State Forest (Flambeau), the Northern Highland-American Legion State Forest (Northern Highland) and the Chequamegon-Nicolet National Forest's Argonne Experimental Forest (Argonne). Four stands were chosen at each site that were approximately 50 ha each, 70-90 years old, and had no management activity in the previous 10 years. Stands were mainly dominated by *Acer saccharum*, with other overstory species including *Fraxinus americana*, *Betula alleghaniensis*, *Tilia americana*, *Acer rubrum*, and *Tsuga canadensis*. See Chapter 2 for site details.

### *Silvicultural Treatments*

Three overstory treatments and two coarse woody debris treatments were implemented at each site in the winter of 2007-2008 (with the exception of the large

gaps/ambient CWD treatment [see description below] at ARGN, which was implemented one year later in winter 2008-2009) in a split plot design. Each stand (whole plot) was divided into two approximately 25 hectare half-stands (split plot), with the entire stand receiving one overstory treatment and each half-stand receiving a different coarse woody debris treatment. Each site also had an approximately 50 hectare uncut control stand, which did not receive any harvest treatment.

The overstory treatments were as follows: (i) small gaps (10.7 m diameter), (ii) large gaps (18.3 m and 24.4 m diameter); and (iii) a multicohort treatment designed to emulate a mesoscale wind disturbance based on the patterns of disturbance documented by Hanson and Lorimer (2007). The three overstory treatments were defined by the size of canopy gaps, number of gaps created per hectare, and additional thinning done to the matrix surrounding gap treatment areas. For the small gap treatment, approximately ten gaps with a 10.7 m diameter were created per hectare and the rest of the stand was thinned to a residual basal area of 18.3-20.7 m<sup>2</sup>/ha. Additionally, these gaps were cleaned of all saplings greater than 2.54 cm diameter at breast height (dbh), a practice that is widely implemented in the region to encourage development of quality hardwood regeneration.

The large gap treatment involved creating one 18.3 m or one 24.4 m diameter gap per 0.4 ha. Areas between large gaps were thinned to achieve a residual basal area of 18.3-20.7 m<sup>2</sup>/ha. Within the large gap treatment, a nested gap-level site preparation treatment was implemented with one of three treatments randomly assigned to each gap: (i) no cleaning (hereafter referred to as “not cleaned”) in which only poorly formed

saplings were removed, (ii) cleaning (hereafter referred to as “cleaned”) in which all saplings greater than 2.54 cm dbh were removed, and (iii) cleaned and scarified gaps (hereafter referred to as “scarified”) in which gaps were cleaned of all saplings greater than 2.54 cm dbh and then scarified with a Salmon blade to expose 70-90% mineral soil. Scarification was performed in September following harvest using a Salmon blade on a crawler bulldozer.

The mesoscale wind treatment included four patches cut as shelterwoods, a heavily thinned matrix area, and a lightly thinned matrix area in each split plot (half stand). Of the four shelterwoods, two were 0.4 ha and two were 1.2 ha in size. Each shelterwood was cut to leave 60-65% residual basal area. The lightly thinned area covered approximately 25% of the stand and remaining portion of the stand was heavily thinned (approximately 65% of the stand). The lightly- and heavily thinned areas were reduced to 20.7-23.0 m<sup>2</sup>/ha and 18.3-20.7 m<sup>2</sup>/ha residual basal area, respectively. A second harvest entry is planned in these stands for six to ten years after the initial harvest. At this time, shelterwoods will be reduced to about 10% crown closure and the heavily thinned area will be reduced to approximately 17.2 m<sup>2</sup>/ha residual basal area. See Fig. 2.1 for aerial photographs of treatment stands.

Coarse woody debris (CWD) treatments were identified as ambient and high. In stands receiving the ambient CWD treatment, no additional CWD was deliberately created. In the stands receiving the high CWD treatment, the number of snags and amount of downed wood were deliberately increased during harvest to approximately 65% of the density and volume found in old-growth northern hardwood stands in the

Sylvania Wilderness in Upper Michigan (Goodburn and Lorimer, 1998), the nearest similar old-growth forests in the region. Snags were created by double-girdling live trees and downed logs were created by felling poorer formed canopy trees.

### *Field Methods*

Ground layer community composition was evaluated to assess the effects of silvicultural treatments on vegetation. Data were collected in the summer of 2012, four years after harvest for all stands except the large gaps/ambient CWD treatment at the Argonne site, which was harvested a year later than the other sites and thus was only in its third growing season after harvest when ground-layer community was surveyed.

In each treatment stand, the ground layer was evaluated at vegetation plots in gaps (small and large gap treatment), shelterwoods (mesoscale wind treatment), or in the forest matrix (control stands). Four replicate plots were sampled for each treatment combination. Treatment combination included overstory treatment, CWD treatment, and, in the large gaps, gap-cleaning treatment. For example, the ground layer was evaluated in a total of eight plots in small (10.7 m diameter) gaps at each site, four in small gaps that had received high CWD treatment and four in small gaps that had received ambient CWD treatment, for a total of 24 sampled vegetation plots in the small gap treatment across the study. At each site in stands receiving the large gap treatment, 48 plots were sampled: four gaps at each gap size (18.3 or 24.4 m diameter) factored by gap-cleaning treatment (not cleaned, cleaned, scarified) and by CWD treatment (ambient or high) (4 replicates x 2 gap sizes x 3 cleaning treatments x 2 CWD treatments = 48 sampled plots), for a total

of 144 plots sampled across the study. At each site in each stand receiving the mesoscale wind treatment, four plots were sampled in shelterwoods receiving the high CWD treatment and four plots were sampled in shelterwoods receiving the ambient CWD treatment, for a total of eight plots sampled at each site. In some stands, two of the vegetation plots were located within the same shelterwood. Data were averaged to the shelterwood level and shelterwoods were treated as individual units of analysis in order to maintain consistency with the small and large gap treatments, in which gaps were treated as individual units of analysis. This resulted in seven sampled shelterwoods at each site and 21 total sampled shelterwoods across the study. In control stands, 10-11 plots were selected randomly from a grid across each stand at each site (31 total plots in the study) and sampled for ground layer vegetation. In some stands, plots had to be dropped due to changes in location of deer enclosure fences or damage to these fences (see Chapter 4), so total sample size was slightly lower than above.

At each vegetation plot, four 0.5 m<sup>2</sup> subplots were sampled. Subplots were placed five meters from plot center in each cardinal direction. In cases where at least 15% of growing space in the subplot was obstructed by rocks or a mature tree, the plot was moved in the direction that eliminated the obstruction while requiring the least deviation from its original placement. Percent cover for all herbaceous plants and woody plants less than 0.5 meters tall was estimated in each subplot using the Braun-Blanquet cover-abundance scale (rare, solitary, with small cover; few, with small cover; numerous, but less than 5% cover or scattered, with cover up to 5%; 5-25%; 25-50%; 50-75%; and >75%) (Braun-Blanquet, 1932). Most plants were identified to species when possible or

genus when species could not be determined. Grasses were only identified to family (Poaceae) and *Carex* spp. were only identified to genus except *Carex pensylvanica* (Pennsylvania sedge), given the known importance of this species in affecting forest regeneration in these systems (Powers and Nagel, 2009).

Presence of exotic earthworms has also been shown to have significant impacts on ground layer community composition and tree regeneration (Holdsworth et al., 2007; Nuzzo et al., 2009; Powers and Nagel, 2008). At each overstory treatment stand, ten randomly located plots were evaluated for earthworm invasion level using the Invasive Earthworm Rapid Assessment Method (Loss et al., 2013). This protocol uses visual assessment of the forest floor to classify earthworm invasion into five stages, stage one being potentially earthworm free and stage five being most affected by earthworm invasion characterized by invasion of *Lumbricus terrestris* (Loss et al., 2013). Since these data were collected on a very coarse scale, we did not use them in analysis, but potential implications are considered in the discussion section of this chapter.

### *Statistical Analyses*

Midpoints of cover classes for individual taxa were used in all calculations. This resulted in cover estimates of 0.01%, 0.1%, 2.5%, 15%, 37.5%, 62.5%, and 87.5%.

Small and large gaps contained one vegetation plot per sampled gap. In these treatments, gaps were treated as individual units of analysis, despite the fact that overstory treatments were applied at the stand level. In the mesoscale wind treatment, shelterwoods were treated as individual units of analysis to maintain consistency with the



large and small gaps. Most shelterwoods contained only one vegetation plot, but at each site one large shelterwood (1.2 ha) contained two vegetation plots which were averaged to the shelterwood level. In controls, vegetation plots were treated as individual units of analysis. The significant distance between vegetation plots (>15 m in small and large gaps treatments and >50 m in mesoscale wind treatment and controls) and the large scale of the treatment stands (~50 ha) allowed us to consider each gap (small and large gaps), shelterwood (mesoscale wind treatment), or vegetation plot (controls) as an independent observation.

Compositional differences between overstory treatments and gap-cleaning treatments were evaluated using distance-based MANOVA (PerMANOVA), with site as the blocking factor and overstory or gap-cleaning treatment as the grouping variable. The Sorenson distance measure was used for these analyses. Since PerMANOVA requires a balanced design, we performed the analysis 1000 times on data sets created by randomly sampling six (overstory treatment analysis) or 13 (gap-cleaning treatment analysis) plots for each site by overstory treatment combination. Mean pseudo F-ratio and p-values for the 1000 bootstrapped samples were reported. Analyses were run in PC-ORD version 6.0 (McCune and Mefford, 2011).

Compositional differences between and among overstory treatments were examined using nonmetric multidimensional scaling ordination (NMS). Sorenson's distance was used to measure compositional dissimilarity and the ordination was performed using PC-ORD with 250 runs of real data, 250 runs of randomized data, and a maximum of 500 iterations per run (McCune and Mefford, 2011). Indicator species

analysis (ISA, Dufrene and Legendre, 1997) was used to determine differences in frequency and abundance of species within overstory treatments and gap-level cleaning treatments using PC-ORD. ISA indicator values (IV) range from 0 (no indication) to 100 (perfect indication). Site was used as a blocking variable and species were considered significant indicators of a treatment when  $p < 0.1$  with 1000 randomizations of a Monte Carlo test. In all of the above analyses (PerMANOVA, NMS and ISA), species present in less than 10% of plots were not included and data for percent cover was relativized by species total.

Coefficient of conservatism (C) values were reported for significant indicator species. Coefficient of conservatism is a measure of likelihood of a species to be present on an unaltered landscape, on a scale from 0 to 10. Species with higher coefficients of conservatism are more likely to be found on relatively unaltered landscapes, presumed to be more similar to presettlement conditions (Wilhelm and Masters, 1995). Since exotic species by definition were not present on presettlement unaltered landscapes, these species do not have C values.

Differences in species richness (number of species per plot), Shannon-Wiener index of diversity (Shannon and Weaver, 1949), and evenness (Pielou, 1969), as well as total cover by functional groups (graminoids, ferns and fern allies, exotic species, other forbs, shrubs, and tree seedlings) and specifically cover of *C. pensylvanica* were determined using analysis of variance (ANOVA). Overstory treatment or gap-cleaning treatment was treated as a fixed variable and site was treated as a random variable. When assumptions of normality and constant variance were not met, data were transformed

using a square root transformation. When significant main effects of fixed variables were found, Tukey's HSD was used to determine pairwise differences between treatments with  $p < 0.1$  considered significant. For all analyses comparing overstory treatments, only large gaps that received the "cleaned" treatment were included in order to maintain comparability between treatments. Coarse woody debris treatment was not a significant factor in any of our analyses, thus these results are not presented.

## Results

### *Overstory treatments*

### *Community composition*

We did not find a significant effect of overstory treatment on ground layer composition (PerMANOVA mean pseudo F-ratio=0.9365, mean  $p=0.5484$ ). This result was also evident in NMS ordinations of ground layer community composition, where we saw a significant amount of overlap in locations of treatments within ordination space. We did however see some separation of the lower and higher disturbance treatments, with the large gaps and mesoscale wind treatment generally occupying similar portions of ordination space distinct from the small gaps and controls (Fig. 3.1).

In this ordination, most of the variation was explained by Axis 1 (44.0%), which ranged from plots with a higher abundance of *Oxalis stricta* (Kendall's  $\tau=-0.5394$ ,  $p=0.0289$ ), *C. pensylvanica* (Kendall's  $\tau=-0.3636$ ,  $p=0.0998$ ), and *Veronica officinalis* (Kendall's  $\tau=-0.4393$ ,  $p=0.0699$ ) toward the negative portion of the axis to generally higher-disturbance mesoscale wind and large gap treatments in the positive portion of this

axis, with higher abundance of 34 different taxa, including many forest interior species (ex. *Trillium* spp. (Kendall's  $\tau=0.4999$ ,  $p=0.0327$ ) and *Mitella diphylla* (Kendall's  $\tau=0.5192$ ,  $p=0.0332$ )) as well as *Carex* spp. (Kendall's  $\tau=0.4848$ ,  $p=0.0282$ ) and disturbance-adapted *Polygonum* spp. (Kendall's  $\tau=0.4122$ ,  $p=0.0635$ ) (Fig. 3.1, also see Appendix A).

The distribution of treatments along Axis 2, which explained 22.2% of total variation, generally ranged from the more severely-disturbed large gaps and mesoscale wind treatment in the lower end of Axis 2 to small gaps and controls on the higher portion of this axis (Fig. 3.1). *Fraxinus* spp. (Kendall's  $\tau=0.5428$ ,  $p=0.0155$ ) were positively associated with this axis, while taxa associated with the negative portion included the exotic invasive species *Taraxacum officinale* (Kendall's  $\tau=-0.4999$ ,  $p=0.0327$ ), *Cirsium arvense* (Kendall's  $\tau=-0.4944$ ,  $p=0.0452$ ), and *Veronica officinalis* (Kendall's  $\tau=-0.3994$ ,  $p=0.0994$ ), and disturbance-adapted *Rubus* spp. (Kendall's  $\tau=-0.4450$ ,  $p=0.0499$ ), as well as grasses (Kendall's  $\tau=-0.6364$ ,  $p=0.0040$ ) and *Arisaema triphyllum* (Kendall's  $\tau=-0.5649$ ,  $p=0.0110$ ) (Fig. 3.1, also see Appendix A).

Several species were identified as significant indicators of a given treatment (per Indicator Species Analysis,  $p<0.1$ ; Table 3.1). Several herbaceous species with higher coefficients of conservatism, including *Streptopus roseus* (C=7), *Lycopodium dendroideum* (C=7), and *Aralia nudicaulis* (C=6), as well as *Osmorhiza claytonii* (C=5) were associated with the less-disturbed small gaps. Additionally, shade-tolerant *A. rubrum* and midtolerant *Fraxinus* spp. were associated with this treatment (Table 3.1). Members of the Poaceae family and *Rubus pubescens* were significant indicators of large

gaps (Table 3.1). The invasive species *Galeopsis tetrahit* and *Polygonum convolvulus* as well as *Carex* spp. and disturbance-adapted *Rubus* spp. (C=2-4) were significant indicators of the mesoscale wind treatment (Table 3.1). There were no significant indicator species for the control stands (Table 3.1).

### *Species diversity and cover*

Measures of plot-level diversity were higher in treated areas than in the controls (Table 3.2). Species richness was significantly higher in the small gaps relative to all of the other treatments (Table 3.2). There was no difference in species richness between the large gaps and mesoscale wind treatment, but both were significantly higher than the controls (Table 3.2). Species evenness was significantly lower in the control stands relative to the mesoscale wind and large gap treatments, which were not different from one another. Evenness in the small gap treatment was not significantly different from the control, large gaps, or mesoscale wind treatments (Table 3.2). Shannon index was significantly higher in the treatment stands than the controls, but there was no significant difference between the treatments (Table 3.2).

Total cover of exotic plants was affected by overstory treatment and increasing canopy disturbance generally led to increasing cover of exotic species (Table 3.3). The most common taxa in this group were *Polygonum* spp. and *Galeopsis tetrahit*, but *Taraxacum officinale*, *Veronica officinalis*, *Hieracium* spp., *Cirsium arvense*, *Myosotis scorpioides*, *Urtica dioica*, *Cirsium palustre*, *Cirsium vulgare*, *Verbascum thapsus*, *Lapsana communis*, *Myosoton aquaticum*, and *Cerastium fontanum* were also found in

the study area. Percent cover of graminoids and shrubs (largely *Rubus* spp.) also generally increased with increasing canopy openness, with the highest cover of graminoids found in large gaps and highest cover of shrub species in the mesoscale wind treatment (Table 3.3). Cover of ferns and fern allies was also highest in the mesoscale wind treatment, significantly higher than the large gaps and controls. Finally, overstory treatment did not have a significant effect of cover by other forbs or tree seedlings less than 0.5 m tall (Table 3.3). Overstory treatment did not have a significant effect on cover by *C. pennsylvanica* (ANOVA,  $F_{3,113}=0.04$ ,  $P=0.9901$ ).

#### *Gap-cleaning treatments*

Gap-cleaning treatments (not cleaned, gaps cleaned of all saplings greater than 2.5cm dbh, and gaps cleaned and scarified to expose mineral soil) did not have a strong effect on composition of the ground layer. PerMANOVA indicated no significant differences in composition between the three treatments (mean pseudo F-ratio=0.2561, mean  $p=0.9654$ ). Indicator species analysis found no indicators for the cleaned gaps, but *Carex* spp. were indicative of the scarified gaps (IV=37.4,  $p=0.0196$ ) and *Trillium* spp. were indicative of the less-disturbed, not cleaned gaps (IV=18.7,  $p=0.0032$ ). There were no differences in any of the diversity measures between the three gap-level treatments (Table 3.4). Gap-cleaning treatments did not have a significant effect on ground-layer cover by any functional group (Table 3.5) or *C. pennsylvanica* ( $F_{2,132}=0.10$ ,  $P=0.9030$ ).

## **Discussion**

Our findings suggest that silvicultural techniques designed to increase structural complexity also have an effect on the composition of the ground-layer community that is largely reflective of the range in disturbance severities being emulated. Overstory removal increased species diversity of the ground layer; however, treatments approximating more moderate levels of canopy disturbance also provided opportunities for the introduction and establishment of exotic and ruderal species. Treatments applied at the gap level to reduce competition from existing advance regeneration and increase exposed mineral soil seedbed conditions had little effect on the ground layer communities in these second-growth northern hardwood forests.

The increased richness and diversity of ground layer plants observed soon after harvest in this study is consistent with findings from other work examining partial harvests (Gálhidy et al., 2006; Goldblum, 1997; Götmark et al., 2005; Schumann et al., 2003), including a meta-analysis of data from 96 studies in North American temperate forests (Duguid and Ashton, 2013). We did not observe significant differences in diversity between overstory treatments, but species richness was actually highest in the small gaps (lowest harvest intensity). This finding is contrary to several other studies that found an increase in richness and/or diversity with increasing harvesting intensity (larger canopy gaps and/or more basal area removed), at least in partial harvests (Burke et al., 2008; Elliott and Knoepp, 2005; Fredericksen et al., 1999; Gálhidy et al., 2006; Hammond et al., 1998). In addition, this finding is counter to expectations based on the

intermediate disturbance hypothesis (Connell, 1978), which would predict the greatest levels of diversity in the large gap or mesoscale wind treatments.

The higher levels of species richness in small gaps relative to more intensive harvest treatments may be due to the positive response of interior forest ground-layer species to the slight increases in resource availability associated with the small gap treatments. In particular, several forest interior and disturbance-sensitive species were associated with the small gaps including *Aralia nudicaulis*, *Streptopus roseus*, *Lycopodium dendroideum*, and *Osmorhiza claytonia*. The fine-scale patterns of disturbance created by the smaller diameter gaps potentially allowed populations of forest interior species to increase without dramatic environmental changes, whereas the higher severity disturbances (large gaps and mesoscale wind treatment) created opportunities for more ruderal species to establish and expand. Nevertheless, these trends may be transient, as other studies have found no effects of single-tree and group selection harvests on the ground layer community up to nine years after harvest (Collins and Pickett, 1988, 1987; Jalonen and Vanha-Majamaa, 2001; Kern et al., 2006).

Ruderal or disturbance-adapted species such as *Rubus* spp. and other shrubs, graminoids, and exotic species including *Polygonum convolvulus*, three *Cirsium* spp., *Galeopsis tetrahit*, and *Myosotis scorpioides*, were more common in treatments with higher canopy openness, especially the mesoscale wind treatment. This increase in non-forest specialist species was likely a contributing factor to the overall increase in richness and diversity found in these stands (Burke et al., 2008; Halpern and Spies, 1995). Many studies have observed increased ruderal species in harvest gaps (Fahey and Puettmann,



2007; Götmark et al., 2005; Schumann et al., 2003; Shields and Webster, 2007), stands where more basal area is removed (Burke et al., 2008; Fredericksen et al., 1999), and managed stands overall (Buckley et al., 2003), with the hypothesis being that open conditions after harvest create an environment that favors r-selected species (Crow et al., 2002). Exotic species, which can increase with harvesting activity (Buckley et al., 2003; Shields and Webster, 2007), exhibited increased cover with increasing harvest intensity in this study as well. Although the emulation of historic mesoscale disturbances may provide conditions to restore structural and compositional conditions absent from contemporary landscapes, these treatments need to also be considered in the context of providing greater opportunity for non-native species to increase in abundance.

While an increase in light with overstory removal may be the most important factor contributing to changes in diversity and composition in the harvested stands in this study, other work has found that many additional factors can affect ground layer composition. In some studies, soil characteristics, including bare soil and soil moisture, were found to be as or more important than overstory characteristics in determining ground layer composition and diversity (Fahey and Puettmann, 2007; Fredericksen et al., 1999; Gálhidy et al., 2006; Gilliam et al., 1995). We did not measure soil moisture, but bare soil created through scarification in the large gaps did not seem to have a significant effect on the ground layer in our study, as we saw no differences in composition or diversity between scarified and non-scarified plots.

Invasive, exotic earthworms and their interactive effects with deer herbivory have increasingly been linked to lower plant richness and changes in native plant communities

in the eastern United States (Holdsworth et al., 2007; Nuzzo et al., 2009). We observed differences in earthworm invasion level (Loss et al., 2013) between stands. Our rough estimate of earthworm invasion was positively correlated with Axis 1 in the NMS ordination (data not shown), suggesting that presence of invasive earthworms may be another significant factor contributing to differences in ground layer composition at these sites. In addition, we found some impacts of deer herbivory on ground layer compositional conditions in these areas in a companion study examining deer exclosures across each overstory treatment (Chapter 4).

*C. pensylvanica* was a species of particular interest in this study because at high densities, this sedge has been shown to form thick mats which reduce density and diversity of tree and shrub regeneration (Johnson, 1992; Powers and Nagel, 2009; Randall and Walters, 2005) as well as cover and diversity of other herbaceous species (Randall and Walters, 2005). Populations of this native sedge have been known to increase dramatically with increased light availability (Zavitkovski, 1976), especially after heavy harvests or clearcutting (Abrams and Dickmann, 1984, 1983; Buckley et al., 1998; Johnson, 1992; Metzger and Tubbs, 1971). We did not observe a significant effect of overstory removal on cover by *C. pensylvanica*, which could be due to the fact that our harvests were not as heavy as those in the studies cited above. Johnson (1992) suggested that canopy openings less than 0.1 ha, which is two times larger than the 24 m diameter (large) gaps in this study, would minimize development of sedge mats. Other factors known to affect sedge densities, especially exotic earthworms (Powers and Nagel, 2008), may also be overriding the influence of overstory disturbance effects on the expansion of

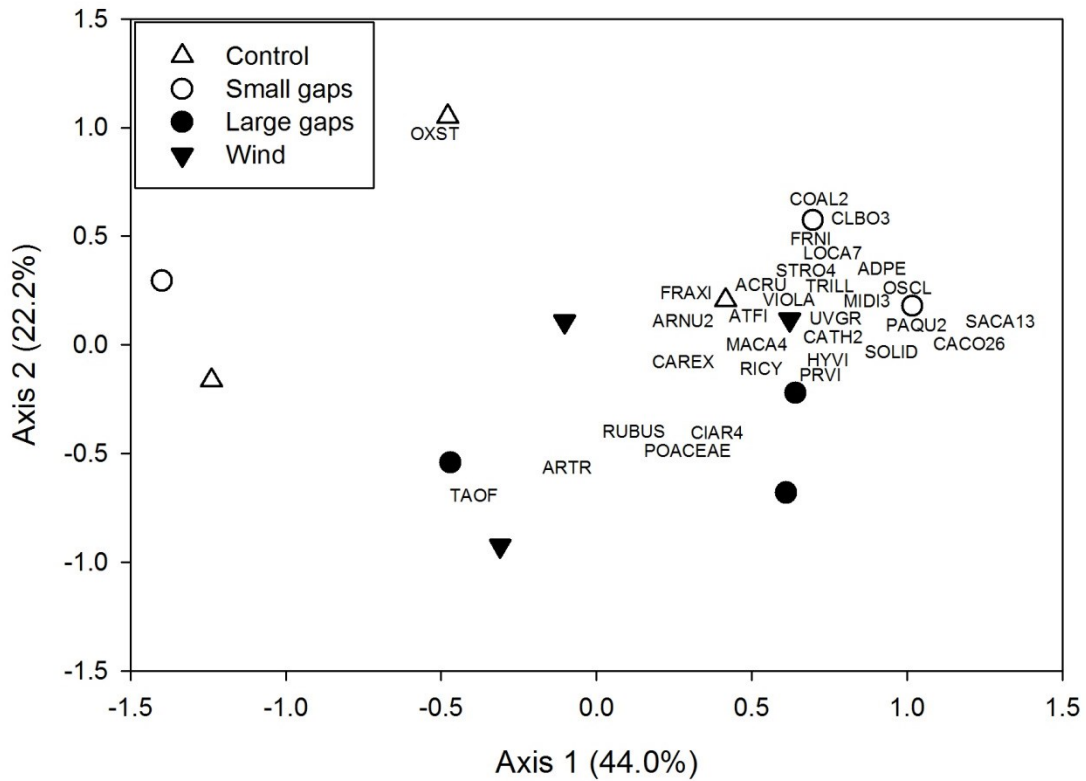
this species. Powers and Nagel (2008) found that effects of harvest intensity alone on *C. pensylvanica* abundance were not significant, but interactions between management and herbivory by white-tailed deer and exotic earthworms did affect percent cover by *C. pensylvanica*. We saw the highest percent cover by *C. pensylvanica* as well as the overall highest exotic earthworm invasion level (Loss et al., 2013, data not shown) at the Northern Highlands site. At the Flambeau site, the mesoscale wind treatment stand had the highest cover by *C. pensylvanica* as well as the highest earthworm invasion level (Loss et al., 2013). These findings suggest a similar mechanism associated with exotic earthworm invasion and sedge mat development may be occurring in our study areas. Additionally, we found some evidence of increased sedge cover in areas with deer compared to browse-protected areas in our companion deer exclosure study (Chapter 4).

#### *Management implications*

Creation of canopy gaps with the objective of increasing structural and compositional diversity did have an effect on the ground layer community in second-growth northern hardwood forests. While canopy gaps caused an increase in species richness and diversity, the highest diversity and richness were actually found in the smallest gaps (10.7 m diameter). More desirable forest interior species increased with the fine-scale disturbance pattern created in these stands, while the majority of species contributing to increased diversity in the large gaps (18.3 and 20.7 m diameter) and shelterwoods were disturbance-adapted exotic species, graminoids, and shrubs. Gaps larger than a certain size, in this case somewhere between 10.7 and 18.3 m diameter

create conditions that are too open for many forest interior species to be competitive. This work also suggests that as canopy openness is increased, the risk of exotic species establishment increases and care should be taken to clean harvest equipment and avoid creating canopy openings around known populations of exotics. Additional forest floor disturbance from deliberate scarification may have minimal effect on herbaceous understory, while possibly allowing for increased establishment of light-seeded tree species such as *Betula alleghaniensis* (see Chapter 2). Additional factors that are not part of the natural dynamic of these stands including exotic earthworm invasion and extreme herbivory by elevated populations of white-tailed deer (see Chapter 4) may interact with treatments designed to emulate natural disturbances and have stronger or unexpected effects on the ground-layer community. Site- or stand-specific consideration of these additional factors is important when making management decisions and may require adjusting expectations regarding the degree to which natural disturbance based approaches can restore native biodiversity given the pervasive influence of these modern stressors.

**Figures**



**Fig. 3.1.** Non-metric multidimensional scaling (NMS) ordination of ground layer vegetation across overstory treatments. All species displayed in the figure are significantly associated with at least one axis at  $p < 0.05$ ; abbreviations follow USDA-PLANTS database (USDA-NRCS, 2013) and are defined in Appendix A. Also see Appendix A for species correlations with axes.

## Tables

**Table 3.1.** Indicator species analysis (Dufrene and Legendre, 1997) for overstory treatments. IV=importance value; all species with  $p < 0.1$  are reported. Coefficient of conservatism ranges from 1 to 10 and species with higher coefficients of conservatism are more likely to be found on relatively unaltered landscapes.

Overstory treatment	Species	IV	p-value	Coefficient of Conservatism (C)
Controls	None	-	-	-
Small gaps	<i>Aralia nudicaulis</i>	23.6	0.0076	6
	<i>Streptopus roseus</i>	15.2	0.0302	7
	<i>Lycopodium dendroideum</i>	18.2	0.0368	7
	<i>Acer rubrum</i>	24.4	0.0416	3
	<i>Fraxinus</i> spp.	25.0	0.0678	5/2
	<i>Osmorhiza claytonii</i>	18.5	0.0680	5
Large gaps	Poaceae	35.0	0.0280	-
	<i>Rubus pubescens</i>	14.7	0.0912	7
Wind	<i>Rubus</i> spp.	58.2	0.0002	2-4
	<i>Polygonum</i> spp.	38.7	0.0002	1 or exotic
	<i>Carex</i> spp.	35.1	0.0116	-
	<i>Galeopsis tetrahit</i>	24.5	0.0184	exotic

**Table 3.2.** Mean species richness (number of species per plot), evenness (Pielou, 1969), and Shannon-Wiener index of diversity (Shannon and Weaver, 1949), for all ground layer species including woody species less than 0.5 m tall in 2m<sup>2</sup> plots. Values in parentheses represent 90% confidence intervals; for control n=31, small gaps n=24, large gaps n=44, and mesoscale wind n=20. Values with different letters are significantly different at P<0.1, using Tukey's HSD.

<b>Overstory</b>			
<b>Treatment</b>	Species richness	Species evenness	Shannon index
Control	7.3 (5.9, 8.7) <sup>a</sup>	0.50 (0.41, 0.59) <sup>a</sup>	1.00 (0.78, 1.22) <sup>a</sup>
Small gaps	13.9 (11.3, 16.5) <sup>b</sup>	0.61 (0.52, 0.70) <sup>ab</sup>	1.64 (1.33, 1.94) <sup>b</sup>
Large gaps	10.6 (9.5, 11.7) <sup>c</sup>	0.65 (0.60, 0.70) <sup>b</sup>	1.52 (1.36, 1.67) <sup>b</sup>
Wind	10.5 (9.3, 11.7) <sup>c</sup>	0.69 (0.66, 0.72) <sup>b</sup>	1.60 (1.47, 1.72) <sup>b</sup>

**Table 3.3.** Mean percent cover of ground-layer vegetation in overstory treatments by functional groups. Values in parentheses represent 90% confidence intervals; for control n=31, small gaps n=24, large gaps n=44, and mesoscale wind n=20. Values with different letters are significantly different within functional groups at P<0.1 using Tukey’s HSD

<b>Overstory treatment</b>	Graminoids	Ferns and fern allies	Exotic spp.	Other forbs	Shrubs	Tree seedlings
Control	15.4 (10.0, 20.7) <sup>a</sup>	9.2 (5.5, 12.9) <sup>a</sup>	0.1 (0.0, 0.3) <sup>a</sup>	18.8 (13.3, 24.4) <sup>a</sup>	0.4 (0.1, 0.8) <sup>a</sup>	5.7 (3.2, 8.3) <sup>a</sup>
Small gaps	17.5 (11.3, 23.6) <sup>ab</sup>	14.8 (9.3, 20.3) <sup>ab</sup>	2.8 (1.0, 4.6) <sup>ab</sup>	26.5 (18.8, 34.3) <sup>a</sup>	3.3 (2.0, 4.7) <sup>b</sup>	7.5 (5.0, 9.9) <sup>a</sup>
Large gaps	27.4 (21.5, 33.2) <sup>b</sup>	8.3 (5.4, 11.2) <sup>a</sup>	6.6 (3.8, 9.3) <sup>bc</sup>	24.3 (18.5, 30.2) <sup>a</sup>	4.8 (3.1, 6.4) <sup>b</sup>	6.1 (3.6, 8.5) <sup>a</sup>
Wind	23.9 (15.6, 32.2) <sup>ab</sup>	17.5 (10.7, 24.2) <sup>b</sup>	9.7 (5.5, 14.0) <sup>c</sup>	20.6 (13.8, 27.5) <sup>a</sup>	7.1 (4.3, 9.9) <sup>c</sup>	5.0 (2.4, 7.6) <sup>a</sup>



**Table 3.4.** Mean species richness (number of species per plot), evenness (Pielou, 1969), and Shannon-Wiener index of diversity (Shannon and Weaver, 1949) for all ground layer species including woody species less than 0.5 m tall in 2m<sup>2</sup> plots in large gaps. Values in parentheses represent 90% confidence intervals; for not cleaned gaps n=44, cleaned gaps n=48, scarified gaps n=45. Values with different letters are significantly different at P<0.1 using Tukey's HSD.

<b>Gap-cleaning</b>			
<b>treatment</b>	Species richness	Species evenness	Shannon index
Not cleaned	10.8 (9.6, 11.9) <sup>a</sup>	0.60 (0.55, 0.65) <sup>a</sup>	1.44 (1.28, 1.59) <sup>a</sup>
Cleaned	10.6 (9.5, 11.7) <sup>a</sup>	0.65 (0.60, 0.70) <sup>a</sup>	1.52 (1.36, 1.67) <sup>a</sup>
Scarified	11.7 (10.6, 12.8) <sup>a</sup>	0.64 (0.60, 0.69) <sup>a</sup>	1.56 (1.42, 1.70) <sup>a</sup>

**Table 3.5.** Mean percent cover of ground-layer vegetation in gap-level cleaning treatments by functional groups. Values in parentheses represent 90% confidence intervals; for not cleaned gaps n=44, cleaned gaps n=48, scarified gaps n=45. Values with different letters are significantly different within functional groups at P<0.1 using Tukey’s HSD.

<b>Gap-cleaning treatment</b>	Graminoids	Ferns and fern allies	Exotic spp.	Other forbs	Shrubs	Tree seedlings
Not cleaned	26.8 (21.2, 32.5) <sup>a</sup>	6.6 (4.2, 9.0) <sup>a</sup>	6.7 (3.2, 10.2) <sup>a</sup>	27.3 (21.6, 33.0) <sup>a</sup>	4.1 (2.9, 5.4) <sup>a</sup>	5.7 (4.0, 7.4) <sup>a</sup>
Cleaned	27.4 (21.5, 33.2) <sup>a</sup>	8.3 (5.4, 11.2) <sup>a</sup>	6.6 (3.8, 9.3) <sup>a</sup>	24.3 (18.5, 30.2) <sup>a</sup>	4.8 (3.1, 6.4) <sup>a</sup>	6.1 (3.6, 8.5) <sup>a</sup>
Scarified	32.9 (27.5, 38.2) <sup>a</sup>	8.0 (5.0, 10.9) <sup>a</sup>	9.2 (5.4, 12.9) <sup>a</sup>	26.6 (21.1, 32.1) <sup>a</sup>	4.3 (2.9, 5.6) <sup>a</sup>	5.3 (3.2, 7.5) <sup>a</sup>

## **Chapter 4 : Effects of browsing by white-tailed deer on tree regeneration and ground-layer community composition in treatments designed for structural complexity restoration**

### **Introduction**

White-tailed deer (*Odocoileus virginianus* Zimmerman) have been identified as a keystone herbivore affecting forest ecosystem structure and function across the eastern United States (Rooney and Waller, 2003; Rooney, 2001; Waller and Alverson, 1997). For example, it is estimated that in the hardwood forests of northern Wisconsin, current deer densities are 2-12 times higher than historical pre-settlement numbers (Rooney, 2001). These high deer densities have been associated with reduced regeneration success in several northern hardwood tree species including *Acer saccharum* (sugar maple) (Kain et al., 2011; Matonis et al., 2011; Powers and Nagel, 2009), *Betula alleghaniensis* (yellow birch) (Horsley and Marquis, 1983), *Quercus rubra* (red oak) (Rooney and Waller, 2003), and *Tsuga canadensis* (eastern hemlock) (Frelich and Lorimer, 1985; Rooney and Waller, 2003). Increased browse pressure by deer has also been associated with homogenization of the understory plant layer through decreases in abundance or local extirpation of browse sensitive species (Goetsch et al., 2011; Rooney, 2001) and increased dominance of browse tolerant woody plants and herbs (Horsley et al., 2003; Matonis et al., 2011; Rooney, 2009). These compositional changes have in turn been linked with alterations to ecosystem processes, including patterns of nutrient cycling (Augustine and McNaughton, 1998).

Changes in community composition due to sustained browsing by high populations of white-tailed deer can have compounding effects on the structure and function of the understory layer in instances when less preferred species directly impact already-reduced populations of preferred browse species (Rooney and Waller, 2003). For example, *Carex pensylvanica* (Pennsylvania sedge) is native to much of the eastern United States (USDA-NRCS, 2013), but under certain conditions including high deer browse, this sedge can form dense mats that decrease density and diversity of tree regeneration and herbaceous plants (Johnson, 1992; Powers and Nagel, 2009, 2008; Randall and Walters, 2005). Non-native plant species, many of which are not preferred by deer, can also outcompete native species and reduce understory diversity (Vavra et al., 2007).

While pressure due to deer browse itself can be considered a low level disturbance, the interaction between browsing and other disturbance events can be complex (Nuttle et al., 2013; Royo and Carson, 2006). Herbivory can increase in harvested areas due to increased biomass near the forest floor (Naaf and Wulf, 2007) and increases in the amount of edge habitat (Alverson et al., 1988). It has been suggested that in some cases, harvest impacts on community composition are strong enough to overshadow herbivore effects (Kraft et al., 2004), while other studies have proposed that effects of browsing can outweigh canopy gap size effects on seedlings (Kern et al., 2012). Density of seedlings and saplings prior to harvest may also play a role in whether or not browsing has a significant effect on regeneration success following harvesting (Jordan, 1967; Marquis, 1974; Miller et al., 2009).

Concerns over loss of diversity and homogenization of forests due to management have led to an increased demand for management strategies that contribute to structural and compositional diversity while still allowing for the extraction of wood products (Franklin et al., 2007; Seymour and Hunter, 1999). Natural disturbance-based silviculture is one potential approach for meeting this objective. With this approach, harvests are designed to emulate the frequency and intensity of natural disturbances (such as insect outbreaks, wind, and fire) to promote stand structures and species compositions that are characteristic of unmanaged ecosystems, thereby promoting native diversity and tree regeneration (Bauhus et al., 2009; Franklin et al., 2007). For northern hardwood ecosystems of the upper Great Lakes region of North America, disturbance regimes are predominantly characterized by small-scale gap disturbances. Mesoscale disturbances, primarily caused by wind events, are also important in determining stand structure and composition, and in upper Michigan were found to have a return interval similar to the lifespan of a single cohort (Frelich and Lorimer, 1991a, 1991b; Hanson and Lorimer, 2007). The effects of these natural disturbances on stand structure and composition may be emulated by using combinations of single tree selection, group selection, and modified shelterwood harvests on stands, as well as through the deliberate creation of standing and downed dead wood during harvest (Keeton, 2006). However, high populations of white tailed deer as well as other factors including exotic earthworms and invasive plant species have created systems without an historical analogue and interactions between these factors and harvests must be better understood in order to make informed management decisions designed to sustain native biodiversity and ecosystem function.

This study examines the effects of white-tailed deer on tree regeneration and ground-layer plant community composition within silvicultural treatments designed to increase structural complexity and compositional diversity in managed northern hardwood stands. Experimental treatments created a range of canopy gap sizes, increased coarse woody debris, and altered microsites for regeneration. We examined composition of the ground layer and regeneration of tree species inside and outside of deer exclosures in order to address the following questions: within harvest treatments, what effect does herbivory by deer have on (i) herbaceous layer composition and diversity and (ii) density and diversity of tree and shrub regeneration, and (iii) do these effects vary across different harvest intensities and regeneration treatments?

## **Methods**

### *Study sites*

This operational-scale study took place at three northern hardwood forest sites in northern Wisconsin, USA. Sites were located at the Flambeau River State Forest (Flambeau), Northern Highland-American Legion State Forest (Northern Highland), and Argonne Experimental Forest within the Chequamegon-Nicolet National Forest (Argonne). Stands at each site were approximately 50 hectares in size, 70-90 years old, and had no management activity in the previous 10 years. Fall deer population densities in this area ranged from 5 to 13 deer/km<sup>2</sup>, with slightly higher densities at the Flambeau and Northern Highland sites than at the Argonne site (Wisconsin Department of Natural Resources, 2012). See Chapter 2 for site details.

### *Silvicultural treatments*

Three overstory treatments and two coarse woody debris treatments were implemented at each site in the winter of 2007-2008 (with the exception of the large gaps/ambient coarse woody debris [CWD] treatment [see description below] at ARGN, which was implemented one year later in winter 2008-2009) in a split plot design. Each stand (whole plot) was divided into two approximately 25 hectare half-stands (split plot), with the entire stand receiving one overstory treatment and each half-stand receiving a different CWD treatment. Each site also had an approximately 50 hectare uncut control stand, which did not receive any harvest treatment.

The overstory treatments were as follows: (i) small gaps (10.7 m diameter), (ii) large gaps (18.3 m and 24.4 m diameter); and (iii) a treatment designed to emulate a mesoscale wind disturbance based on the patterns of disturbance documented by Hanson and Lorimer (2007). The three overstory treatments were defined by the size of canopy gaps, number of gaps created per hectare, and additional thinning done to the matrix surrounding gap treatment areas. For the small gap treatment, approximately ten gaps with a 10.7 m diameter were created per hectare and the rest of the stand was thinned to a residual basal area of 18.3-20.7 m<sup>2</sup>/ha. Additionally, these gaps were cleaned of all saplings greater than 2.54 cm diameter at breast height (dbh), a practice that is widely implemented in the region to encourage the development of quality hardwood regeneration.

The large gap treatment involved creating one 18.3 m or one 24.4 m diameter gap per 0.4 ha. Areas between large gaps were thinned to achieve a residual basal area of

18.3-20.7 m<sup>2</sup>/ha. Within the large gap treatment, a nested gap-level site preparation treatment was implemented with one of three treatments randomly assigned to each gap: (i) no cleaning (hereafter referred to as “not cleaned”) in which only poorly formed saplings were removed, (ii) cleaning (hereafter referred to as “cleaned”) in which all saplings greater than 2.54 cm dbh were removed, and (iii) cleaned and scarified gaps (hereafter referred to as “scarified”) in which gaps were cleaned of all saplings greater than 2.54 cm dbh and then scarified with a Salmon blade to expose 70-90% mineral soil. Scarification was performed in September following harvest using a Salmon blade on a crawler bulldozer.

The mesoscale wind treatment included four patches cut as shelterwoods, a heavily thinned matrix area, and a lightly thinned matrix area in each split plot (half stand). Of the four shelterwoods, two were 0.4 ha and two were 1.2 ha in size. Each shelterwood was cut to leave 60-65% residual basal area. The lightly thinned area covered approximately 25% of the stand and remaining portion of the stand was heavily thinned (approximately 65% of the stand). The lightly- and heavily thinned areas were reduced to 20.7-23.0 m<sup>2</sup>/ha and 18.3-20.7 m<sup>2</sup>/ha residual basal area, respectively. A second harvest entry is planned for this treatment six to ten years after initial harvest which will include a shelterwood removal cut and additional thinning in the heavily thinned portions of the stand.

Coarse woody debris (CWD) treatments were identified as ambient and high. In stands receiving the ambient CWD treatment, no additional CWD was deliberately created. In the stands receiving the high CWD treatment, the number of snags and



amount of downed wood were deliberately increased during harvest to approximately 65% of the density and volume found in old-growth northern hardwood stands in the Sylvania Wilderness in Upper Michigan (Goodburn and Lorimer, 1998), the nearest similar old-growth forests in the region. Snags were created by double-girdling live trees and downed logs were created via felling poorer formed canopy trees.

### *Field methods*

#### *Plot selection*

A series of 25 m<sup>2</sup> plots were established in each stand one year prior to treatment implementation for measuring tree regeneration (Fig. 2.2). All regeneration plots were 5 m by 5 m except mid-distance plots in 24.4 m diameter gaps, which were 7.19 m by 3.48 m in order to sample a larger portion of the variation from gap edge to gap center (Fig. 2.2). In treatment stands, regeneration plots were located within harvest gaps and shelterwoods, as described below. Sampling was also done in the thinned matrix of all harvest stands, but this study focuses only on plots from the gaps and shelterwoods.

Small gaps (10.7 m diameter) each contained one sampled regeneration plot in one of five possible locations (Fig. 2.2a). Each gap was treated as a separate unit of analysis. Thirty-six small gaps were sampled in each stand for a total of 108 small gaps sampled across the study. Large gaps (18.3 m and 24.4 m diameter) contained three or four sampled regeneration plots in nine possible locations in order to sample areas with different light levels within each gap (Fig. 2.2b and c). Measurements from the 25 m<sup>2</sup> regeneration plots were averaged within each gap and each gap was treated as an

individual unit of analysis. In each stand, 24 gaps were sampled for each gap-level cleaning treatment (twelve 18.3 m diameter gaps and twelve 24.4 m diameter gaps) for a total of 72 large gaps sampled in each stand and 216 large gaps sampled across the study, divided equally across each gap-level cleaning treatment (not cleaned, cleaned, scarified). Shelterwoods in the mesoscale wind treatment contained one (0.4 ha shelterwoods) or two (1.2 ha shelterwoods) square 32 m by 32 m macro-plots with a sampled 5 m by 5 m regeneration plot located at three or four corners of the larger macro-plot (Fig. 2.2d). Measurements were averaged to the shelterwood level and shelterwoods were treated as individual units of analysis. Twenty-four total shelterwoods were sampled in this study, eight shelterwoods in each stand. The control stands contained 27 (Flambeau), 29 (Northern Highland), or 33 (Argonne) macro-plots arranged in a grid pattern across the stand. Exact number of macro-plots depended on the shape of the stand as well as presence of wet areas and vernal ponds, which were not sampled. Similar to the sampling scheme for the mesoscale wind treatment, sampled 5 m by 5 m regeneration plots were located randomly at one or two corners of each larger macro-plot in the control stands (Fig. 2.2d). Measurements from regeneration plots were averaged for each macro-plot and macro-plots were treated as individual units of analysis. A total of 89 control stand macro-plots were sampled across the study.

### *Deer exclosures*

In order to study the effects of herbivory by white-tailed deer, exclosures were erected around a subset (approximately 18%) of the regeneration plots using T-posts and

hog wire. These exclosures were designed to exclude deer, but not rabbits or rodents. Fences were approximately 1.5 m tall and located 0.25 m outside of regeneration plot boundaries. Exclosures of this height were found to be effective in keeping deer out of a small enclosed area (Martin, 2006). In each treatment stand, the exclosure treatment was replicated four times for each treatment combination. Treatment combination included overstory treatment, CWD treatment, and, in the large gaps, gap-cleaning treatment. For example, within the small gap treatment, deer exclosure fences were erected around a total of eight regeneration plots at each site, four in small gaps that had received high CWD treatment and four small in gaps that had received ambient CWD treatment, for a total of 24 exclosures across the study. At each site in stands receiving the large gap treatment, 48 regeneration plots were protected from browsing: four plots at each gap size (18.3 or 24.4 m diameter) factored by gap-cleaning treatment (not cleaned, cleaned, scarified) and by CWD treatment (low or high) (4 gaps x 2 sizes x 3 cleaning treatments x 2 CWD treatments = 48 protected regeneration plots at each site), totaling 144 exclosures in large gaps across the study. In each mesoscale wind treatment stand, four plots in shelterwoods receiving the high CWD treatment and four plots in shelterwoods receiving the low CWD treatment were protected from browsing at each site, for a total of eight exclosures at each site. In some stands, two of the exclosures were located within the same shelterwood. Data were averaged to the shelterwood level and shelterwoods were treated as individual units of analysis in order to maintain consistency with the small and large gap treatments, in which gaps were treated as individual units of analysis. This resulted in seven shelterwoods with exclosures at each site and 21 total shelterwoods

with exclosures across the study. Eleven exclosures were established around regeneration plots in each control stand resulting in 33 total control stand exclosures.

Fences were checked periodically for damage from animals or fallen trees and branches and repaired. Evidence that deer had accessed exclosure areas when the fence was damaged was found for one plot in the mesoscale wind treatment at the Flambeau site in spring 2011 and one control plot at the Argonne site in spring 2012.

#### *Sampling of woody regeneration*

Regeneration of woody species was measured in fenced and unfenced regeneration plots in June-August prior to harvest (2007), as well as June-August three years after treatments had been implemented (2011 for all stands except large gaps/ambient CWD at the Argonne site, which had been harvested one year later and thus was measured in 2012). Stem counts of seedlings and saplings in three size classes: small seedlings (0.1 m to <0.5 m tall), large seedlings (0.5 m tall to <2 cm dbh), and saplings (2cm dbh to <10 cm dbh) were tallied by species. See Chapter 2 for sampling details.

#### *Ground-layer community sampling*

Ground-layer community composition was evaluated at paired subplots inside and outside of deer exclosures. These data were collected in June-August 2012, three (Argonne, large gaps/low CWD) or four (all other stands) years after harvest. At each fenced regeneration plot, eight 0.5 m<sup>2</sup> subplots were sampled, four inside of the exclosure and four outside. Subplots inside exclosures were placed 0.5 m from plot center in each

cardinal direction. Outside subplots were placed 5 m from plot center in each cardinal direction, except in rectangular exclosures in 24.4 m diameter gaps where outside subplots were placed 4.24 m from plot center along long sides (7.19 m) of regeneration plots and 6.1 m from center along short sides (3.48 m) of regeneration plots. These distances resulted in outside subplots that were all approximately 1.5 m outside of the exclosure fences. In cases where at least 15% of growing space in the subplot was obstructed by rocks or a mature tree, the plot was moved in the direction that eliminated the obstruction while requiring the least deviation from its original placement. Percent cover of all herbaceous and woody species less than 0.5 m tall was estimated for each subplot using the Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1932). Most plants were identified to species when possible or genus when species could not be determined. Grasses were only identified to family (Poaceae) and *Carex* spp. were only identified to genus except *C. pensylvanica*. Midpoints of cover classes were used in all calculations.

Between the tree regeneration sampling in summer 2011 and ground-layer community sampling in summer 2012, some exclosures were moved from their original locations to new plots within the same site, due to initially being installed in incorrect locations. Since browsers were not excluded from these plots for the entire ground-layer community study period, they were not used in these analyses. This meant that seven plots in large gaps (three at the Flambeau site, three at the Argonne site, and one at the Northern Highland site) and one plot in the control stand at the Flambeau site were not used in analysis of ground-layer community composition.

### *Statistical analyses*

In addition to the plots above that were dropped from ground-layer community composition analysis because of exclosures being moved, the two plots that had evidence of deer access were also dropped from analysis. The Flambeau mesoscale wind treatment exclosure, which was accessed by a deer in spring 2011, was not used in any analyses. The Argonne control exclosure, which was accessed by a deer in spring 2012, was dropped from analysis of ground-layer community composition. See Table 4.1 for sample sizes for analysis.

Gaps (small and large gaps treatments), shelterwoods (mesoscale wind treatment), and macro-plots (control stands) were treated as individual units of analysis, despite the fact that overstory treatments were applied at the stand level. The significant distance between these units (>15 m in small and large gaps treatments and >50 m in mesoscale wind treatment and controls) and the large scale of the treatment stands (~50 ha) allowed us to consider each gap, shelterwood, and control stand macro-plot as an independent observation. When comparing effects of overstory treatment, only the “cleaned” gaps were used for the large gap treatment, since the other within-gap treatments were not applied to the smaller gaps or shelterwoods. Effects of gap-cleaning treatments were analyzed only within the large gap treatment. See Table 4.1 for sample sizes.

Compositional differences between browse-protected and unprotected plots were evaluated using permutation-based MANOVA (PerMANOVA) with Sorenson distance measures (Anderson, 2001) in PC-ORD version 6.0 (McCune and Mefford, 2011).

Exclosure treatment was used as the grouping variable and macro-plot, shelterwood, or gap number was used as the blocking variable so that each block contained paired plots inside and outside of exclosures. Blocked indicator species analysis (Dufrene and Legendre, 1997) was also performed using PC-ORD to identify species associated with protected and unprotected plots. The factor level combination of site and overstory treatment was used as the blocking variable because using macro-plot, shelterwood, or gap number as the blocking variable created too many blocks for analysis. Exclosure treatment was used as the grouping variable. Species present in less than 10% of plots were dropped for each analysis; data for percent cover was relativized by species.

We were particularly interested in differences in cover of *C. pensylvanica* and exotic species as a group because of their potential to have a strong influence on understory composition and structure. Effects of deer herbivory within overstory and gap-level treatments on cover of *C. pensylvanica* and the sum of percent cover of all exotic species were analyzed using mixed-model analysis of variance (ANOVA). Exclosure treatment, overstory treatment or gap-cleaning treatment, and their interaction were treated as fixed variables, while site and gap (small and large gap treatments), shelterwood (mesoscale wind treatment), or macro-plot (controls) nested within sites were treated as random variables. When assumptions of normality and constant variance were not met, data were transformed using a square root transformation. When a significant main effect was found, Tukey's HSD was used to determine pairwise differences between exclosure treatments within each overstory or gap-cleaning treatment. Differences with  $p < 0.1$  were considered significant.

Differences in species richness (number of species per plot), Shannon-Wiener index of diversity (Shannon and Weaver, 1949), and evenness (Pielou, 1969) were also evaluated using mixed-model analysis of variance (ANOVA). The same parameters were used as described above for *C. pensylvanica* and exotic species.

Mixed model analysis of covariance (ANCOVA) was used to determine effects of deer exclosures on post-treatment densities of tree seedlings and saplings. In these analyses, stem densities inside and outside of exclosures were averaged to the gap, shelterwood, or macro-plot level; exclosure treatment (protected or not protected), overstory treatment or gap-cleaning treatment, and the interaction between the two variables were treated as fixed variables, site was treated as a random variable, and pretreatment stem densities for the same size class were used as the covariate. When assumptions of normality and constant variance were not met, data were transformed using a square root transformation or aligned rank transformation (Mansouri, 1999). When a significant main effect was found, Tukey's HSD was used to determine pairwise differences inside and outside of exclosures within each overstory treatment or gap-cleaning treatment. Any difference with  $P < 0.1$  was considered significant. Coarse woody debris treatment was not a significant factor in any of our analyses, thus these results are not presented.



## Results

### *Ground-layer plant communities*

PerMANOVA indicated significant compositional differences between plots protected from deer browse and unprotected plots ( $F_{1, 118}=3.1741$ ,  $p=0.0002$ ). Indicator species analysis found *Trillium* spp. to be indicative of protected plots and *C. pennsylvanica* to be associated with unprotected plots (Table 4.2). Percent cover of *C. pennsylvanica* was also higher in unprotected plots, but this difference was only significant in the large gaps that had been cleaned (Table 4.3). Percent cover of exotic species was not affected by browse protection in any overstory or gap-cleaning treatment (Table 4.3).

### *Diversity measures*

Despite compositional differences between browse protected and unprotected plots suggested by the significant PerMANOVA analysis, there was little difference between these conditions in terms of plot-level diversity measures (Table 4.4-4.6). Species richness was significantly higher in unprotected plots than protected plots in small gaps as well as in all large gap cleaning treatments (Table 4.4). Species diversity was also slightly higher in unprotected plots in large gaps that were scarified (Table 4.5). Species evenness was not significantly affected by browsing within any overstory or gap-cleaning treatments (Table 4.6).

## *Woody vegetation*

### *Overstory treatments*

Exclosures did not have a strong effect on overall regeneration densities of tree species within the different overstory treatments. In the mesoscale wind treatment, there were significantly higher densities of large seedlings outside of exclosures than inside. No other significant differences in browse-protected and unprotected plots were found (Fig. 4.1).

Browse protection did not have a uniform effect across species. *A. saccharum* seedlings and saplings, found at high densities in all stands, were not negatively impacted by deer browse (Fig. 4.2a-c). In the mesoscale wind treatment, small and large *A. saccharum* seedlings were present at higher densities in unprotected plots than protected plots; the difference in *A. saccharum* density between protected and unprotected plots was also significant for small seedlings in large gaps (Fig. 4.2a and b). Effects of browse protection on *Fraxinus* spp. varied with overstory treatment and regeneration size class. Large *Fraxinus* spp. seedlings were at lower densities in protected plots in the controls and higher densities in protected plots in the large gaps (Fig. 4.2e). *Fraxinus* spp. saplings benefitted from browse protection in the controls and small gaps, but were at higher densities in unprotected plots in the mesoscale wind treatment (Fig. 4.2f). *O. virginiana*, a species of low browse preference, was generally found at higher densities in unprotected plots. This difference was significant for small seedlings in the large gaps and mesoscale wind treatment, large seedlings in the mesoscale wind treatment, and saplings in small gaps (Fig. 4.2g-i). However, large *O. virginiana* seedlings in small gaps were at higher

densities in browse-protected plots (Fig. 4.2h). Effects of browse protection on *A. rubrum* were also variable; small seedlings in the controls and large seedlings in the small gaps were at higher densities in protected plots, while large *A. rubrum* seedlings in the large gaps were at higher densities in unprotected plots (Fig. 4.2j-l). Density of *B. alleghaniensis* regeneration was very low in all treatments, but browse protection slightly increased densities of both small and large *B. alleghaniensis* seedlings in the large canopy gap treatment (Fig. 4.2m and n).

In the higher overstory disturbance treatments, where densities of *Rubus* spp. were much greater than the other stands, *Rubus* spp. densities were higher in plots not protected from browse (Fig. 4.3). Small seedling-sized *Rubus* spp. attained higher densities outside exclosures in both the large canopy gaps and mesoscale wind treatment, while large seedling-sized *Rubus* spp. were only significantly denser outside exclosures in the large canopy gaps (Fig. 4.3). At low densities in the small gaps and controls, *Rubus* spp. seemed to benefit from browse protection. Small seedling-sized *Rubus* spp. were at higher densities in browse-protected plots in the controls and large seedlings-sized *Rubus* spp. were at higher densities in browse-protected plots in the small gaps (Fig. 4.3).

#### *Gap-cleaning treatments*

In large gaps, overall density of small and large seedlings was not affected by browsing by white-tailed deer (Fig. 4.4). Saplings were found at higher densities in protected plots in gaps that had not been cleaned, but no other differences were significant (Fig. 4.4).

Within the large gaps, *A. saccharum* was the most abundant regenerating tree species and was affected very little by deer browsing (Fig. 4.5a-c). In cleaned gaps, small *A. saccharum* seedlings were found at significantly higher densities in unprotected plots than browse-protected plots (Fig. 4.5a and b). *Fraxinus* spp. had mixed responses to browsing. Small *Fraxinus* seedlings and saplings in gaps that had not been cleaned, as well as large seedlings in cleaned gaps, were at higher densities in browse-protected plots (Fig. 4.5d-f). Small and large *Fraxinus* seedlings in scarified gaps, as well as large seedlings in gaps that had not been cleaned, were at higher densities in unprotected plots (Fig. 4.5d and e). *O. virginiana* regeneration was generally negatively affected by browse protection. Differences in *O. virginiana* regeneration density between browse-protected and unprotected plots were significant for small seedlings in cleaned gaps, large seedlings in gaps that were not cleaned, and small seedlings and saplings in scarified gaps (Fig. 4.5g-i). Large *A. rubrum* seedlings were negatively affected by browse protection, while *A. rubrum* saplings increased in browse-protected plots (Fig. 4.5k and l). These differences were significant for large seedlings in cleaned and not cleaned gaps, and for saplings in gaps that had not been cleaned and scarified gaps (Fig. 4.5k and l). Finally, *B. alleghaniensis* regeneration benefitted from browse protection in all size classes (Fig. 4.5m-o). Small and large *B. alleghaniensis* seedlings had increased densities with browse protection in cleaned gaps and *B. alleghaniensis* saplings benefitted from browse protection in gaps that had not been cleaned (Fig. 4.5m-o).

Within large gaps, densities of *Rubus* spp. were generally lower in browse protected plots than unprotected plots. This difference was significant for both size

classes of *Rubus* spp. in cleaned gaps and for large seedling-sized *Rubus* spp. in gaps that had not been cleaned (Fig. 4.6). Differences in *Rubus* spp. density inside and outside of exclosures were not significant in scarified gaps for any size class (Fig. 4.6).

## **Discussion**

In addition to the effects of harvesting treatments designed to increase structural and compositional heterogeneity on ground-layer composition and tree regeneration that were discussed in Chapters 2 and 3, we found additional effects of herbivory by white-tailed deer within these treatments. Herbivory had a significant effect on ground-layer composition, namely *C. pensylvanica* was more abundant and *Trillium* spp. less abundant in plots that had been browsed. We did not see an increase in ground-layer richness or diversity with browse protection and in some cases richness and/or diversity were lower in browse-protected plots. Deer browsing had very little effect on overall density of tree regeneration, but densities of individual species were affected by browsing, both positively and negatively depending on species and overstory or gap-cleaning treatment. These findings are consistent with the ever-growing body of literature on the pervasive and often complex impacts of elevated levels of deer herbivory on regeneration dynamics and underscore the importance of accounting for these impacts in the design of forest management approaches aimed at restoring and maintaining native biodiversity (Hidding et al., 2013; Kain et al., 2011; Matonis et al., 2011; Nuttle et al., 2014, 2013; Powers and Nagel, 2009; Royo and Carson, 2006; Tanentzap et al., 2012).

Changes in composition of ground-layer plants with deer herbivory have been observed in many other studies. Specifically, several studies have documented increased cover by *C. pensylvanica* and *Carex* spp. in general in areas with significant deer browsing. Powers and Nagel (2008) found that deer density alone had a significantly positive effect on cover by *C. pensylvanica*, but that the interaction between deer density and stand management was also significant. This is supported by our finding that cover of *C. pensylvanica* was higher in browsed plots than protected plots for all treatments, but this effect was only significant in large gaps that had been cleaned. We also found *Trillium* spp. to be an indicator of browse-protected plots, which is supported by several studies suggesting that leaf area and flowering of *Trillium* spp. are decreased by deer browsing (Anderson, 1994; Augustine and Frelich, 1998; Goetsch et al., 2011; Kraft et al., 2004; Rooney and Waller, 2001; Royo et al., 2010b) and that high deer densities may even cause local extirpation of this herb (Anderson and Katz, 1993; Augustine and Frelich, 1998).

Herbivory by deer did not have a negative effect on ground-layer species richness or diversity; conversely, species richness was significantly higher in browsed plots in both small and large gaps. Species diversity was higher with browsing in scarified large gaps. While many studies cite reduced diversity and some local extirpations of ground-layer plants with deer herbivory (Goetsch et al., 2011; Horsley et al., 2003; Rooney and Waller, 2003; Rooney, 2009; Royo and Carson, 2006), Royo et al. (2010a) found that browsing increased herbaceous diversity under moderate deer densities (4.6-7.7 deer/km<sup>2</sup>), and other studies have suggested that reduction in densities of seedlings and

saplings with browsing allows the herbaceous layer to increase in richness and diversity (Hegland et al., 2013; Naaf and Wulf, 2007).

Although we did find some differences in tree regeneration with deer exclosures, these results were not as consistent or strong as may have been expected based on the findings of other studies. In particular, there is a significant body of research supporting the hypothesis that herbivory by white-tailed deer can decrease overall levels of regeneration or of specific tree species in hardwood or hemlock-hardwood forests (e. g. Anderson and Katz, 1993; Horsley and Marquis, 1983; Horsley et al., 2003; Jordan, 1967; Kain et al., 2011; Marquis, 1981, 1974; Rooney, 2009). The lack of dramatic differences in tree regeneration inside and outside of exclosures with any harvesting treatment in this study may be due to several factors, the first being length of time the exclosures were in place. In our study, tree regeneration inside of exclosures had only been protected from browsing for three years. While Jordan (1967) found significant effects of deer browsing on regeneration after three years of browse protection and Marquis (1974) saw significant differences after four to five years, Horsley and Marquis (1983) and Horsley et al. (2003) found that differences inside and outside of deer exclosures increased with time of protection and that most differences were not significant until at least three years after exclosures were established. Other studies that found significant effects of deer exclosures on regeneration had times of protection ranging from nine years (Marquis, 1981) to sixty years (Kain et al., 2011).

Ambient deer densities in study areas during the time of this research were not excessively high, and ranged from 5-13 deer/km<sup>2</sup> (Wisconsin Department of Natural

Resources, 2012). According to enclosure studies in the Alleghany hardwood region of Pennsylvania, these densities may be near the threshold for deer populations to have significant effects on tree regeneration (Horsley et al., 2003; Tilghman, 1989). Holladay et al. (2006) did not find an effect of deer herbivory on regeneration in a southern bottomland hardwood forest when densities were estimated to be about 7 deer/km<sup>2</sup>, and Hidding, Tremblay, and Côté (2012) saw no significant effect of herbivory on height or survival of balsam fir seedlings and saplings at densities  $\leq 15$  deer/km<sup>2</sup>.

Aside from current deer populations, legacy effects of historically high deer populations may also be as or more important in determining ground-layer community composition and tree regeneration (Balgooyen and Waller, 1995; Nuttle et al., 2014). Although deer populations during the time of our study were not excessively high at 5-13 deer/km<sup>2</sup>, estimates of population densities in the mid to late 1990s, 15-20 years previously, were as high as 14-18 deer/km<sup>2</sup> in this area (Wisconsin Department of Natural Resources, unpublished data). This period of high deer densities may have homogenized pre-exclosure regeneration and understory plant conditions and prevented the detection of a short-term browse effect once exclosures were erected.

Despite the lack of overarching, significantly negative effects of browsing seen in this study, *B. alleghaniensis* was negatively affected by browsing by white-tailed deer. This effect was only significant in large gaps where conditions favored regeneration of this shade midtolerant species. In large gaps that had been cleaned, where there was presumably enough ground-layer light due to canopy openness and reduced competition of advance regeneration, there were significantly more small and large *B. alleghaniensis*



seedlings in protected plots than plots that were not protected from browse. In large gaps that had not been cleaned, and where *B. alleghaniensis* advance regeneration present prior to treatment was not removed, *B. alleghaniensis* saplings also benefitted from browse protection. This species is known to be sensitive to deer browsing (Anderson and Katz, 1993; Balgooyen and Waller, 1995; Horsley and Marquis, 1983; Horsley et al., 2003; Kern et al., 2012), and has very specific seedbed and light requirements for germination and survival (Bolton and D'Amato, 2011; Erdmann, 1990; Shields and Webster, 2007; Webster and Lorimer, 2005). Balgooyen and Waller (1995) found that presence of *B. alleghaniensis* regeneration was better predicted by recent deer density than historic deer density, suggesting that it is less affected by legacies of historically high deer densities. Because it is only midtolerant of shade, *B. alleghaniensis* seedlings do not survive as long as advance regeneration as associated species, such as *A. saccharum* (Bolton and D'Amato, 2011; McClure et al., 2000; Webster and Lorimer, 2002). As a result, efforts to increase the representation of this species on the landscape need to provide adequate browse protection, as well as understory light conditions via canopy opening and removal of understory competition.

*T. canadensis*, a historically important component of forests in this region, does depend on advance regeneration and can survive as seedlings or saplings under a closed canopy for over 50 years and sometimes as long as 200 years (Webster and Lorimer, 2002). This species is likely affected by both past and current deer populations in a given area (Anderson and Katz, 1993; Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Rooney, 2001), and was found very rarely in the understory in our study sites, despite

making up as much as 19% of the overstory by basal area in some stands. In the entire sample area (675 sampled regeneration plots), we found only five *T. canadensis* seedlings and no saplings. While deer are likely a factor affecting *T. canadensis* regeneration in these stands, other factors including availability of well-decomposed coarse woody debris (CWD) seedbeds are also important (Marx and Walters, 2008). As the CWD created during harvest in this study (three years prior to regeneration data collection) reaches higher decay classes, the combination of seedbed and protection from browsing may allow for some regeneration of *T. canadensis*.

Densities of less palatable species, including *O. virginiana* and *Rubus* spp. were often negatively affected by browse protection. This pattern was also true for *A. saccharum*, which was the most common tree species regenerating on these sites. *A. saccharum* is often not browsed when other, more desirable species are available (Anderson and Katz, 1993; Anderson and Loucks, 1979) and when browsed it can resprout multiple times in a growing season (Switzenberg et al., 1955). Since we saw few differences in total stem densities of regeneration with exclosure treatments, it is likely that in plots not protected from browse these less-palatable and browse-tolerant species are taking up growing space that would otherwise be occupied by *B. alleghaniensis* and other species under low browsing regimes. This pattern is particularly evident in the large gap and mesoscale wind treatments, where increased light caused increased overall regeneration and potentially increased competition for space and other resources. Other work has found that woody species not preferred by deer increase with the reduction of browse-sensitive species under high levels of herbivory and can lead to reduced richness

and diversity in tree regeneration (Horsley et al., 2003; Kain et al., 2011; Matonis et al., 2011)

### *Management implications*

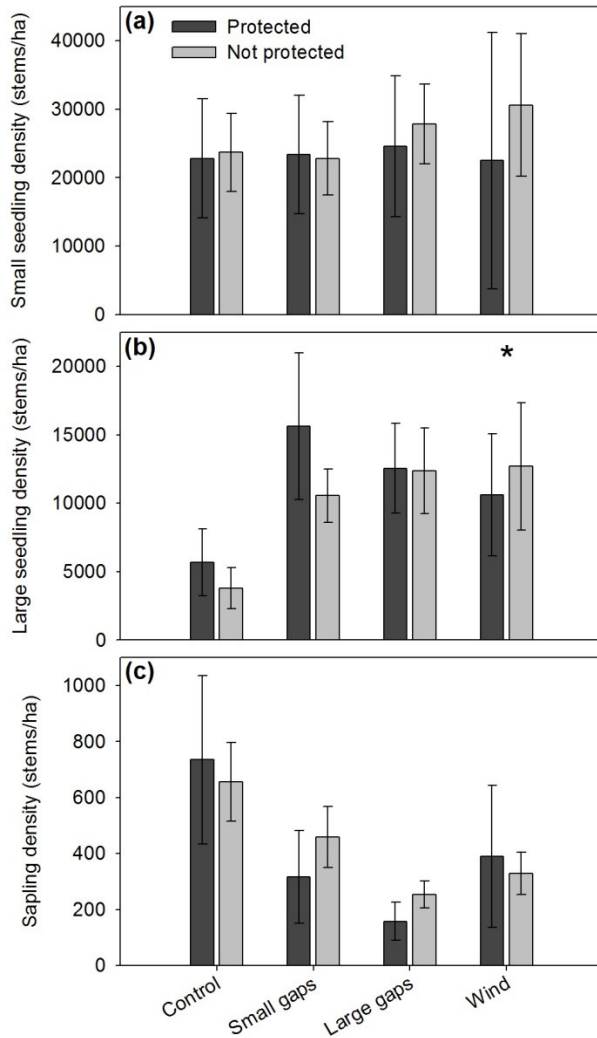
Elevated deer herbivory levels have been well documented as a challenge to maintaining and restoring plant diversity and tree regeneration. By consuming specific species, deer act as a selective filter that affects tree regeneration and ground layer community composition. Legacy effects of high deer populations as well as interactions among deer, harvesting, and exotic or invasive species can cause complex responses that need to be considered when making management decisions. These complex effects are illustrated by the high plot-level variability in the effects of deer exclosures on understory community composition and structure found in this study (Fig. 4.7).

Regeneration of *B. alleghaniensis* was reduced in plots not protected from deer browsing. Additionally, browse-sensitive *T. canadensis* regeneration was nearly absent from all stands. In addition to being sensitive to deer browsing, both of these species are highly dependent on downed woody debris (DWD) as a regeneration substrate (Bolton and D'Amato, 2011; Shields et al., 2007). Densities of *B. alleghaniensis* and *T. canadensis* could be increased in the understory if DWD in advanced decay classes was increased in addition to protection from high rates of browsing. Such increases in the regeneration of these species may be realized as the DWD created in the high CWD treatments in this study reaches higher decay classes; however, only if appropriate browse protection is provided.

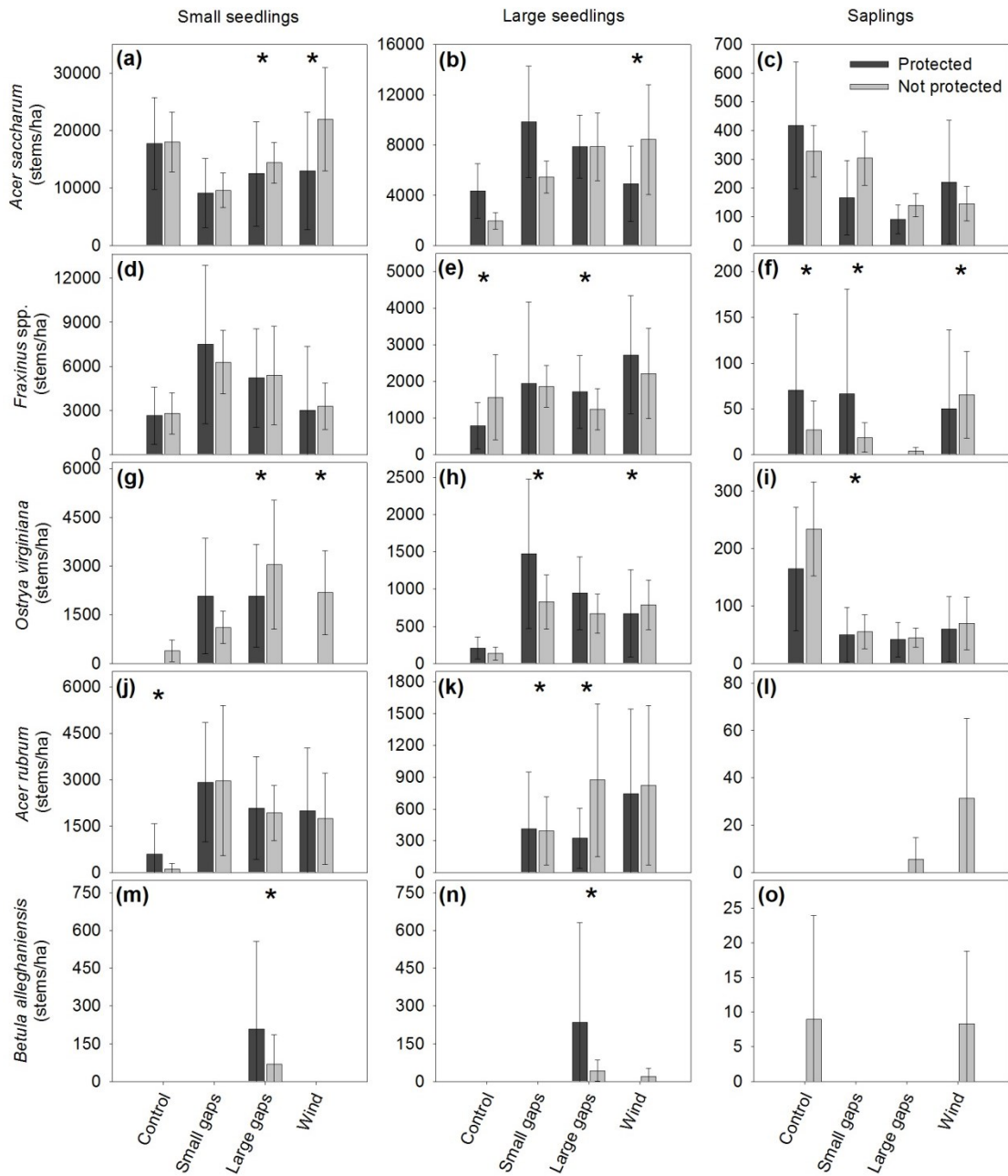
The interaction among *C. pensylvanica*, harvesting, and deer density is important to consider when creating harvest openings in northern hardwood systems. We saw increased cover by *C. pensylvanica* in browsed plots, but the difference was only significant in large, cleaned gaps. If selective browsing by high deer populations and increased canopy openness with harvesting allow thick mats of this species to form, it can reduce tree regeneration as well as richness and diversity of other species (Powers and Nagel, 2009, 2008; Rooney, 2009; Schumann et al., 2003). As such, the use of smaller canopy openings or the application of gap-level site preparation treatments may be necessary to limit the impacts of *C. pensylvanica* on tree regeneration and other understory species.

While many other studies of effects of white-tailed deer on the understory focus on sites with higher deer population densities (e. g. about 20 deer/km<sup>2</sup> or as high as 60-100 deer/km<sup>2</sup>, Anderson and Loucks, 1979; Kain et al., 2011; Matonis et al., 2011; Powers and Nagel, 2009, 2008), we found significant impacts of deer on both ground layer communities and tree regeneration at densities of 5 to 13 deer/km<sup>2</sup>. Managing deer populations by increasing regional deer harvest goals during regular hunting seasons or targeted hunting while stands are regenerating could allow for increased regeneration of underrepresented and browse-sensitive species. Given the logistical and financial constraints related to fencing large areas to protect regeneration and understory plant communities, the coordination of wildlife and forest management in these areas will be critical for ensuring the long-term ecological sustainability of northern hardwood systems.

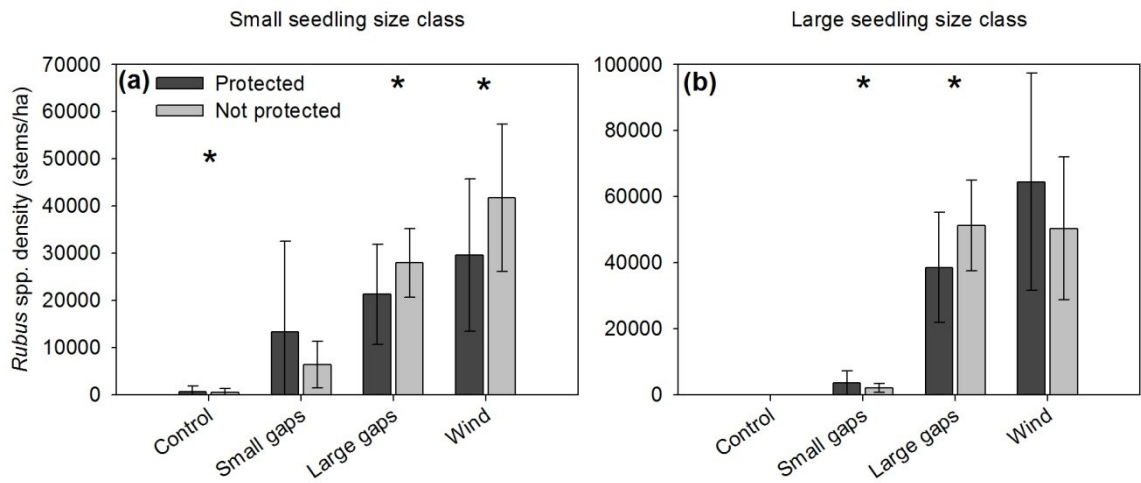
## Figures



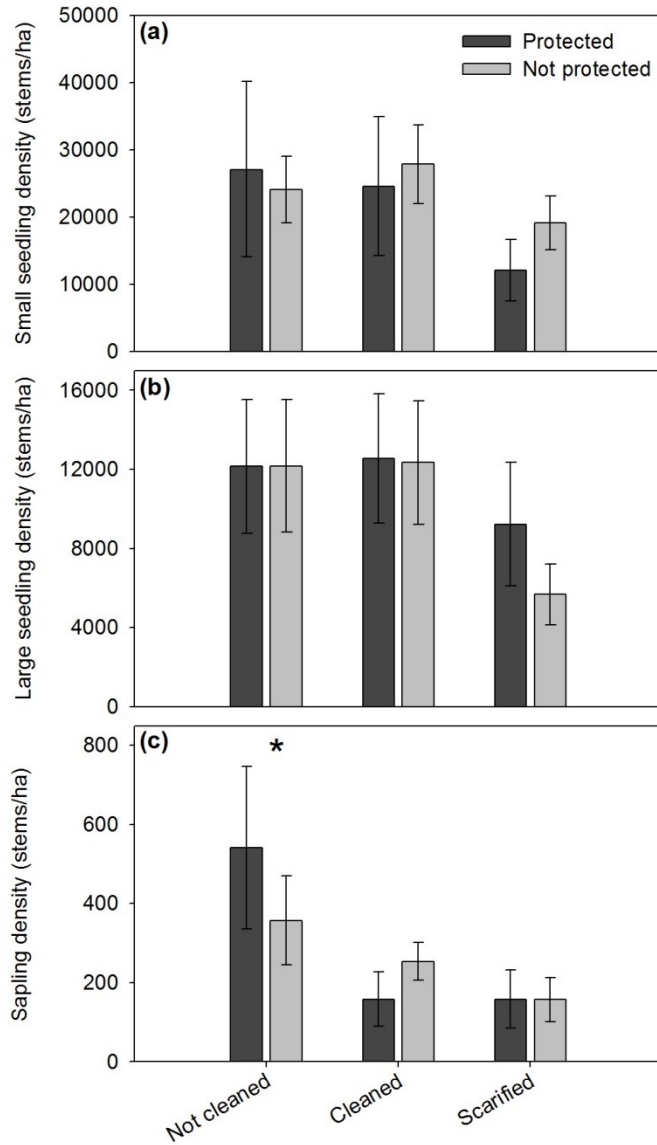
**Fig. 4.1.** Mean densities of (a) small tree seedlings (0.1 m to <0.5 m tall), (b) large tree seedlings (0.5m tall to <2 cm dbh), and (c) saplings (2 cm dbh to <10 cm dbh) within overstory treatments in browse protected (dark bars) and unprotected plots (lighter bars). Error bars represent 90% confidence intervals; asterisks represent significant effects of browse protection within overstory treatments at  $p < 0.1$  using ANCOVA and Tukey's HSD.



**Fig. 4.2.** Mean densities of (a-c) *Acer saccharum*, (d-f) *Fraxinus* spp., (g-i) *Ostrya virginiana*, (j-l) *Acer rubrum*, and (m-o) *Betula alleghaniensis* regeneration by size class and overstory treatment. Error bars represent 90% confidence intervals; asterisks represent significant effects of browse protection within overstory treatments at  $p < 0.1$  using ANCOVA and Tukey's HSD. See Fig. 4.1 for size class definitions.

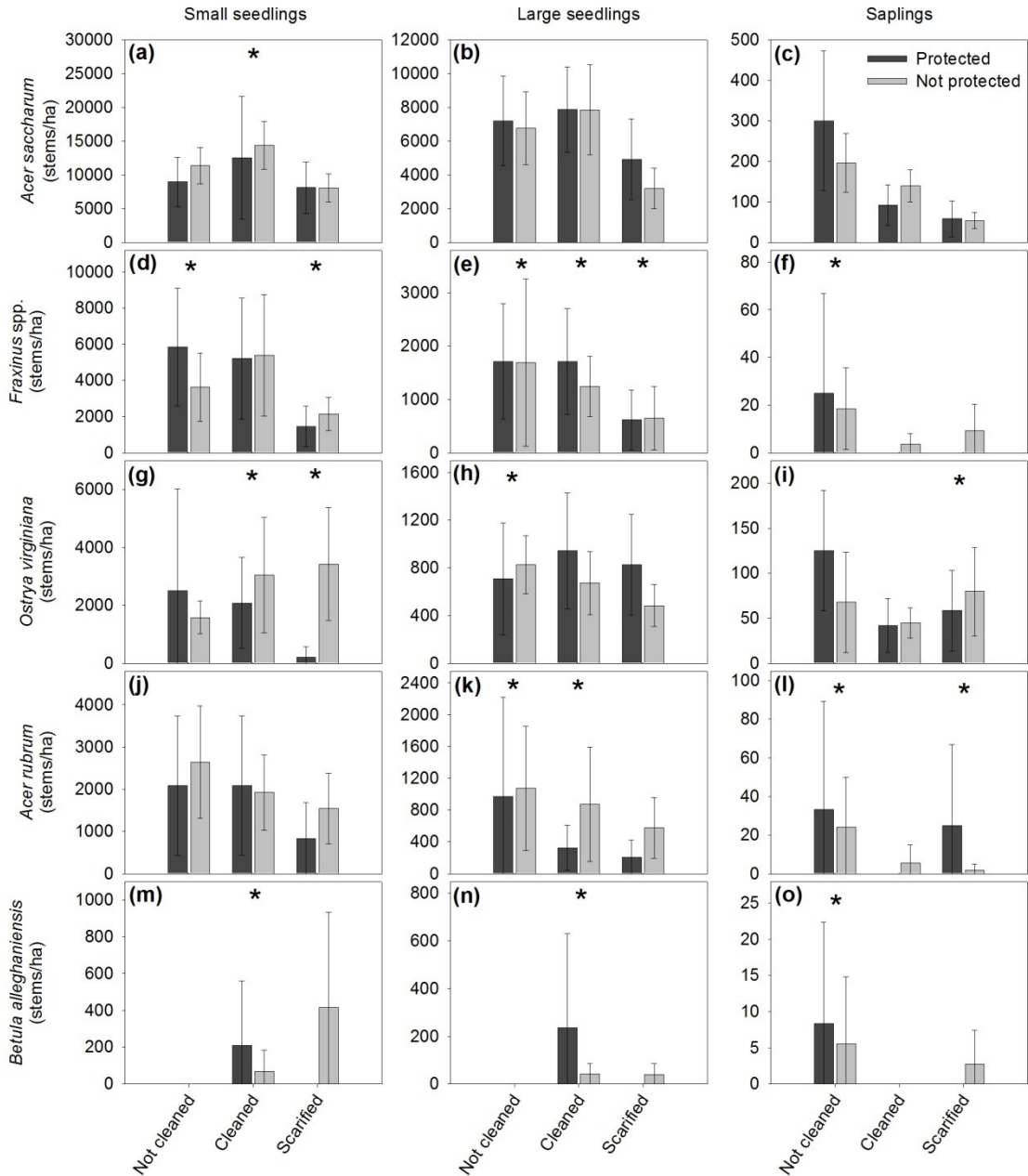


**Fig. 4.3.** Mean densities of *Rubus* spp. (a) 0.1 to <0.5 m tall and (b) >0.5 m tall in overstory treatments with and without protection from deer browsing. Error bars represent 90% confidence intervals; asterisks represent significant effects of browse protection within overstory treatments at  $P < 0.1$  using ANCOVA and Tukey's HSD.

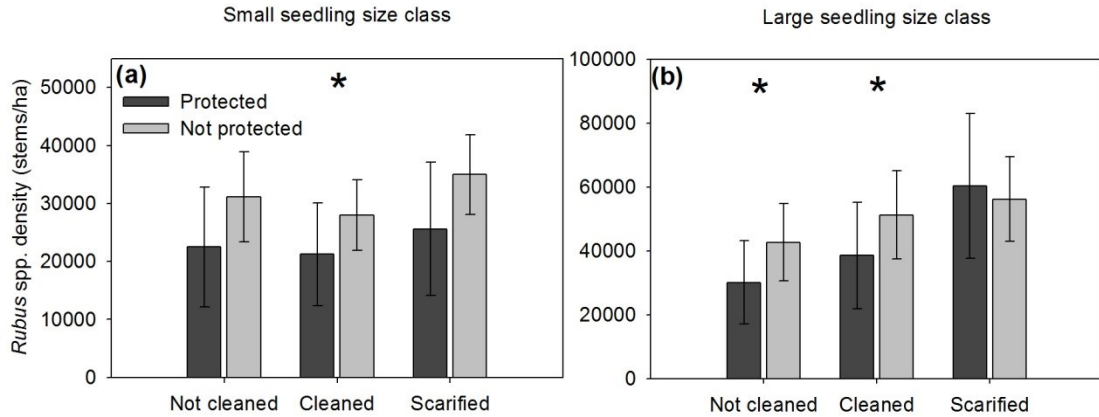


**Fig. 4.4.** Mean densities of (a) small tree seedlings, (b) large tree seedlings, and (c) saplings by gap-cleaning treatments in browse protected (dark bars) and unprotected plots (lighter bars). Error bars represent 90% confidence intervals; asterisks represent significant effects of browse protection within gap-cleaning treatments at  $P < 0.1$  using ANCOVA and Tukey's HSD. See Fig. 4.1 for size class definitions.

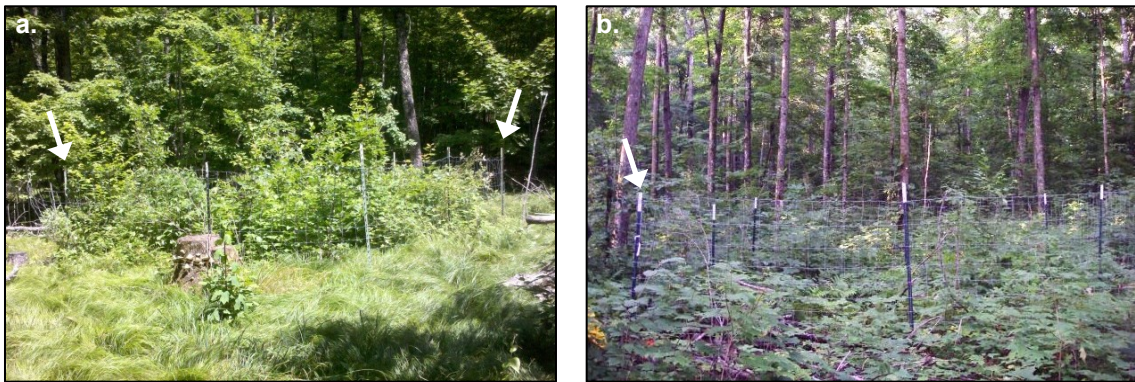




**Fig. 4.5.** Mean densities of (a-c) *Acer saccharum*, (d-f) *Fraxinus* spp., (g-i) *Ostrya virginiana*, (j-l) *Acer rubrum*, and (m-o) *Betula alleghaniensis* regeneration by size class and gap-cleaning treatment. Error bars represent 90% confidence intervals; asterisks represent significant effects of browse protection within gap-cleaning treatments at  $P < 0.1$  using ANCOVA and Tukey's HSD. See Fig. 4.1 for size class definitions.



**Fig. 4.6.** Mean densities of *Rubus* spp. (a) 0.1 to <0.5m tall and (b) >0.5m tall in by gap-cleaning and browse protection treatments. Error bars represent 90% confidence intervals; asterisks represent significant effects of browse protection within gap-cleaning treatments at P<0.1 using ANCOVA and Tukey's HSD.



**Fig. 4.7.** Differences in regeneration densities and understory plant community composition inside and outside of exclosures were quite variable with stark differences at some plots (a), but not at others (b). White arrows show edges of deer exclosures.

## Tables

**Table 4.1.** Sample size (n) for analysis of woody regeneration and ground-layer community composition for browse-protected and unprotected plots.

	Woody regeneration data		Ground-layer community data	
	Protected	Not protected	Protected	Not protected
<b>Overstory treatment</b>				
Control	34	89	31	31
Small gaps	24	108	24	24
Large gaps	48	72	44	44
Wind	20	24	20	20
<b>Gap-cleaning treatment</b>				
Not cleaned	48	72	48	48
Cleaned	48	72	44	44
Scarified	48	72	45	45

**Table 4.2.** Indicator species analysis (Dufrene and Legendre, 1997) for browse protection treatments. IV=importance value; species with  $P < 0.1$  are reported.

	Species	IV	p-value
Not Protected	<i>Carex pensylvanica</i>	48.1	0.0002
Protected	<i>Trillium</i> spp.	16.6	0.0048

**Table 4.3.** Mean percent cover of *Carex pensylvanica* and mean total percent cover of exotic species in browse protected and unprotected plots by overstory treatment and gap-cleaning treatment. Values in parentheses are 90% confidence intervals; p-values less than 0.1 are written in bold.

	<i>Carex pensylvanica</i>			Exotic species		
	Protected	Not protected	p-value	Protected	Not protected	p-value
<b>Overstory treatment</b>						
Control	9.7 (4.7, 14.6)	13.7 (8.1, 19.2)	0.3872	0.8 (0.0, 2.3)	0.1 (0.0, 0.3)	1.0000
Small gaps	9.5 (3.0, 16.1)	12.1 (5.7, 18.5)	0.9980	4.4 (1.4, 7.4)	2.8 (1.0, 4.6)	0.9584
Large gaps	11.0 (4.8, 17.2)	15.9 (9.9, 21.8)	<b>0.0477</b>	5.9 (3.5, 8.3)	6.6 (3.8, 9.3)	0.9868
Wind	8.7 (3.4, 14.0)	13.8 (6.5, 21.1)	0.7346	8.7 (2.2, 14.1)	9.7 (5.5, 14.0)	0.6599
<b>Gap-cleaning treatment</b>						
Not cleaned	11.1 (6.0, 16.3)	15.4 (9.5, 21.2)	0.5140	7.7 (3.9, 11.5)	6.7 (3.2, 10.2)	0.9906
Cleaned	11.0 (4.8, 17.2)	15.9 (9.9, 21.8)	<b>0.0278</b>	5.9 (3.5, 8.3)	6.6 (3.8, 9.3)	0.9826
Scarified	9.7 (4.7, 14.6)	14.6 (9.5, 19.6)	0.6392	10.6 (5.4, 15.9)	9.2 (5.4, 12.9)	0.8398

**Table 4.4.** Mean plot-level species richness (number of species per 2 m<sup>2</sup>) by browse protection treatment and by overstory and gap-cleaning treatments. Values in parentheses are 90% confidence intervals; p-values less than 0.1 are written in bold.

	Protected	Not protected	p-value
<b>Overstory treatment</b>			
Control	6.7 (5.7, 7.8)	7.3 (5.9, 8.7)	0.9968
Small gaps	11.0 (9.1, 12.8)	13.9 (11.3, 16.5)	<b>0.0664</b>
Large gaps	8.9 (7.8, 10.1)	10.6 (9.5, 11.7)	0.2607
Wind	8.7 (7.4, 10.1)	10.5 (9.3, 11.7)	0.7238
<b>Gap-cleaning treatment</b>			
Not cleaned	8.6 (7.7, 9.5)	10.8 (9.6, 11.9)	<b>0.0063</b>
Cleaned	8.9 (7.8, 10.1)	10.6 (9.5, 11.7)	<b>0.0841</b>
Scarified	9.3 (8.2, 10.6)	11.7 (10.6, 12.8)	<b>0.0037</b>

**Table 4.5.** Mean plot-level species diversity (Shannon and Weaver, 1949) by browse protection treatment and by overstory and gap-cleaning treatments. Values in parentheses are 90% confidence intervals; p-values less than 0.1 are written in bold.

	Protected	Not protected	p-value
<b>Overstory treatment</b>			
Control	1.13 (0.95, 1.32)	1.00 (0.78, 1.22)	0.9114
Small gaps	1.46 (1.21, 0.72)	1.64 (1.33, 1.94)	0.8391
Large gaps	1.35 (1.21, 1.49)	1.52 (1.36, 1.67)	0.5705
Wind	1.42 (1.25, 1.60)	1.60 (1.47, 1.72)	0.8931
<b>Gap cleaning treatment</b>			
Not cleaned	1.33 (1.19, 1.46)	1.44 (1.28, 1.59)	0.7479
Cleaned	1.35 (1.21, 1.49)	1.52 (1.36, 1.67)	0.3262
Scarified	1.28 (1.13, 1.43)	1.56 (1.42, 1.70)	<b>0.0084</b>

**Table 4.6.** Mean plot-level species evenness (Pielou, 1969) by browse protection treatment and by overstory and gap-cleaning treatments. Values in parentheses are 90% confidence intervals; p-values less than 0.1 are written in bold.

	Protected	Not protected	p-value
<b>Overstory treatment</b>			
Control	0.60 (0.53, 0.68)	0.50 (0.41, 0.59)	0.4723
Small gaps	0.60 (0.51, 0.69)	0.61 (0.52, 0.70)	1.0000
Large gaps	0.63 (0.59, 0.67)	0.65 (0.60, 0.70)	0.9950
Wind	0.68 (0.64, 0.73)	0.69 (0.66, 0.72)	1.0000
<b>Gap-cleaning treatment</b>			
Not cleaned	0.62 (0.57, 0.67)	0.60 (0.55, 0.65)	0.9879
Cleaned	0.63 (0.59, 0.67)	0.65 (0.60, 0.70)	0.9676
Scarified	0.57 (0.52, 0.63)	0.64 (0.60, 0.69)	0.3594

## Chapter 5 : Conclusions

Our findings suggest that restoring diversity of tree regeneration and ground-layer community in second-growth northern hardwoods using silvicultural techniques may be challenging. Larger canopy openings increased densities of tree regeneration, but also caused increases in exotic and disturbance-adapted ground-layer species. Midtolerant and shade intolerant tree regeneration was more likely to be present in large gaps and shelterwoods of the mesoscale wind treatment, but all treatments generally served to release advance regeneration of shade-tolerant *Acer saccharum* and there was no difference in diversity of regeneration between the overstory treatments. Cleaning gaps of large advance regeneration and scarifying soil surface slightly increased densities of *Betula alleghaniensis*, while having little effect on composition of the rest of the ground layer. White-tailed deer affected both herbaceous and woody plants in the understory and acted as a selective filter preferentially browsing certain species and eliciting complex interactions with silvicultural treatments.

These results underscore the importance of many factors, including overstory disturbance, microsite availability, exotic or invasive species, and herbivores that affect understory composition and diversity. The following sections provide suggestions for management when goals include increasing structural and compositional heterogeneity as well as limitations of this study and suggestions for future research.

### *Management implications*

Simply creating larger canopy openings that mimic multiple-tree fall gaps and mesoscale wind disturbances may not be enough to increase compositional heterogeneity and occurrence of underrepresented species in second-growth northern hardwood stands in the face of modern issues and stressors affecting these forests. Challenges include recalcitrant understory layers (Royo and Carson, 2006), exotic invasive plants and earthworms, persistently high rates of herbivory by elevated populations of white-tailed deer, and the interactions between these factors, which can generate complex responses in the forest understory. Given this suite of challenges, management objectives associated with increasing the representation of historically important species may require more targeted approaches that minimize the influence of each challenge through competition control, protection measures, and the use of artificial regeneration. Although more costly than historic approaches to managing these species, these approaches may be one of the only ways to ensure adequate representation of species, including *B. alleghaniensis* and *Tsuga canadensis*, in future forests.

We saw some success in increasing regeneration of underrepresented species, especially *B. alleghaniensis*, when larger advance regeneration of competing species was removed or reduced through gap cleaning and mineral soil was exposed through scarification in large gaps. Gap cleaning released small *B. alleghaniensis* advance regeneration, while scarification allowed for the establishment of new seedlings. However, densities of *B. alleghaniensis* were still low in all stands, and it may be necessary to apply these treatments more deliberately in order to have substantial *B.*



*allegghaniensis* regeneration. Scarification near mature seed trees, retention of within-gap seed sources (Poznanovic et al., 2013), and gap-cleaning and release treatments around established seedlings might further benefit this species. Deliberately increasing DWD across managed areas may also benefit this species, as advance regeneration may establish on well-decayed wood seedbeds and ultimately be released by the creation of future gaps. In cases where the goal of increasing diversity of regeneration is complicated by the fact that there is little seed source of desired species in the overstory, planting may be necessary in order to increase the representation of these species.

Protection from deer or a reduction of deer populations, even in areas where current populations around 10 deer/km<sup>2</sup> may be considered only moderately high, is also likely to be necessary to increase presence of underrepresented species. In this study, we saw increased *B. allegghaniensis* with browse protection, but only when overstory and microsites were also altered to benefit this species. Precise goals for a deer population that allows sufficient regeneration would vary locally with habitat quality, browse availability, and other factors.

In the larger canopy openings generally required for the regeneration of midtolerant tree species (Leak, 1999; Nuttle et al., 2013; Shields et al., 2007), invasion by exotic species becomes an increasing threat to understory diversity. When performing harvest and management operations, care should be taken to clean equipment to avoid transport of these species between sites. Additionally, knowing and marking locations of populations of exotic species and avoiding creating canopy openings in these areas could reduce the possibility that they will take over a site. The use of chemical or manual

methods to remove or reduce these populations prior to gap formation may also limit their influence on post-harvest communities.

### *Study limitations and research recommendations*

There were several limitations to this study. The first is the relatively short time period examined (3-4 years after harvest). Initial responses to natural disturbance-based management may be transient and distinctly different from long-term results where multiple harvest entries continue to change conditions (Arseneault et al., 2011; Tilman, 1989). Only a few years after harvesting, deliberately-created CWD had not reached high decay classes and most newly-established regeneration was small. Continued, long-term monitoring of this study will allow researchers to see additional changes with increased CWD in high decay classes, longer-term protection from deer, and effects of additional harvest entries including the shelterwood removal cut in the mesoscale wind treatment.

While potentially the simplest way to study effects of white-tailed deer and other browsers, exclosures that completely eliminate browsers from an area do not create a natural condition. Exclosure studies only allow the comparison of ambient deer populations (which in most cases are high due to human impacts) to an artificial condition without browsers, which is also not representative of the conditions these communities are evolutionarily adapted to. Several studies have examined effects of deer herbivory at varying population densities using population differences on islands (Balgooyen and Waller, 1995; Mudrak et al., 2009), sites with differences in hunting pressure or regulations (Anderson and Katz, 1993; Filazzola et al., 2014; Matonis et al.,

2011; Pedersen and Wallis, 2004; Powers and Nagel, 2009), experimental deer herd reduction within a site (Royo et al., 2010b; Tanentzap et al., 2011), or fenced deer enclosures that keep populations at specific densities (Hidding et al., 2012; Horsley et al., 2003; Nuttle et al., 2014; Tilghman, 1989; Tremblay et al., 2006). However, experiments such as these can be expensive, have limited possibilities for site selection, and/or must be examined over long periods of time. It is important to compare results of enclosure experiments to those of experiments that analyze the impacts of a range of deer densities to identify the degree of departure of these deer-free conditions from communities experiencing various levels of herbivore pressure.

Large-scale and landscape-level experiments such as this allow researchers to assess impacts of treatments across the range of environmental conditions that would be present at an operational scale, but they also present challenges. Significant within-site and site-to-site differences introduce a high level of variability, decreased ability to detect significant differences with experimental treatments, and smaller portions of explained variability by the factors studied. However, since one of the goals of studies such as this is to develop practical recommendations for management, studies done at the same scale as operational harvests are more realistic than smaller scale studies. Moreover, the degree of variation generated across these scales provides a realistic portrayal of the range of conditions that might be expected following large-scale implementation of like treatments.

The impact that invasive earthworms can have on northern hardwood and other forests is a topic that has recently received increased attention (Bohlen et al., 2004;

Holdsworth et al., 2007; Nuzzo et al., 2009; Powers and Nagel, 2008). We briefly discussed possible impacts of earthworms on these sites, but sampling effort for earthworm impacts was very minimal and not included in statistical analysis of data. Sampling of earthworms at the plot level, possibly using an extraction sampling method, could lead to more conclusive evidence about the impacts of earthworms at these sites and better recommendations for management at sites with differing earthworm impacts.

While the sites in this study were selected to represent the range of site quality of northern hardwood forests in this region, all of the sites were relatively nutrient-rich. All three study sites contained some ATD (*Acer-Tsuga/Dryopteris*) habitat type, but the Flambeau and Argonne sites also contained AH (*Acer/Hydrophyllum*) and AOCa (*Acer/Osmorhiza-Caulophyllum*) habitat types, which are more nutrient rich than ATD (Kotar et al., 2002). The ATM (*Acer-Tsuga/Maianthemum*) habitat type is also very common in northern Wisconsin, but was not included in this study. The slightly lower nutrient status of ATM sites does not favor *A. saccharum* as much as the aforementioned habitat types and allows more tree species to be competitive (Kotar et al., 2002). If ATM sites had been included in this study, we might have seen increased diversity of regeneration and increased representation of *B. alleghaniensis* and other tree species in the understory (Matonis et al., 2011; Webster and Lorimer, 2005).

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**Appendix A.** Correlations (Kendall's  $\tau$ ) between percent cover of ground-layer species and NMS axes (Fig. 3.1). Values in bold are significant at  $P < 0.05$ ; values in italics are significant at  $p < 0.1$ .

Species	Symbol	Axis 1	Axis 2	Species	Symbol	Axis 1	Axis 2
<i>Abies balsamea</i>	ABBA	0.24	-0.40	<i>Laportea canadensis</i>	LACA3	0.36	0.09
<i>Acer rubrum</i>	ACRU	<b>0.50</b>	0.05	<i>Lonicera canadensis</i>	LOCA7	<b>0.63</b>	0.22
<i>Acer saccharum</i>	ACSA3	0.24	0.24	<i>Lycopodium annotinum</i>	LYAN2	0.08	<i>0.40</i>
<i>Actaea</i> spp.	ACTAE	0.13	-0.13	<i>Lycopodium dendroideum</i>	LYDE	0.39	0.13
<i>Adiantum pedatum</i>	ADPE	<b>0.63</b>	0.30	<i>Maianthemum canadense</i>	MACA4	<b>0.58</b>	0.15
<i>Allium tricoccum</i>	ALTR3	-0.17	<i>0.44</i>	<i>Maianthemum racemosum</i>	MARA7	0.24	-0.40
<i>Amphicarpae bracteata</i>	AMBR2	<i>0.45</i>	0.09	<i>Matteuccia struthiopteris</i>	MAST	0.22	-0.40
<i>Anemone acutiloba</i>	ANAC10	0.40	0.13	<i>Mitella diphylla</i>	MIDI3	<b>0.52</b>	0.12
<i>Anemone quinquefolia</i>	ANQU	-0.03	-0.33	<i>Osmorhiza claytonii</i>	OSCL	<b>0.63</b>	0.20
<i>Apocynum androsaemifolium</i>	APAN2	0.35	-0.19	<i>Osmunda claytoniana</i>	OSCL2	0.32	0.04
<i>Aralia nudicaulis</i>	ARNU2	<b>0.72</b>	0.20	<i>Ostrya virginiana</i>	OSVI	<i>0.39</i>	-0.08
<i>Aralia racemosa</i>	ARRA	<i>0.46</i>	0.13	<i>Oxalis stricta</i>	OXST	<b>-0.54</b>	0.31
<i>Arisaema triphyllum</i>	ARTR	0.08	<b>-0.56</b>	<i>Parthenocissus quinquefolia</i>	PAQU2	<b>0.51</b>	-0.03
<i>Athyrium filix-femina</i>	ATFI	<b>0.67</b>	0.14	<i>Phegopteris connectilis</i>	PHCO24	<i>0.42</i>	0.20
<i>Betula alleghaniensis</i>	BEAL2	0.08	-0.30	<i>Poaceae</i>	POACEAE	0.33	<b>-0.64</b>
<i>Carex pensylvanica</i>	CAPE6	<i>-0.36</i>	-0.24	<i>Polygonatum biflorum</i>	POBI2	0.12	0.00
<i>Carex</i> spp.	CAREX	<b>0.48</b>	-0.24	<i>Polygonatum pubescens</i>	POPU4	<i>0.41</i>	0.25
<i>Carya cordiformis</i>	CACO26	<b>0.49</b>	0.04	<i>Polygonum</i> spp.	POLYG4	<i>0.41</i>	-0.26
<i>Caulophyllum thalictroides</i>	CATH2	<b>0.64</b>	0.17	<i>Prunus serotina</i>	PRSE2	0.00	-0.22
<i>Circaea alpina</i>	CIAL	0.13	-0.13	<i>Prunus virginiana</i>	PRVI	<b>0.61</b>	0.02
<i>Circaea lutetiana</i>	CILU	0.28	0.08	<i>Quercus rubra</i>	QURU	0.22	-0.29
<i>Cirsium arvense</i>	CIAR4	0.04	<b>-0.49</b>	<i>Ribes cynosbati</i>	RICY	<b>0.56</b>	-0.10
<i>Clintonia borealis</i>	CLBO3	<b>0.51</b>	0.35	<i>Ribes triste</i>	RITR	<i>0.45</i>	0.00
<i>Cornus alternifolia</i>	COAL2	<b>0.51</b>	0.35	<i>Rubus pubescens</i>	RUPU	0.35	-0.28
<i>Diervilla lonicera</i>	DILO	-0.08	-0.03	<i>Rubus</i> spp.	RUBUS	0.22	<b>-0.44</b>
<i>Dirca palustris</i>	DIPA9	0.00	-0.36	<i>Sanguinaria canadensis</i>	SACA13	<b>0.51</b>	-0.03
<i>Dryopteris intermedia</i>	DRIN5	0.24	0.30	<i>Solidago</i> spp.	SOLID	<b>0.72</b>	0.24
<i>Eurybia macrophylla</i>	EUMA27	<i>0.45</i>	-0.09	<i>Streptopus roseus</i>	STRO4	<b>0.60</b>	0.12
<i>Fraxinus nigra</i>	FRNI	<i>0.43</i>	<b>0.47</b>	<i>Taraxacum officinale</i>	TAOF	-0.12	<b>-0.50</b>
<i>Fraxinus</i> spp.	FRAXI	0.29	<b>0.54</b>	<i>Tilia americana</i>	TIAM	0.11	0.14
<i>Galeopsis tetrahit</i>	GATE2	0.17	-0.39	<i>Trientalis borealis</i>	TRBO2	-0.05	-0.11
<i>Galium</i> spp.	GALIU	<i>0.45</i>	0.09	<i>Trillium</i> spp.	TRILL	<b>0.50</b>	0.22
<i>Geum aleppicum</i>	GEAL3	<i>0.46</i>	-0.08	<i>Ulmus</i> spp.	ULMUS	<i>0.45</i>	0.00
<i>Gymnocarpium dryopteris</i>	GYDR	0.06	-0.19	<i>Uvularia grandiflora</i>	UVGR	<b>0.57</b>	0.17
<i>Hieracium</i> spp.	HIERA	0.27	-0.36	<i>Uvularia sessifolia</i>	UVSE	0.28	0.06
<i>Hydrophyllum virginianum</i>	HYVI	<b>0.49</b>	0.04	<i>Veronica officinalis</i>	VEOF2	<i>-0.44</i>	<i>-0.40</i>
<i>Impatiens capensis</i>	IMCA	0.28	-0.12	<i>Viola</i> spp.	VIOLA	<b>0.56</b>	0.33