Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest

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ABSTRACT

Natural regeneration in canopy gaps is a key process affecting long-term dynamics of many forests, including northern hardwood forests. The density and composition of regenerating trees are often highly variable, reflecting sensitivity to a suite of driving factors operating at different scales (e.g., harvest gap to regional landscape), including production of seeds, physical characteristics of gaps and stands, competition with non-tree vegetation, and browsing by animals. Multivariate analyses over broad geographic areas provide insights into the relative effects of these factors and permit exploration of spatial patterns in regeneration. We examined the effects of gap-, stand-, and landscape-scale factors on densities of tree seedlings (<1 m tall) and saplings (1–2 m tall) in 59 selection-harvested northern hardwood stands located across a 4500 km^2 region of Michigan's Upper Peninsula. We used Bayesian multilevel modeling to account for the hierarchical structure of the data and assess uncertainty in parameter estimates. Sugar maple (*Acer saccharum*) saplings were absent from 61% of 154 m^2 plots centered in harvest gaps (n = 347) despite its high shade tolerance and overstory dominance, but densities were high in other gaps. Densities of sugar maple seedlings and/or saplings were negatively associated with a combination of greater stand-scale densities of white-tailed deer (*Odocoileus virginianus*), greater gap-scale cover of non-tree vegetation, and lower gap-scale light availability, with deer density having the greatest effect. Densities of unpalatable and commercially less valuable ironwood (*Ostrya virginiana*), the second most common regeneration species, were positively related to gap-scale seed-production potential but were unrelated to factors affecting sugar maple. Ironwood tended to replace sugar maple saplings in areas with high deer density. At the landscape scale, densities of sugar maple seedlings and saplings decreased with decreasing latitude and snow depth and increasing winter deer densities. These inverse spatial patterns suggest that deer herbivory can lead to landscape-scale variation in regeneration success. However, the spatial distribution of habitat types (a proxy for soil moisture and nutrient conditions) confound this observation, with higher densities of sugar maple generally located on stands with less nutrient-rich habitat types. Results demonstrate that combinations of factors operating at different scales, and with different relative magnitudes of impact, contribute to high variation in regeneration composition and density following timber harvest. Selection silvicultural practices, as currently applied, do not ensure regeneration of desirable species; practices might require modifications in general (e.g., increasing gap size) and to match them to regionally varying factors like deer density.

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1. Introduction

The formation of canopy gaps creates pulses of resources (e.g., light and water) that provide opportunities for tree regeneration. Natural regeneration in gaps is a key feature of the long-term development of forests in areas where larger-scale disturbances are uncommon (Runkle, 1982; Yamamoto, 2000; McCarthy, 2001).

Canopy gaps form naturally due to mature-tree mortality from old age, windfall, lightning, diseases, and insects (McCarthy, 2001), but the primary mode by which these gaps are created in many managed forests is tree removal from selection harvesting. Selection harvesting, often part of uneven-aged silviculture systems characterized by partial overstory removal and explicit provisions for regeneration, has been practiced and studied in many forest types around the world (Nyland, 1998; Fredericksen and Mostacedo, 2000; McCarthy, 2001; Newbery et al., 2007; Yoshida and Noguchi, 2009). In northern hardwood forests of North America, single-tree and group selection harvesting are recommended to create and/or maintain an uneven-aged structure and sustain the production

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of high quality timber (Arbogast, 1957; Nyland, 1998). This recommendation is based on evidence that partial cutting promotes regeneration of economically valuable, shade-tolerant species such as sugar maple (*Acer saccharum* Marsh.) (Tubbs, 1977).

However, northern hardwood stands can have low densities of saplings of desired species following harvesting, even species such as sugar maple that are dominant in the overstory (Stoeckeler et al., 1957; Marquis and Brenneman, 1981; Jenkins, 1997; Miller, 2004; Donovan, 2005). Failure of dominant overstory species to regenerate in gaps should lead to substantial changes in future stand composition and structure (Seagle and Liang, 2001; Pedersen and Wallis, 2004). Regeneration failure alters habitat for non-tree vegetation and wildlife and poses economic concerns for communities that depend on timber industry (Donovan, 2005; Racevskis and Lupi, 2006).

Intense browsing by white-tailed deer (*Odocoileus virginianus* (Zimmermann)) is often cited as the major cause of regeneration failure after harvesting (Stoeckeler et al., 1957; Shafer et al., 1961; Marquis and Brenneman, 1981; Donovan, 2005). Selective browsing by deer, and differences in species tolerance to browsing, affect the density and species richness of understory tree-layers (Stoeckeler et al., 1957; Horsley et al., 2003; Rooney and Waller, 2003). Browsing can occasionally cause the near elimination of species preferred by deer such as sugar maple and eastern hemlock (*Tsuga canadensis* (L.) Carrièr) and the dominance of unpalatable or browse-tolerant species such as ironwood (*Ostrya virginiana* (Mill.) K. Koch) and American beech (*Fagus grandifolia* Ehrh.) (Stoeckeler et al., 1957; Rooney et al., 2000; Horsley et al., 2003; Sage et al., 2003; Côté et al., 2004; Miller, 2004). Deer densities are heterogeneous across some landscapes due to variations in the presence and abundance of favorable summer and winter habitat characteristics, agricultural land, and understory forage (Côté et al., 2004; Felix et al., 2004; Millington et al., 2010) and landscape-scale variation in snow depth and predation pressure (Doepker et al., 1994; Côté et al., 2004). Spatial variation in deer densities can translate into spatial variation in the density of saplings of species heavily utilized as forage (Rooney et al., 2000).

The density and species composition of seedling and sapling layers in harvest gaps are affected by many other factors in addition to deer herbivory. Densities of seedlings are initially constrained by local seed production and availability of suitable seedbeds. Generally positive relationships among tree size, seed production, and seedling densities (Tubbs, 1977; Ribbens et al., 1994; Garrett and Graber, 1995; Fei and Steiner, 2008) imply that management decisions regarding the retention of large, mature seed-trees can impact future regeneration. Once seeds germinate, availability of soil moisture, nutrients, and light affect seedling growth (Walters and Reich, 1997; Schreeg et al., 2005; Kobe, 2006), survival (Caspersen and Kobe, 2001; Schreeg et al., 2005), and species richness (Tubbs, 1977; Runkle, 1982; Burger and Kotar, 2003; Schumann et al., 2003).

Increases in canopy gap size and understory light availability are expected to benefit tree seedling survival and growth, but they can also increase cover of non-tree understory vegetation (Collins et al., 1985; Schumann et al., 2003). This in turn can reduce the survival and growth of seedlings and saplings (Horsley and Marquis, 1983; Romagosa and Robinson, 2003; Fei and Steiner, 2008) via competition for light and soil resources (George and Bazzaz, 1999; Randall, 2007). Selective browse pressure in areas with high deer densities might exacerbate these effects by increasing the abundances of unpalatable species including some gramanoids and ferns (Wiegmann and Waller, 2006; Randall and Walters, 2011), placing browsed tree seedlings and saplings at a greater competitive disadvantage (Randall, 2007).

Given the suite of factors that affect seedlings and saplings throughout their ontogeny, multivariate assessments of multiple stands across broad geographic areas are critical for determining the relative contributions of different factors (Fredericksen et al., 1998; Rooney et al., 2000, 2002; Powers and Nagel, 2009). This approach also reduces the risk of assigning significance to factors that simply correlate with unmeasured variables that directly influence regeneration. Identifying the most important bottlenecks to tree regeneration at stand to regional scales can help inform forest management practices to improve economic and ecological sustainability.

This paper presents results from a study that examined the relative effects of gap-scale seed-production potential, light availability, and cover of non-tree vegetation and stand-scale winter deer density on densities of seedlings (<1 m tall) and saplings (1–2 m tall) within harvest gaps across a large portion of the Western Upper Peninsula of Michigan. We also explored the correlation between landscape-scale patterns in these gap- and stand-scale factors with spatial patterns in the densities of seedlings and saplings. We predicted that densities of sugar maple saplings would increase with increasing latitude due to lower browse pressure in areas with lower winter deer density. A south to north gradient of decreasing winter deer density across our study area is caused in part by the southern seasonal migration of deer to avoid deep lake-effect snow (Doepker et al., 1994; VanDeelen et al., 1998).

2. Methods

2.1. Study area

The 59 northern hardwood stands included in this study were located across a 4500 km² area of the Western Upper Peninsula of Michigan (Fig. 1; Appendix A) that is the focus of an ongoing interdisciplinary research project integrating ecology and economics to better understand managed forest landscapes (Laurent et al., 2005; LeBouton et al., 2005; Racevskis and Lupi, 2006; Shi et al., 2006; Millington et al., 2010). This area is dominated by forest cover, with little agricultural or urban/suburban land use, and shows a strong gradient in deer densities and snow depth (Doepker et al., 1994; Shi et al., 2006). Since at least the 1960s, winter deer densities have been particularly high in the southeastern portion of the study area (Doepker et al., 1994). This is likely due to the lower snow depths and higher concentration of lowland conifer stands, both of which contribute to variation in winter deer density across this landscape (Millington et al., 2010). Doepker et al. (1994) also suggest that increased pulpwood harvesting in this area might contribute to elevated deer densities.

We selected stands primarily based on their date of harvest (no more than 15 years prior to sampling in summer 2008) and secondarily based on their location. We sought to maximize the extent of the geographic area from which we were sampling. We had no prior knowledge of sapling densities when selecting stands. Stands were selected from a set of over 100 northern hardwood stands previously visited by collaborators in the study area and a set of about 80 additional stands provided by managers with the Michigan Department of Natural Resources and private industrial timber companies. We determined the date of harvest for each stand by analyzing releases in the radial growth of felled saplings (see Matonis, 2009 for details) or from stand inventory data when available.

Ownership of stands is divided among state (28 of 59 stands), private industrial (30 of 59 stands), and non-industrial private (1 of 59 stands) owners. The overstories of these stands were dominated by sugar maple (55 of 59 stands) or American basswood (*Tilia americana* L.) (4 of 59 stands) and had various components of other species, including balsam fir (*Abies balsamea* (L.) Mill.), black cherry (*Prunus serotina* Ehrh.), eastern hemlock, paper birch (*Betula papyrifera* Marshall), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), white spruce (*Picea glauca* (Moench) Voss), and
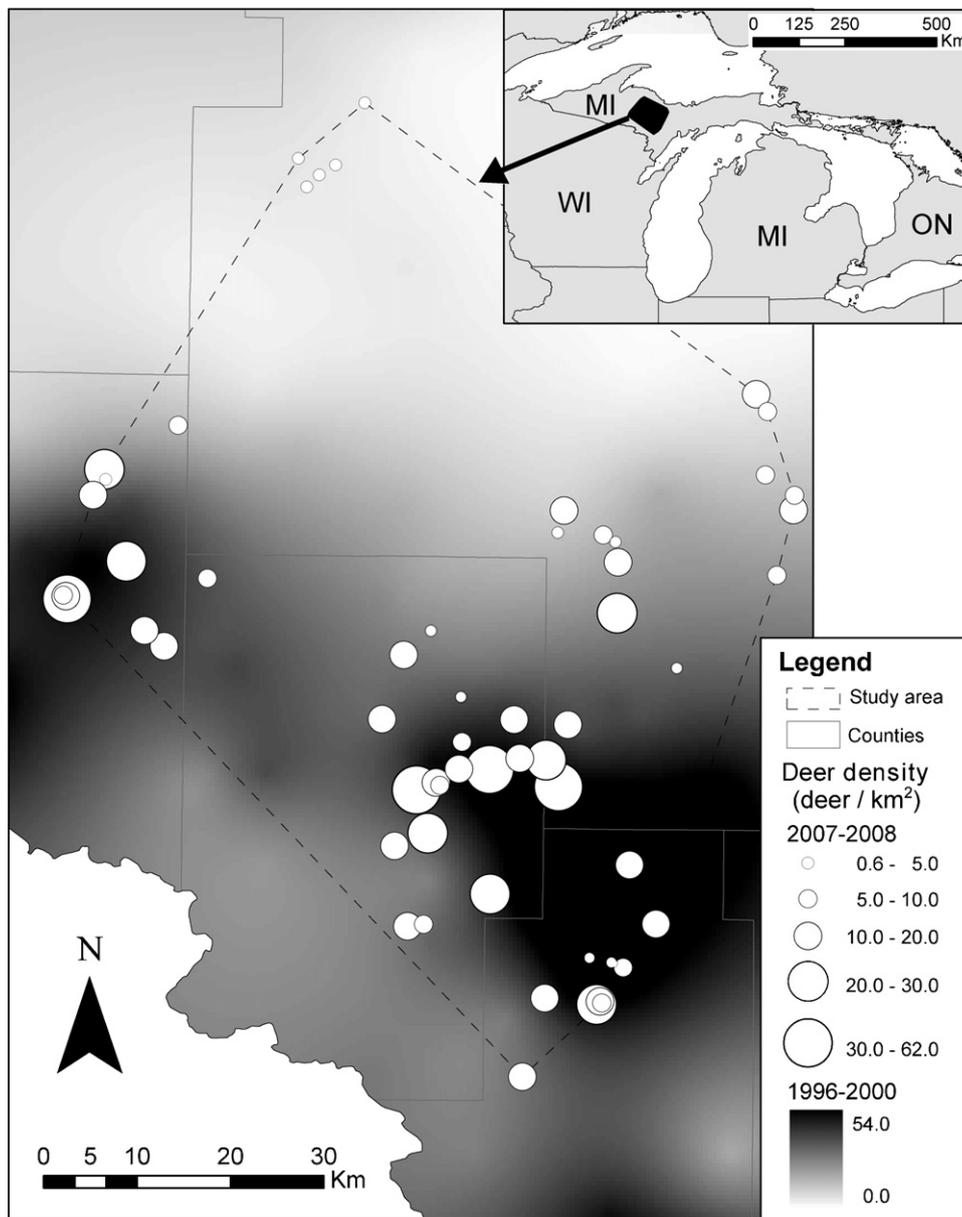
Fig. 1. Map of study area and northern hardwood stand locations ($n = 59$ stands). The graduated symbols show estimated deer density (deer/km^2) based on our fecal pellet surveys from winter 2007 to 2008 and the smoothed surface shows predicted mean deer density from 1996 to 2000 based on Michigan Department of Natural Resources fecal pellet surveys (Hill, 2001; see Matonis, 2009 for universal kriging details). Estimates for winter 2007–2008 are positively correlated with the predicted 1996–2000 estimates at the same location (Kendall's $\tau = 0.27$, *p*-value<0.01). MI: Michigan, WI: Wisconsin, ON: Ontario, Canada.

yellow birch (*Betula alleghaniensis* Britton) (Appendix A). Stands were located on ground moraines, disintegration moraines, and till-floored lake plains, with soil drainage varying from very poor to excessive. Annual snow fall varies from 1600 mm in the southern portion of the Western Upper Peninsula to 4350 mm in the northern portion (National Climatic Data Center 2009, *public communications*) due to lake-effect snowfall driven by Lake Superior.

2.2. Field methods

We measured light availability, cover of non-tree vegetation, and seed-production potential at the gap scale ($n = 347$ gaps) because these variables can exhibit great variability among gaps within a stand. Sampling at the gap scale permitted us to capture the impacts of light availability and cover of non-tree vegetation on the microhabitat experienced by saplings regenerating in gaps of various sizes. Seed-production potential could arguably be mea-

sured at the stand scale, but we collected data at the gap scale to focus on the impact of local seed-trees around each gap. This is justified since a large majority of seeds disperse only a short distance from parent trees for many species in northern hardwood forests (e.g. <20 m) (Ribbens et al., 1994; Clark et al., 1998). We collected data on winter deer density, habitat type, and snow depth at the stand scale ($n = 59$ stands). These factors generally demonstrate greater variability among stands than within a stand. When these gap- and stand-scale factors vary across the landscape in a systematic fashion, we also consider them to be landscape-scale factors.

Six harvest gaps were systematically sampled at each stand, with the exception of five stands where fewer gaps were measured because fewer existed or very high sapling densities made data collection prohibitively time-intensive. Gaps were defined as canopy openings created by the removal of one or more trees that were no farther than 100 m from the center point used for the fecal pellet

survey. All gaps had a diameter of least 10 m between the boles of gap-edge trees (i.e., inter-bole diameter $\geq$10 m), and were sampled from three size strata (shortest inter-bole diameter <12.5 m, 12.5–15 m, and >15 m) when present. Extended gap area (i.e., the area between the boles of gap-edge trees) was estimated using the method of Runkle (1981).

Tree seedlings (<1 m tall) were tallied by species and height (to the nearest 0.25 m) in two 1 m^2 quadrats located 1 m east and west of the gap center. Tree saplings (1–7 m tall) were tallied by species and height (to the nearest 0.25 m) in one 154 m^2 gap-centered circular plot (7 m radius). Our plots are about the size of a large single-tree gap, and nearly equivalent to the median observed extended gap area. In gaps with extreme densities of saplings (>200 saplings/gap plot), only one-fourth to three-fourths of the gap plot was sampled for efficiency, and estimates were scaled up to the entire plot. We express sapling densities as saplings/100 m^2 because this area is more comparable to the size of a harvest gap than either 1 m^2 or 1 ha.

Canopy openness, a proxy for light availability (Kobe and Hogarth, 2007), was estimated from hemispherical photographs (Canham et al., 1990) taken at a height above the tree sapling layer that responded to the recent harvest and/or the non-tree vegetation. Photos were analyzed with Gap Light Analyzer v 2.0 (Frazer et al., 1999) using an automatic threshold value determined by Side-Look v. 1.1.01 (Nobis and Hunziker, 2005). Canopy openness could not be estimated for ten gaps due to overexposure of the photograph. We visually estimated percent ground cover of shrubs, ferns, and graminoids in the two seedling quadrats and in three additional 1 m^2 quadrats randomly located within each gap. We did not estimate forb cover because it was generally low at our stands.

Seed-production potential (SPP) was estimated for sugar maple, ironwood, and other species by summing the quotient of the squared diameter-at-breast-height (dbh; breast height = 1.4 m) and the squared distance of each mature tree to the center of the gap (Σdiameter^2/distance^2). The rarity and low densities of species other than sugar maple and ironwood necessitated that we pool them for analysis. Our estimation of SPP is based on the expectation that a tree's contribution to SPP increases with dbh and decreases with distance in a quadratic fashion (Ribbens et al., 1994). Trees and stumps within 20 m of the gap center and with dbh $\geq$ 20 cm were used for this estimate. Ironwood trees with dbh $\geq$ 5 cm were also used because this species is smaller at maturity than other species. We determined the species identity of stumps in the field or in the laboratory from wood samples (see Marx, 2005 for methodology). Stump basal diameter was converted to dbh using relationships developed by Demaerschalk and Omule (1978). Estimates of seed-production potential were developed for the sampling year (SPP$_{2008}$) based on the current dbh of living trees and for the time of harvest (SPP$_{Harvest}$) based on stump dbh and "grown back" dbh of living trees. Radial growth equations from the Lake States Variant of the Forest Vegetation Simulator (Bush and Brand, 1993) were used to "grow back" mature tree dbh in 2008 to dbh at the time of harvest (see Matonis, 2009 for detailed methodology).

Alternative approaches to SPP that directly measure seed production were impractical given the scale of our experiment, and as we collected field measurements over one summer, they could possibly be misleading given high interannual variation in seed production (Graber and Leak, 1992; Garrett and Graber, 1995). Our SPP estimates are intended only as an index of relative differences in seed-production potential among gaps; however, it might make a fairly poor index of potential seed supply for the other species category due to differences among stands in overstory species composition and large interspecific differences in factors like dispersal patterns and substrate requirements (Burns and Honkala, 1990; Ribbens et al., 1994; Clark et al., 1998). In contrast, SPP likely works well as a relative index for potential seed supply of sugar maple

and ironwood because their individual dispersal patterns should not vary substantially among stands. These two species are also relatively unparticular about establishment substrates (Burns and Honkala, 1990).

Winter deer density was estimated at each stand using fecal pellet surveys in spring 2008. Although fecal pellet surveys can be imprecise because they are sensitive to forage intake, forage moisture content, percentage of young in the herd, and sampling design (Neff, 1968), they are reasonably accurate (Neff, 1968; Forsyth et al., 2007; but see Fuller, 1991). They are also the only practical method for estimating relative differences in deer densities among multiple sites across broad geographic areas. Pellet groups were double counted along ten transects (50 m × 4 m) oriented around one randomly selected center point in each stand. Counts were averaged across the ten transects and converted to an estimate of deer density following the methods of Hill (2001). Visible pellets were deposited after leaf-off, so deer density estimates correspond to deer presence from the beginning of November 2007 to the end of April 2008. We also noted evidence of deer browsing on sugar maple saplings to directly measure herbivory; however, we were unable to collect these measurements at many stands due to the absence of saplings in the understory. For this reason, our analyses only use estimates of deer density from fecal pellet counts.

Habitat type, a proxy for soil moisture and nutrient regimes (Walters and Reich, 1997; Burger and Kotar, 2003), was determined for each stand based on diagnostic assemblages of understory vegetation. The five different habitat types for northern hardwood stands in the Western Upper Peninsula of Michigan are AOCa (mesic soil moisture regime; rich to very rich soil nutrient regime), ATD-Hp (mesic; medium to rich), ATD (mesic; medium to rich), ATM (dry-mesic to mesic; medium), and TMC (mesic to wet-mesic; medium) (Burger and Kotar, 2003; Appendix B). Given the demands of our landscape-wide data collection, the use of habitat type classification was more practical than collecting the soils information necessary to adequately characterize nutrient and water regimes. Also, managers in our study area and beyond are utilizing the habitat type classification system as a tool to inform management decisions, so using this method facilitates the translation of our results into management implications.

Mean daily snow depth from November to April 2008 was determined for each stand from the Snow Data Assimilation System (SNODAS) produced by the National Snow and Ice Data Center (see Barrett, 2003 for details).

2.3. Statistical analyses

Statistical analyses focused on densities of seedlings (<1 m tall) and saplings (1–2 m tall) of sugar maple, ironwood, and a combination of all other, less common species. The other species category is heavily dominated by red maple, white ash, and black cherry, with these species representing 55%, 26%, and 6% of seedlings and 30%, 49%, and 12% of saplings in this category, respectively. We focused our analysis on saplings 1–2 m tall because they are, or recently were, within the range of deer browse (Fredericksen et al., 1998) and are thus more likely than taller saplings to show responses to recent browse pressure and relationships with our estimates of deer density. These shorter saplings also dominate the regeneration layer, with saplings 1–2 m tall accounting for nearly 75% of saplings 1–7 m tall measured across all gap plots.

To determine the association of gap- and stand-scale variables with densities of seedlings and saplings, we developed generalized linear multilevel models (GLMMs). Unlike linear regression, GLMMs incorporate information about the clustering of observations (i.e., gaps nested within stands) to produce estimates of standard errors that account for non-independence in hierarchi-

Table 1
Densities and occurrence of seedlings (<1 m tall) and saplings (1–2 m tall) in gap-centered plots in 347 harvest gaps across 59 northern hardwood stands in the Western Upper Peninsula of Michigan.

Species[a]	Mean	Median	Range	Coefficient of variation	Occurrence in gap plots (% of plots)
	Seedlings per m^2/saplings per 100 m^2				
Sugar maple	7.1/18.3	3/0	0–79/0–260	1.4/2.3	78/39
Ironwood	0.5/5.0	0/0	0–16/0–91	3.0/2.6	28/46
Red maple	0.8/2.5	0/0	0–24/0–167	3.6/4.9	18/14
White ash	0.4/4.1	0/0	0–10/0–157	3.3/4.8	16/18
Black cherry	0.1/1.0	0/0	0–8/0–41	6.2/3.3	6/31
All species	9.0/31.5	5/8	0–82/0–296	1.2/1.6	89/78

[a] The following species were observed as seedlings and saplings in less than 5% of gaps with mean densities <0.1 seedling/m^2 and <1 sapling/100 m^2: American basswood, American beech, American elm (*Ulmus americana* L.), balsam fir, black ash (*Fraxinus nigra* Marsh), northern red oak (*Quercus rubra* L.), quaking aspen (*Populus tremuloides* Michx.), white spruce, and yellow birch. Eastern hemlock and eastern white pine (*Pinus strobus* L.) were observed as seedlings but not as saplings, and balsam poplar (*Populus balsamifera* L.), bigtooth aspen (*Populus grandidentata* Michx.), paper birch, and tamarack (*Larix laricina* (Du Roi) K. Koch) were observed as saplings but not as seedlings.

cally structured and non-normal data (Goldstein, 1995; Bolker et al., 2009). Bayesian inference with Markov chain Monte Carlo sampling is recommended for GLMM parameter estimation since it produces credible intervals that incorporate uncertainty in both fixed- and random-effect parameters (Zhao et al., 2006; Bolker et al., 2009). We present Bayesian credible intervals (i.e., posterior intervals) in our results to indicate the uncertainty and reliability of our parameter estimates. Credible intervals are similar to classical confidence intervals, but they are calculated and interpreted differently (Willink and Lira, 2005). Credible intervals represent the range of values that contain the actual parameter value given a certain level of certainty (e.g., 95% credible interval).

In our GLMMs, we used a negative binomial error structure and a log link to model densities of seedlings and saplings as a linear combination of a stand-scale random intercept (α_j) and gap-scale fixed effects (canopy openness, cover of non-tree vegetation, and seed-production potential). We modeled α_j using a normal distribution error structure, with the mean being the linear combination of an overall intercept and stand-scale fixed effects (deer density and time since harvest). Null models were developed for comparison, in which seedling and sapling densities were modeled using only an overall intercept and α_j drawn from a normal distribution with a mean of zero.

Gap- and stand-scale variables were standardized to improve model convergence. The cover of shrubs, ferns, and graminoids were summed to create the composite metric "cover of non-tree vegetation" to reduce the number of parameters. We used SPP_{2008} as the seed-production potential metric for the seedling analyses since it is unlikely that trees represented by stumps were the seed source for individuals in our seedling category except at the most recently harvested stands. We used $SPP_{Harvest}$ for the sapling analyses since both residual, extant trees and trees removed in the last harvest likely contributed to the pool of older, larger trees constituting our sapling category.

In our GLMMs, we used normal priors for all gap- and stand-scale fixed-effects with a mean of 0 and variance of 10,000 (i.e., noninformative priors) (Bolker et al., 2009). As recommended by Gelman (2006), we used a uniform prior with a range of 0–50 for the standard deviation of the stand-scale random intercept (σ_α). Our estimate of σ_α was not sensitive to the prior distribution used (see Matonis, 2009). Model estimation was performed using WinBUGS v.1.4.3 (Spiegelhalter et al., 2003) run through R v.2.10.1 (R Development Core Team, 2009) with the package *R2WinBUGS* (Sturtz et al., 2005) (see Appendix C for model code). For all models, we ran three parallel chains with dispersed, randomly selected starting values for 70,000 iterations with a burn-in of 10,000 and a thinning rate of 5. We diagnosed convergence using the R package *coda* (Plummer et al., 2009). All models showed strong evidence of convergence based on the Gelman–Rubin diagnostic and the Raftery–Lewis diagnostic (Bolker, 2008).

We determined Deviance Information Criterion (DIC) for full models with gap- and stand-scale covariates and for null models to determine if predictor variables improved model performance. DIC is a method of assessing model performance in terms of fit and complexity (Spiegelhalter et al., 2002), with a decrease in DIC of five or more indicating better model performance (Bolker, 2008).

Habitat type was not included in the GLMMs to reduce the number of parameters. Differences in the densities of seedlings and saplings among habitat types were assessed using Kruskal–Wallis rank sum test.

To explore landscape-scale trends in densities of seedlings and saplings and gap- and stand-scale variables, we determined the correlation between stand latitude and longitude with stand-mean densities of seedlings and saplings, stand-mean values for gap-scale independent variables, and stand-scale independent variables. Nonparametric Kendall's tau rank correlation coefficient was used due to the non-normality of many of the variables.

3. Results

3.1. Characterization of regeneration and gap- and stand-scale variables

A total of 16 species were present as seedlings (<1 m tall) and 18 as saplings (1–2 m tall) in gap plots across the study area, but seedling populations were heavily dominated by sugar maple and sapling populations by sugar maple and ironwood (Table 1). Median densities of seedlings and saplings were low (e.g., 3 seedlings/m^2 and 0 saplings/100 m^2 for sugar maple) and their distributions were right skewed (e.g., densities of sugar maple were as high as 79 seedlings/m^2 and 260 saplings/100 m^2). Sugar maple saplings were absent from 61% of gap-centered plots and ironwood saplings from 54% of gap plots. Twenty-two percent of gap plots contained no saplings of any species.

Mean number of trees (dbh ≥ 20 cm) removed to create harvest gaps was 3 (range 1–13 trees) and mean extended gap area was 190 m^2 (range 80–915 m^2) (Table 2). Extended gap area and canopy openness (mean 13%, range 2–55%) were positively correlated with each other (Table 3) and with cover of non-tree vegetation (mean 40%, range 0–95%). Mean winter deer density was estimated at 14 deer/km^2, ranging from 1 to 62 deer/km^2, and it was negatively correlated with snow depth (mean 27 cm, range 16–48 cm). Across the range of observed deer density and snow depth, deer density decreased on average 2 deer/km^2 as snow depth increased 10 cm along a generally south to north gradient. Time since harvest and SPP_{2008} for sugar maple were positively correlated with each other and negatively correlated with cover of non-tree vegetation and canopy openness.

Some gap- and stand-scale variables varied among habitat types. Snow depth differed by habitat type (Kruskal–Wallis rank sum

Table 2
Summary of gap- and stand-scale independent variables.

Variable[a]	Mean	Median	Coefficient of variation	Range
Gap-scale (n = 347 harvest gaps)				
Canopy openness (%)	13	12	0.5	2–55
Extended gap area (m^2)	190	155	0.5	80–915
Cover of non-tree vegetation (%)	40	40	0.5	0–95
SPP$_{2008}$ sugar maple	220	205	0.4	25–510
SPP$_{Harvest}$ sugar maple	770	410	1.9	55–14,130
SPP$_{2008}$ ironwood	5	0	2.8	0–125
SPP$_{Harvest}$ ironwood	35	0	8.1	0–4,135
SPP$_{2008}$ other species	60	25	1.5	0–655
SPP$_{Harvest}$ other species	235	55	3.9	0–13,575
Stand-scale (n = 59 stands)				
Winter deer density (deer/km^2)	14	12	0.8	1–62
Mean snow depth (cm)	27	23	0.3	16–48
Time since harvest (years)	9	9	0.3	2–15

[a] SPP: seed-production potential (Σdiameter^2/distance^2) for 2008 and at time of harvest.

$\chi^2_{df=4,\ p\text{-value}<0.01} = 22.1$), with the median snow depth on ATD-Hp stands being 8 cm less than on ATD and 10 cm less than on ATM. Seed-production potential of other species at the time of harvest varied by habitat type ($\chi^2_{4,0.02} = 11.3$), with the median seed-production potential being about 80% lower on AOCa stands than on ATM. If TMC was excluded from the analysis because of low sample size (n = 2 stands), sugar maple seed-production potential at the time of harvest marginally varied among the remaining four habitat types ($\chi^2_{3,0.08} = 6.8$), with the median seed-production potential being about 35% lower on ATD-Hp stands than on ATD. Deer density did not significantly vary among habitat types ($\chi^2_{4,0.13} = 7.2$).

3.2. Association of gap- and stand-scale variables with densities of seedlings and saplings

The association of gap- and stand-scale factors with regeneration densities varied by species and size class (Figs. 2 and 3). The inclusion of gap- and stand-scale variables improved our ability to explain variation in regeneration densities of sugar maple seedlings and saplings, ironwood seedlings, and saplings of other species (i.e., reduced model DIC by >5 compared with the null model) (Table 4).

Gap-scale canopy openness was positively associated with densities of saplings of sugar maple and other species. Gap-scale cover of non-tree vegetation was negatively associated with densities of seedlings and saplings of sugar maple and other species, and it tended towards a negative association with ironwood seedlings. Gap-scale seed-production potential had a significant positive association with densities of ironwood seedlings, and it tended towards a positive association with densities of sugar maple seedlings.

Stand-scale winter deer density was negatively associated with densities of sugar maple seedlings and saplings. Stand-scale time since harvest was not associated with regeneration densities.

The overall intercept was positive for the model of sugar maple seedlings, making it more likely to predict a non-zero density than the models for sugar maple saplings and seedlings and saplings of ironwood and other species. These other models had overall intercepts either close to zero or negative, making them more likely to predict densities of zero unless the stand-scale random intercept is large. The standard deviation for the stand-scale random intercept was generally larger in magnitude than any of the fixed-effects for all seedling and sapling models. This indicates that densities of seedlings and saplings varied greatly among stands, and that the random intercept is necessary to capture additional variation not explained by measured gap- and stand-scale covariates, especially for the model of sugar maple saplings.

Densities of seedlings varied by habitat type for sugar maple ($\chi^2_{4,<0.01} = 17.6$), ironwood ($\chi^2_{4,0.01} = 14.1$), and other species ($\chi^2_{4,0.04} = 10.3$), as did densities of sugar maple saplings ($\chi^2_{4,<0.01} =$

37.5) (Fig. 4). The median density of sugar maple seedlings on AOCa stands was 11 seedlings/m^2 less than on ATD, and the median density of sugar maple saplings on AOCa and ATD-Hp stands was 15 saplings/100 m^2 less than on ATM and 48 saplings/100 m^2 less than on ATD. No other pairwise comparisons of seedling and sapling densities between habitat types were significant unless TMC was excluded from the analysis, in which case, the median density of ironwood seedlings on ATD stands was 0.3 seedlings/m^2 less than on AOCa.

3.3. Landscape-scale trends in regeneration and gap- and stand-scale variables

Spatial patterns were observed in densities of seedlings and saplings (Fig. 5). Densities increased with latitude for sugar
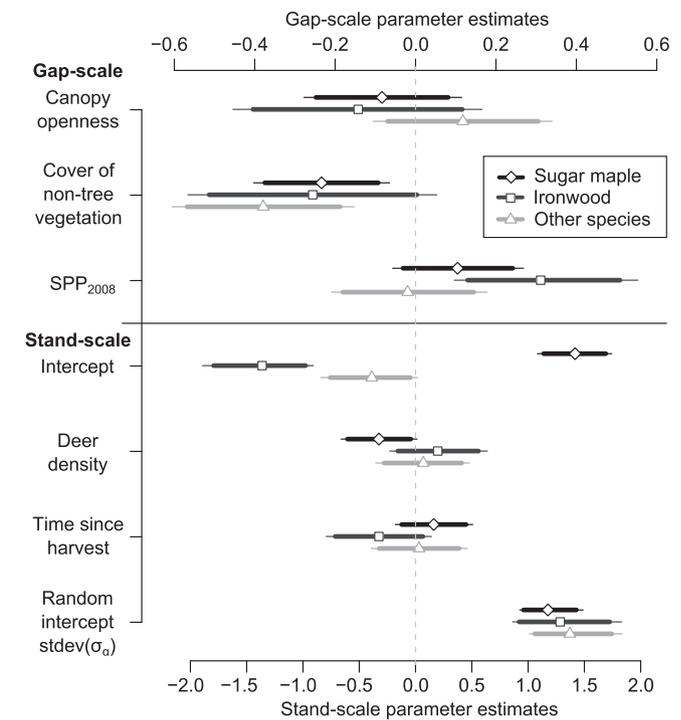

Fig. 2. Effects of gap- and stand-scale variables on densities of seedlings (<1 m tall)/m^2: mean parameter estimates (diamond, square, or triangle symbol), 95% credible interval (thin line), and 90% credible interval (thick line) from posterior distributions. Positive values indicate increases in seedling density (on the log scale) with a one standard deviation increase in that covariate. Random intercept stdev (σ_α): standard deviation for the random stand-scale intercept. SPP$_{2008}$: seed-production potential for 2008.
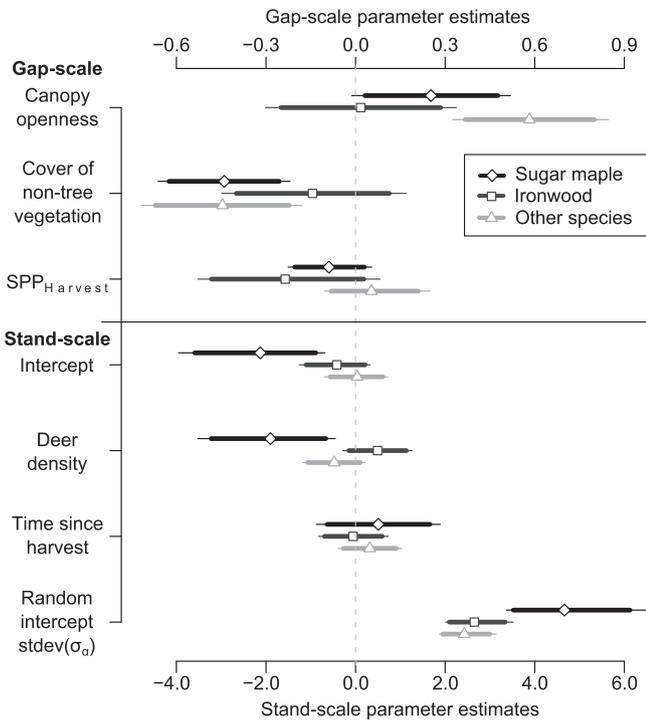
Fig. 3. Effects of gap- and stand-scale variables on densities of saplings (1–2 m tall)/100 m^2: mean parameter estimates (diamond, square, or triangle symbol), 95% credible interval (thin line), and 90% credible interval (thick line) from posterior distributions. Positive values indicate increases in sapling density (on the log scale) with a one standard deviation increase in that covariate. Random intercept stdev (σ_α): standard deviation for the random stand-scale intercept. SPP$_{Harvest}$: seed-production potential at time of harvest.

maple seedlings (Kendall's $\tau = 0.43$, p-value < 0.01) and saplings of sugar maple ($\tau = 0.58$, p-value < 0.01) and other species ($\tau = 0.22$, p-value $= 0.02$). Densities of ironwood seedlings decreased with latitude ($\tau = -0.31$, p-value < 0.01). Densities of seedlings of other species decreased with longitude ($\tau = -0.19$, p-value $= 0.04$). The strongest latitudinal gradient was in densities of sugar maple saplings. Sugar maple saplings were present in only 4% of gap plots ($n = 163$) in stands located south of latitude 46.13°N, with a total of eight saplings across all southern gap plots. In contrast, they were present in 71% of gap plots ($n = 184$) in the stands north of 46.13°N, with densities as great as 260 saplings/100 m^2. In contrast, saplings of ironwood and other species were present in 54% and 39% of southern gap plots with densities as high as 83 and 157 saplings/100 m^2, respectively.

Spatial patterns were also observed in various gap- and stand-scale factors. Winter deer density and ironwood seed-production potential at the time of harvest and in 2008 decreased with latitude, while snow depth and sugar maple seed-production potential at the time of harvest increased with latitude (Table 3). Cover of non-tree vegetation increased with longitude, but no other east-west trends were observed in gap- and stand-scale variables.

Habitat types were spatially segregated (Fig. 6), with latitude and longitude being significantly different among habitat types ($\chi^2_{4, <0.01} = 34.1$ and $\chi^2_{4, <0.01} = 18.1$, respectively). ATD and ATM stands were generally located farther north than AOCa and ATD-Hp stands, and ATD stands were generally located farther east than AOCa.

4. Discussion

4.1. Multiple gap- and stand-scale variables affect densities of seedlings and saplings

Densities of seedlings and saplings in harvest gaps are highly variable. Regeneration failure in many of the stands studied
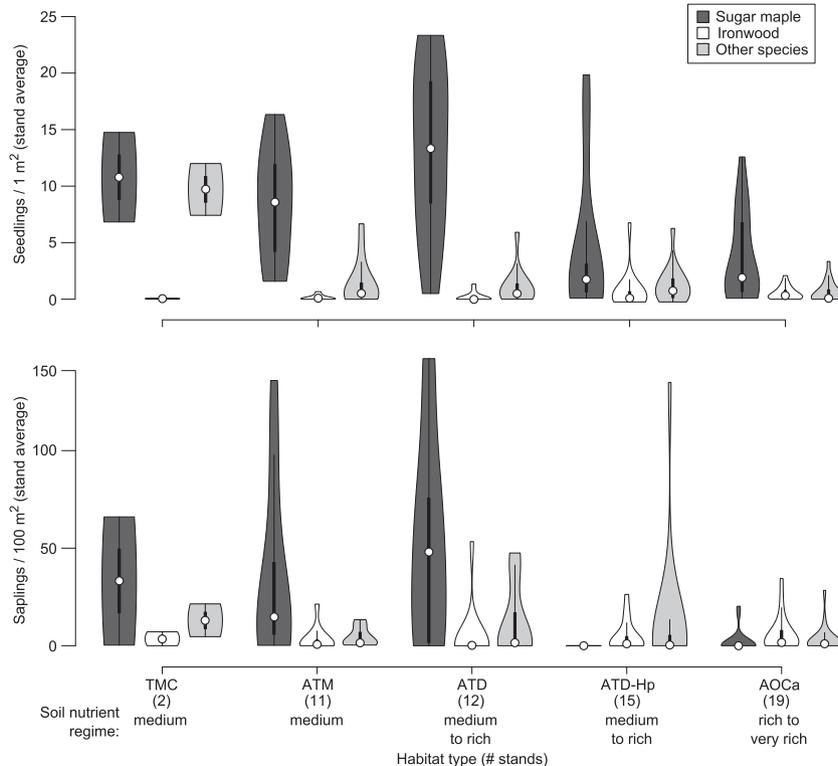

Fig. 4. Stand-mean densities of seedlings (<1 m tall) and saplings (1–2 m tall) by habitat type. Violin plots show the distribution of values, median (white dot), interquartile range (thick vertical line), and range of values 1.5× interquartile range (thin vertical line).
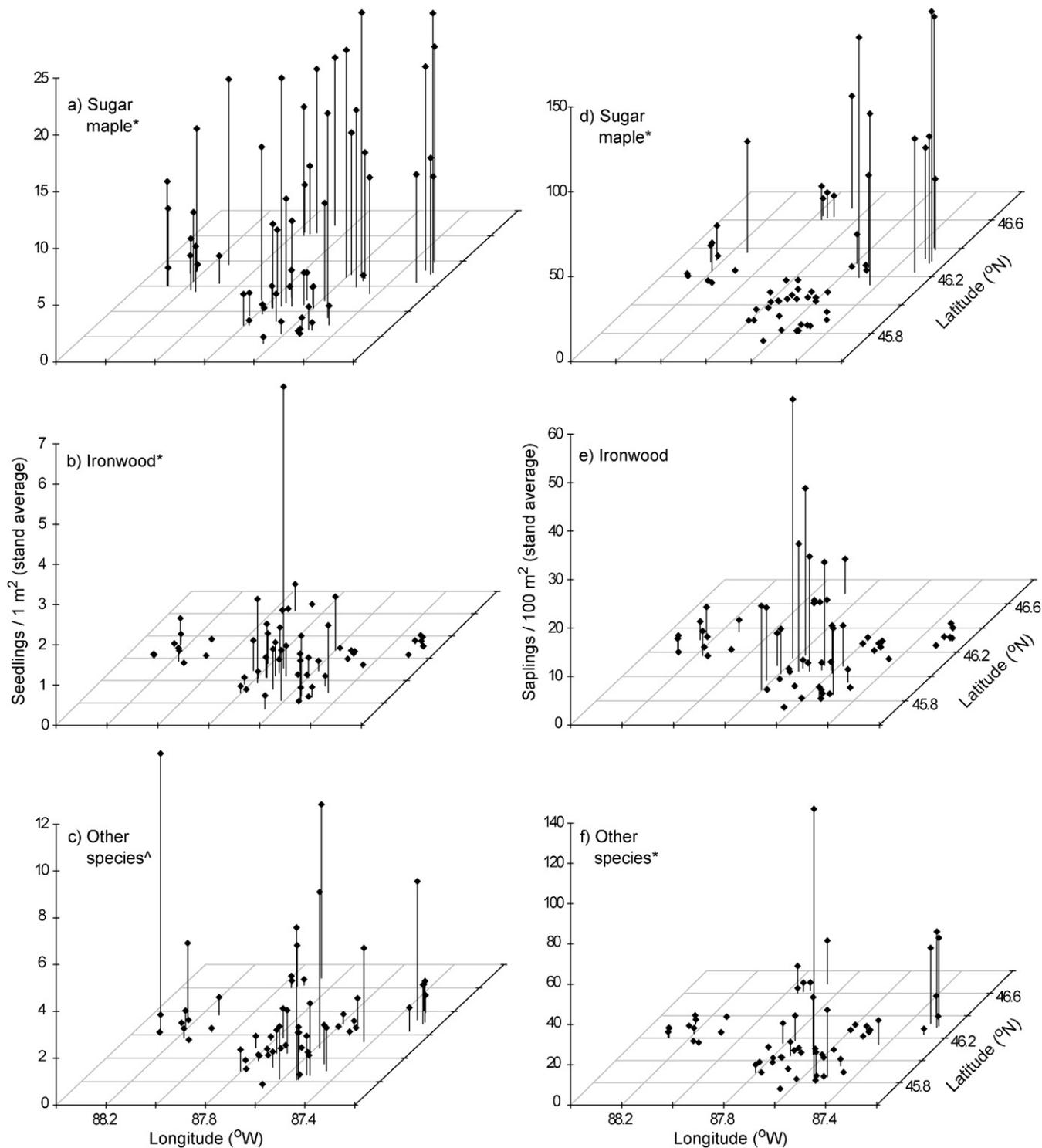
Fig. 5. Spatial patterns in stand-mean densities of seedlings (<1 m tall) (a–c) and saplings (1–2 m tall) (d–f) of sugar maple, ironwood, and other species. *Significant ($p < 0.05$) correlation with latitude. ^Significant ($p < 0.05$) correlation with longitude.

here is implied by low densities of saplings (<10 saplings of all species/100 m^2) in 46% of gap plots and the absence of saplings of shade-tolerant, overstory-dominant sugar maple from 61% of gap plots. Harvest gaps were generally created by the removal of several large trees, so regeneration and recruitment of multiple saplings would be necessary to restore pre-harvest stand densities. Taller saplings (2–7 m tall) of sugar maple are uncommon as well, being absent in 56% of our gap plots, despite observations that this species is well suited for regeneration below canopy gaps

following timber harvest (Tubbs, 1977). Poor regeneration of dominant species has consequences for forest composition and density, with various, potentially large-scale impacts on timber-dependent economies and forest ecosystems.

We identified multiple factors associated with highly variable densities of seedlings and saplings on stands dispersed across a large geographic area. Canopy openness, cover of non-tree vegetation, seed-production potential, and deer density explain some of the variability observed among stands, with species showing dif-
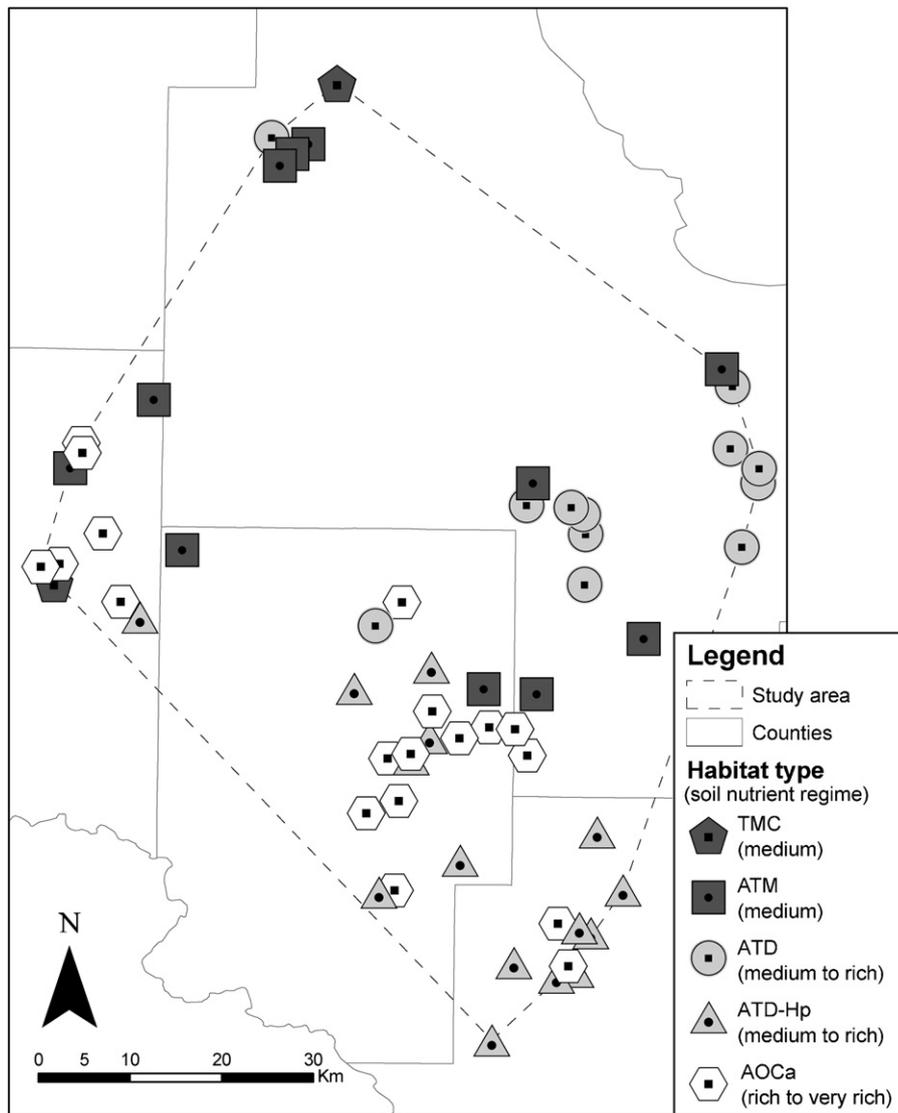
Fig. 6. Habitat types of the northern hardwood stands included in this study (n = 59 stands). Habitat types were determined using Burger and Kotar (2003).

ferent levels of sensitivity to these gap- and stand-scale factors. Our results demonstrate that a single factor cannot be implicated as the cause of regeneration failure; various interacting factors stack the odds against the maturation of seedlings to saplings and saplings to overstory trees. In our study area, the relative effect of deer density ($-$) on densities of sugar maple saplings was greatest, followed by the effects of cover of non-tree vegetation ($-$) and canopy openness ($+$) (Table 5).

Regenerating tree-layers are adversely affected by competition from both overstory trees and from understory non-tree vegetation. Consistent with our observations, densities of seedlings and saplings have been shown to increase with increasing gap size/light availability (Schumann et al., 2003; Runkle, 1982) and decrease with increasing cover of non-tree vegetation (Yawyney and Carl, 1970; Horsley and Marquis, 1983; George and Bazzaz, 1999; Fei and Steiner, 2008). Taller saplings can affect the cover of non-tree vegetation through competition and shading (Collins et al., 1985), complicating efforts to determine cause and effect relationships between densities of tree saplings and cover of non-tree vegetation. However, short-statured tree seedlings are more likely to be affected by, rather than affect, non-tree vegetation. Our finding of a negative relationship between cover of non-tree vegetation and densities of saplings and, in particular, densities of seedlings

supports the notion that non-tree vegetation can inhibit the regeneration of tree species.

Gaps with lower cover of non-tree vegetation and greater light availability can serve as more suitable regeneration sites for saplings, regardless of their shade tolerance ranking. The density of saplings of even shade-tolerant sugar maple increased with increasing canopy openness, as did the densities of saplings of other species, which was a conglomerate of shade-tolerant (American beech and balsam fir), intermediate (American basswood, American elm, red maple, red oak, white ash, white spruce, and yellow birch), and shade-intolerant species (balsam poplar, bigtooth aspen, black ash, black cherry, paper birch, quaking aspen, and tamarack). If canopy openness is standardized by cover of non-tree vegetation, it is positively correlated with densities of saplings of shade-tolerant (Kendall's τ = 0.15, p-value < 0.01), intermediate (τ = 0.15, p-value < 0.01), and shade-intolerant (τ = 0.08, p-value = 0.06) species in the other species category.

The potential for source limitations to impact regeneration success is suggested by increases observed in densities of seeds and seedlings with increasing density, size, and proximity of mature seed-trees in the overstory (Ribbens et al., 1994; Garrett and Graber, 1995; Clark et al., 1998). In contrast, we did not observe a significant contribution of potential seed supply to regeneration variation

Table 3

Association between gap- and stand-scale variables based on Kendall's tau rank correlation ($n = 347$ gaps, 59 stands). Comparisons between gap- and stand-scale variables use stand-means for gap-scale variables to comply with independence assumptions.

	Cover of non-tree vegetation	Extended gap area	Canopy openness	Winter deer density	Time since harvest	Snow depth	SPP$_{Harvest}$ other species	SPP$_{2008}$ other species	SPP$_{Harvest}$ ironwood	SPP$_{2008}$ ironwood	SPP$_{Harvest}$ sugar maple	SPP$_{2008}$ sugar maple
Latitude	0.03	0.00	0.12	−0.27**	−0.03	0.55**	0.04	−0.03	−0.15*	−0.24**	0.28**	−0.02
Longitude	0.21**	0.09	0.00	0.08	0.09	0.14	0.00	0.11	0.11	0.10	0.12	−0.11
SPP$_{2008}$ sugar maple	−0.16*	0.02	−0.15*	0.14	0.26**	−0.07	−0.32**	−0.44**	−0.08	−0.07	0.17*	
SPP$_{Harvest}$ sugar maple	0.03	0.00	0.11	−0.01	−0.02	0.20**	−0.28**	−0.27**	−0.04	0.05		
SPP$_{2008}$ ironwood	−0.01	0.11	−0.01	0.09	−0.03	−0.24**	−0.05	−0.01	0.77**			
SPP$_{Harvest}$ ironwood	0.02	0.13	−0.02	0.08	−0.05	−0.25**	−0.02	0.06				
SPP$_{2008}$ other species	0.02	−0.06	−0.02	−0.14	0.01	−0.04	0.51**					
SPP$_{Harvest}$ other species	0.02	0.02	0.10	−0.12	−0.02	0.08						
Snow depth	0.13	0.06	0.17*	−0.21**	−0.03							
Winter deer density	−0.23**	−0.05	−0.30**	0.16*								
Time since harvest	0.06	0.08	−0.04									
Canopy openness	0.28**	0.30**										
Extended gap area	0.18**											

SPP: seed-production potential ($\sum$ diameter^2/distance^2) for 2008 and at time of harvest.
* p-value <0.10.
** p-value <0.05.

Table 4

Comparing model performance: Deviance Information Criterion (DIC) for full models that include all gap- and stand-scale covariates and null models that include only the overall intercept and random stand-scale intercept. A decrease in DIC of five or more indicates improved performance for the full model over the null model.

Variable	Full model DIC	Null model DIC
Seedling (<1 m tall) density		
Sugar maple	1769	1781
Ironwood	583	591
Other species	921	920
Sapling (1–2 m tall) density		
Sugar maple	1094	1109
Ironwood	1150	1149
Other species	1307	1328

in northern hardwood stands in our study area, except for ironwood. As an important caveat, various factors could weaken the relationship we observed between seed-source potential and densities of seedlings and saplings. For example, high interannual variation in seed production, seed viability, seed predation, and seedling survival and spatial variation in the availability of seedling establishment substrates (Graber and Leak, 1992; Houle, 1992; Garrett and Graber, 1995) could uncouple or obscure the relationship between overstory tree sizes and distances with gap-scale seedling densities.

In our study area, ironwood saplings regenerate across all habitat types, regardless of light availability, cover of non-tree vegetation, and deer densities. Densities of ironwood seedlings might be limited by seed source, but this does not appear to translate into the absence of saplings, potentially due to high survivorship. Ironwood is not a browse preferred species and can increase in relative dominance in areas with high winter deer densities (Miller, 2004, but see Powers and Nagel, 2009). In this study area, densities of sugar maple saplings were generally lower in gaps with higher densities of ironwood saplings (Kendall's $\tau = -0.16$, p-value < 0.01). This pattern likely does not reflect differences in stand suitability for the two species because the relationship is not significant between densities of sugar maple and ironwood seedlings ($\tau = -0.07$, p-value = 0.13). Rather, observations support a relation-

Table 5

Effect sizes from the generalized linear mixed model (GLMM) for sugar maple saplings: mean predicted changes in density of sugar maple saplings (95% credible interval [CI]) for changes in gap- or stand-scale variables (+/- one standard deviation from the observed mean). The log link used in the GLMM causes increases and decreases in the value of covariates to have asymmetrical effects on predicted densities of saplings. Effect sizes are shown for two different values of the random stand-scale intercept (α_j) that cause the predicted density of sugar maple to equal 0 or 20 saplings/100 m^2 when all gap- and stand-scale variables are at their observed means.

Change in gap- or stand-scale variables[a]	Change in predicted density of sugar maple saplings (saplings/100 m^2) (95% CI)	
	$\alpha_j = 0.0$[b]	$\alpha_j = 4.9$[c]
Deer density		
14 → 26 deer/km^2	0 (0–0)	−16 (−50 to −2)
14 → 2 deer/km^2	1 (0–5)	141 (5–604)
Canopy openness		
13 → 20%	0 (0–0)	6 (0–24)
13 → 6%	0 (0–0)	−4 (−16–0)
Cover of non-tree vegetation		
40 → 65%	0 (0–0)	−7 (−23 to −1)
40 → 15%	0 (0–0)	11 (1 – 38)

[a] All other variables held at observed means (Table 2).
[b] Mean predicted density of sugar maple saplings is 0 saplings/100 m^2 (95% CI = 0–1) when all gap- and stand-scale variables are at their observed means.
[c] Mean predicted density of sugar maple saplings is 20 saplings/100 m^2 (95% CI = 2–63), close to the mean observed density of sugar maple saplings, when all gap- and stand-scale variables are at their observed means.

ship mediated by an herbivory-competition interaction in which ironwood replaces sugar maple in areas with higher winter browse pressure.

Knowledge about gap- and stand-scale conditions confers partial ability to predict densities of seedlings and saplings, but considerable levels of variation in regeneration densities remain unaccounted for. Additional sources of variation might be temporal and spatial variability in patterns of seed dispersal and seedling establishment (Clark et al., 1998), heterogeneity in the suitability and availability of seed-bed microhabitats (Houle, 1992; Marx and Walters, 2008), individual-scale variation in sapling growth rates, the chance presence of advanced regeneration saplings in the location of harvest gaps (Brokaw and Busing, 2000), and the influence of previous harvests or other disturbances on advanced regeneration structure.

4.2. Inverse landscape-scale gradients in winter deer density and density of sugar maple saplings

Spatial patterns in the density of white-tailed deer during the winter appear to be partially responsible for a landscape-scale gradient in the density of palatable saplings within the zone of browse susceptibility (i.e., <2 m tall). In the Western Upper Peninsula of Michigan, stands potentially experiencing regeneration failure of sugar maple were generally located in the south and west where winter deer densities were higher. Others have also noted a similar trend in this region (Miller, 2004; Donovan, 2005). The spatial pattern we observed in winter deer density is consistent with estimates from fecal pellet surveys independently collected by the Michigan Department of Natural Resources (Fig. 1) and has been documented across the study area for at least half a century (Doepker et al., 1994). In contrast, landscape-scale variation in deer densities does not appear to influence landscape-scale variation in sugar maple regeneration across northern New York State, potentially because deer density is lower in this region or the spatial-scale used by previous studies was too great to capture the relationship (Didier and Porter, 2003).

Covariance among deer density, snow depth, and vegetation habitat types limit our ability to conclusively say how each of these factors contributes to the overall patterns we observed in regeneration. Densities of sugar maple seedlings and saplings were greater on ATD, ATM, and TMC stands, which were generally located farther north and had deeper snow than AOCa and ATD-Hp stands. Despite this, a deer-driven gradient in densities of sugar maple saplings seems more likely than a habitat type-driven gradient for several reasons. These include: (1) Densities of sugar maple saplings were most dissimilar between ATD and ATD-Hp stands, even though these habitat types are predicted to have similar soil moisture and nutrient conditions (Burger and Kotar, 2003). (2) Growth rates of sugar maple saplings are either positively related or insensitive to soil nutrient and water availability (Walters and Reich, 1997; Bigelow and Canham, 2002; Kobe, 2006), and sapling growth rates are positively related to survival (Caspersen and Kobe, 2001). These relationships between resources and sapling performance are at odds with the pattern of lower sugar maple sapling densities on the more resource rich, southerly distributed habitat types. (3) Despite being presently depauperate of saplings, sugar maple dominates the overstory of AOCa and ATD-Hp stands, suggesting that resource conditions at these stands supported sugar maple regeneration at one point. (4) Sugar maple seedlings were far more abundant than sugar maple saplings, and differences in their densities among habitat types were weaker than differences in densities of saplings, potentially because winter browsing by deer interrupts the transition from seedling to sapling.

Sugar maple seed-production potential at the time of harvest increased with latitude, also being greater on ATD compared with ATD-Hp stands, but this is unlikely to account for the gradient in densities of saplings. Our estimates of seed-production potential had no to low value in predicting densities of sugar maple seedlings and saplings.

Our results contribute to a growing body of evidence that sugar maple might be decreasing in dominance across its range in northeastern United States and parts of Canada. Negative impacts on seedling, sapling, and/or overstory sugar maples are attributed to deer browsing, competition from unpalatable species, nutrient stress (i.e., calcium, potassium, and magnesium limitations), defoliation by native and exotic insects, and changes to soil conditions caused by exotic earthworms (Horsley et al., 2000; Sage et al., 2003; Juice et al., 2006; Powers and Nagel, 2009; Larson et al., 2010). Our results suggest that herbivory by white-tailed deer, light availability, and competition from non-tree vegetation affect densities of sugar maple saplings following selection harvesting. Winter deer herbivory might have the potential to create a landscape-scale gradient in sugar maple regeneration success, with implications for the sustainability of selection harvesting in some stands.

4.3. Management implications

Forest managers are concerned by low densities of saplings in northern hardwood stands and the potential replacement of commercially valuable sugar maple by non-valuable ironwood (Miller, 2004; Donovan, 2005). Our observations of the absence of sugar maple saplings from 61% of gap plots challenge the notion that "securing some sort of commercially important natural regeneration is usually a simple matter in most northern hardwood stands" (Tubbs, 1977, p1). Although early work on selection harvesting in the region supports this statement (Eyre and Zillgitt, 1953), increasing deer density across the area since the 1970s (Doepker et al., 1994) and/or the potential unsuitability of selection harvesting for securing regeneration on some habitat types might reduce the ability to apply this technique ubiquitously across northern hardwood stands. If regeneration cannot be secured by forest managers, some stands might be converted to conifer plantations or sold for development (Donovan, 2005), with potentially large-scale impacts on the economy, wildlife habitat, and biodiversity.

Larger gap sizes with higher light availability are associated with higher densities of seedlings and saplings; however, the positive effect of light availability on cover of non-tree vegetation reduces the effectiveness of increasing gap size as a means to improve regeneration. Even ten years after harvest, the cover of non-tree vegetation was as high as 93% (up to 79% for *Rubus* spp, 65% for ferns, and 67% for graminoids). The results of other studies suggest that removal of non-tree vegetation might be necessary to ensure successful regeneration in some stands (Yawyney and Carl, 1970; Horsley and Marquis, 1983; Romagosa and Robinson, 2003).

Browsing by white-tailed deer had stronger effects on densities of sugar maple saplings than canopy openness or cover of non-tree vegetation, indicating that attention should be devoted to quality deer management that maintains populations in balance with their habitat (Frawley, 2005). Targeted hunting to reduce deer for several years in areas where deer overwinter could allow seedlings and saplings an opportunity to outgrow browse susceptibility (Sage et al., 2003; Millington et al., 2010), helping to strike a balance between deer and other forest resources such as timber production and understory bird habitat.

Stratifying northern hardwood management practices by deer density and/or habitat type might lead to better regeneration success. For example, silvicultural systems characterized by larger harvest openings, such as shelterwood or group selection systems, might be more appropriate than single-tree selection systems in stands where deer density is high (Marquis and Brenneman, 1981; Sage et al., 2003). The development of harvest recommendations

specific to each habitat type could facilitate ecosystem management by coordinating appropriate silvicultural techniques with considerations of deer habitat potential (Felix et al., 2004). Further research to disentangle the impacts of forest harvest intensity, deer herbivory, and habitat types on regeneration, potentially through soil fertilization treatments and deer exclosures, would help determine which factors require modifications in management.

Our snapshot observations of deer and regeneration densities are based on conditions during one season; however, regeneration dynamics are not static, with the impact of deer on plant communities developing over time (Côté et al., 2004; Wiegmann and Waller, 2006; Royo et al., 2010). Monitoring the development of regeneration and herbivory following timber harvests is therefore important to indicate when management intervention might be needed to mitigate deer impacts. In addition to the fecal-pellet count methods we used, measurements of height, abundance, cover, and browse damage on phytoindicator species (e.g., *Trilium* and *Maianthemum* spp.) can provide useful information about trends in deer impacts (Royo et al., 2010).

Despite the limitations of our snapshot-in-time approach, we believe that our results adequately represent and foreshadow long-term trends in vegetation dynamics, such as the potential for declines in important overstory species due to poor regeneration. Our single-year estimates of deer density generally corroborate multi-decade Michigan Department of Natural Resources pellet count data. We also focused on a size class of saplings that are susceptible to the factors we measured, including deer herbivory. Furthermore, we sampled recent harvest gaps, ranging from a few years to a decade post-harvest, where regeneration is expected and required for sustainable management practice.

By measuring many variables across a large number of stands we were able to develop valuable insight into the relative contribution of different factors impacting regeneration. Overall, our results demonstrate that holistic silvicultural-systems that match harvest practices to local deer densities and habitat types and consider interactions between light levels and non-tree vegetation will be most successful at encouraging the regeneration of commercially valuable species.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.03.034.

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