

Ungulate exclusion accentuates increases in woody species richness and abundance with canopy gap creation in a temperate hardwood forest

Autumn E. Sabo^{a,*}, Jodi A. Forrester^b, Julia I. Burton^c, Phillip D. Jones^d, David J. Mladenoff^a, Eric L. Kruger^a

^a Dept. of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Dr., Madison, WI 53706, USA

^b Dept. of Forestry and Environmental Resources, North Carolina State University, 2800 Faucette Dr., Raleigh, NC 27695, USA

^c Wildland Resources Dept., Utah State University, 5230 Old Main Hill, NR 206, Logan, UT 84322, USA

^d Dept. of Wildlife, Fisheries and Aquaculture, Mississippi State University, Box 9690, Mississippi State, MS 39762, USA



ARTICLE INFO

Keywords:

Canopy openness

Gaps

Nonparametric multi-dimensional scaling (NMDS)

Northern hardwood forest

Species richness

Tree regeneration

Understory

White-tailed deer (*Odocoileus virginianus*)

ABSTRACT

Forest biodiversity is declining due to a wide variety of anthropogenic factors. Forest and wildlife management can be part of the problem or part of the solution. Our objective was to examine the influence of white-tailed deer exclusion on the response of understory communities to a gradient in overstory disturbance. We expected that greater overstory disturbance would act synergistically with deer exclusion to increase understory species richness and abundance. In northern Wisconsin, USA, we monitored changes in understory vegetation in a temperate hardwood forest following four overstory treatments (no-harvest controls and three gap sizes) and two deer treatments (deer access or exclusion). By the seventh year following gap creation, understory species richness and the abundance of multiple species groups had increased, especially when deer were excluded. Effects were most pronounced in larger gaps, particularly among saplings of less shade-tolerant tree species. The tree seedling community responded similarly, but less strongly, to treatments. In contrast, change in the short-stature shrub and herbaceous community seven years following gap and deer treatments was limited and species-specific. Environmental conditions at the groundlayer, such as light availability and soil moisture content, rarely differed by treatment in our study. Increased density of understory vegetation at seven years post-treatment may have negated early pulses in resource availability resulting from gap creation. Gap creation alone increased species richness and abundance of woody taxa, whereas deer exclusion alone had little effect on the understory community. When treatments were applied in combination, we saw the greatest change in the plant community. Our study provides evidence that, when accompanied by a reduction in deer population density, relatively intense overstory disturbance (e.g., group-selection harvest) may be an effective management strategy for restoring forest heterogeneity.

1. Introduction

Anthropogenic changes to the environment and movement of species beyond their native ranges lead to a global phenomenon, biotic homogenization, where a few species increase in abundance as many others decline (e.g., McKinney and Lockwood, 1999). Such homogenization has been documented across plant guilds in temperate forests of North America (e.g., Wiegmann and Waller, 2006; Schulte et al., 2007; Rooney, 2009; Schumacher and Carson, 2013). For example, *Acer* spp. are replacing species like *Quercus* spp., *Pinus* spp. *Betula* spp. and *Tsuga canadensis* (e.g., Shotola et al., 1992; Stearns and Likens, 2002; Schulte et al., 2007; Nowacki and Abrams, 2008; Rogers et al., 2009;

Schumacher and Carson, 2013), likely due to factors such as fire suppression and white-tailed deer (*Odocoileus virginianus*) herbivory.

A narrow distribution of canopy opening sizes in even-aged forests compared to unmanaged forests, e.g., old-growth stands (Goodburn, 1996), may also play a role in biotic homogenization. Creating gaps in a range of sizes serves to better mimic natural disturbance regimes (Seymour et al., 2002) and may be necessary for the successful regeneration of shade-intolerant and mid-tolerant tree species (McClure and Lee, 1993; Kobe et al., 1995; Webster and Lorimer, 2005; Gasser et al., 2010). Gaps can also stimulate growth of herb species that are more shade intolerant (e.g., Collins et al., 1985; Moore and Vankat, 1986; Burton et al., 2014). In a northern Wisconsin forest, small-seeded,

Abbreviations: SWC, soil water content; D_x, diameter at breast height size class x; H_x, height class x'; C, horizontal percent cover

* Corresponding author at: Environmental Science Program, Sweet Briar College, 128 Chapel Road, Sweet Briar, VA 24595, USA.

E-mail address: asabo@sbcc.edu (A.E. Sabo).

<https://doi.org/10.1016/j.foreco.2018.11.004>

Received 27 July 2018; Received in revised form 31 October 2018; Accepted 3 November 2018

0378-1127/ © 2018 Published by Elsevier B.V.

less shade-tolerant species were more common as gap size increased in a thinned forest matrix (Kern et al., 2013), and graminoids were more abundant in medium to large-sized gaps three years after their creation in the experiment we utilized for this study (Burton et al., 2014). Similarly, light availability was a key driver of understory spatial patterning in a study comparing old-growth and second-growth hardwood stands (Scheller and Mladenoff, 2002), and of understory diversity in an experiment testing uneven-aged silvicultural techniques (Smith et al., 2008).

The response of forest vegetation to canopy gaps may also depend on the abundance of herbivores, particularly ungulate species. In recent study areas across eastern deciduous forests, white-tailed deer densities often averaged ≥ 8 deer km^{-2} (e.g., Anderson and Loucks, 1979; Van Deelen et al., 1996; Waller and Alverson, 1997; Rooney et al., 2002; Kain et al., 2011). Overabundant deer are regarded as a key threat to eastern deciduous forests (Waller and Alverson, 1997), causing declines or regeneration failures of palatable tree species. Deer also preferentially browse many forbs (Miller et al., 1992; Anderson, 1994; Balgooyan and Waller, 1995; Fletcher et al., 2001), some of which are particularly intolerant to browsing because they produce only one flush of growth. Thus, a subset of native forbs, shrubs and trees may decrease relative to less-palatable, more-tolerant grasses, sedges, and clonal ferns in areas with an abundance of deer (Gill, 1992; Rooney, 2001; Wiegmann and Waller, 2006; Goetsch et al., 2011; Frerker et al., 2014). Dominance by ferns or graminoids, which can form “recalcitrant layers” because they block the development of more diverse communities, are particularly problematic when heavy deer browsing is concurrent with overstory removal (Royo and Carson, 2006).

In this study, we focused on two potential methods for reversing homogenization of understory plant communities: reducing deer pressure and creating overstory gaps. We capitalized on extensive pre-treatment data about both the woody and herbaceous components of the understory, and report how our longer-term results compare to short-term treatment effects reported previously (Burton et al., 2014; Forrester et al., 2014). We hypothesized that deer exclusion and increasing gap size would act synergistically to increase species richness and the abundance of understory species. To test our hypothesis, we compared changes in vegetation seven years after applying a combination of deer exclosures, three sizes of gaps, and deer-access and intact (no-harvest) overstory controls.

2. Materials and methods

2.1. Study site

Our project was set on 280 ha within the Flambeau River State Forest, Wisconsin, USA (45.617778, -90.785556) where average (1971–2000) air temperatures in January and July are -13°C and 19°C , and mean annual precipitation is 84 cm (Midwest Regional Climate Center, <http://mcc.sws.uiuc.edu>). Topography at the site is flat to gently sloping. Soils are Aquic or Oxyaquic Glossudalfs that comprise deep silt loams overlaying dense till (David Hvizdak, USDA, NRCS), and that experience seasonally perched or high water tables. The site was clearcut in the mid-1920s. It is now dominated by second-growth *Acer saccharum* (Forrester et al., 2014), which represents 56% of the stand's basal area (BA), as well as *Tilia americana* (16%) and *Fraxinus americana* (12%). On average, our sampling area had a basal area of $29\text{ m}^2\text{ ha}^{-1}$ prior to treatment (Sabo et al., unpublished). For additional site details, see Forrester et al. (2014). From 2006 to 2013, deer population densities in the area were 8–12 deer km^{-2} , according to post-hunt estimates by the Wisconsin Department of Natural Resources (Robert Rolley, personal communication).

2.2. Experimental design

We worked within a long-term experiment that was designed to test

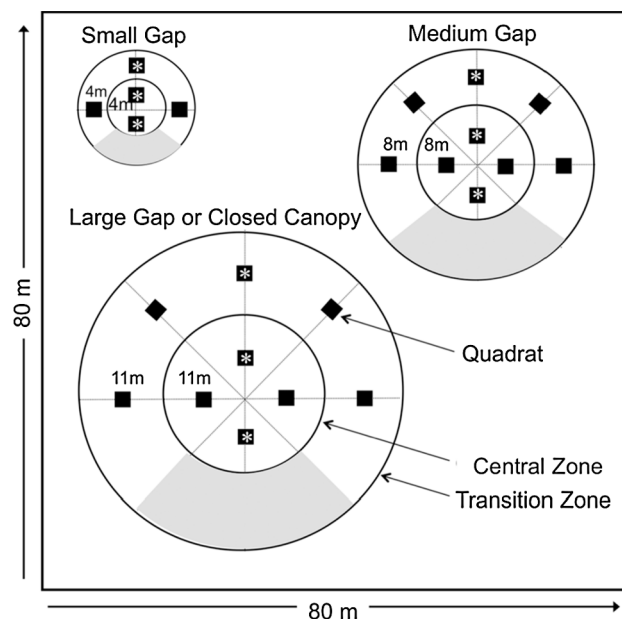


Fig. 1. Plot layout indicating the 4-m^2 quadrats (squares) in the central (inner circle) and transition (outer circle) zones in each subplot within the plots. In no-harvest plots, we sampled the 9 quadrats in the large circular subplot only. The radii of the subplot zone widths are 4 m for small, 8 m for medium, and 11 m for large. Light availability, soil compaction and soil moisture were only measured in quadrats along north to south transect (those marked with *). The shaded areas indicate where saplings were not measured in the harvested plots. In no-harvest plots, we only sampled saplings in the central zone.

the effects of forest structure on ecosystem processes by creating variable-sized gaps and excluding deer (as well as other manipulations that were not used during our study) (Dyer et al., 2010). Each treatment (deer-access/gap, exclosure/gap, exclosure/no-harvest, and deer-access/no-harvest) was replicated five times using 0.64 ha plots. In January 2007, when the ground was frozen and under snow, gap subplots of three different sizes (small = 50 m^2 , medium = 200 m^2 , and large = 380 m^2) were created in each gap treatment plot by cutting and removing all trees and saplings with a diameter at breast height (DBH) $> 5\text{ cm}$ (central, circular zone of subplot; Fig. 1). Uncut “transition” zones of 4, 8 and 11 m surround the 50-m^2 , 200-m^2 and 380-m^2 gaps, respectively.

Canopy gaps were not created in the remaining two treatments (no-harvest, with and without exclosure), but subplots identical in dimensions to the 380-m^2 gap subplots (380-m^2 central zone and 11-m-wide transition zone) were established. Exclosure treatments were applied during the fall of 2007, by installing high-density polypropylene fence ($5 \times 5\text{ cm}$ mesh), at a 2.1-m height, around the perimeter of each plot to exclude deer (Forrester et al., 2014). Plots were randomly assigned treatments and, within them, subplots were randomly oriented.

2.3. Data collection

Pre-treatment (2006) and seven years after treatment (2013), percent cover of the understory vegetation (herbs, shrubs and trees less than 1.4 m in height) was estimated within a series of 4-m^2 permanent quadrats (Fig. 1). We sampled nine quadrats in each of the 380-m^2 and 200-m^2 gap subplots, and five in each of the 50-m^2 gap subplots. In no-harvest treatments, we sampled nine quadrats (Fig. 1) per plot. In all quadrats, we estimated mid-summer % cover of all vascular plants by species and height (h) class ($h_1 < 30\text{ cm}$, $30 \leq h_2 < 100\text{ cm}$, $100 \leq h_3 < 140\text{ cm}$, and $h_4 > 140\text{ cm}$) using a scale consisting of 11 cover (c) classes: $c_1 < 0.5\%$, $0.5 \leq c_2 < 1\%$, $1 \leq c_3 < 2.5\%$, $2.5 \leq c_4 < 5\%$, $5 \leq c_5 < 15\%$, $15 \leq c_6 < 25\%$, $25 \leq c_7 < 50\%$,

$50 \leq c_8 < 75\%$, $75 \leq c_9 < 95\%$, $95 \leq c_{10} < 100\%$, and $c_{11} = 100\%$ (Gauch, 1982).

Saplings ($0.5 \text{ cm} \leq \text{DBH} < 5 \text{ cm}$) were tallied by species and DBH (D) class ($0.5 \text{ cm} \leq D_1 < 1.0 \text{ cm}$, $1.0 \text{ cm} \leq D_2 < 2.5 \text{ cm}$, $2.5 \text{ cm} \leq D_3 < 5.0 \text{ cm}$) within the entire central zone and the north, east and west transition quadrants of gap treatments. Owing to their location, the sampled areas adjacent to but outside of the central gap area in the north, east and west transition zones received additional solar radiation and had higher soil moisture availability than those within intact forest (Raymond et al., 2006; Schatz et al., 2012), which is why we included these as part of the treatment area. In no-harvest plots, similar sapling measurements were made, but only in the (intact) central subplot zone (i.e., not the north, east or west transition zone).

Prior to treatment (2006), in addition to measuring all saplings in the manner described above, we measured the basal area of small trees ($5 \leq \text{DBH} < 10 \text{ cm}$) and large trees ($\text{DBH} \geq 10 \text{ cm}$) within the same areas to characterize structure of the pre-treatment overstory (Dyer et al., 2010). Since the environment of 50-m² gap subplots was likely to be influenced by large trees beyond the 4-m transition zone boundaries, we included, for these subplots only, trees with $\text{DBH} \geq 10 \text{ cm}$ in an additional 5-m wide radius beyond the north, east and west transition zones.

In 2013, we assessed treatment effects on light availability and soil characteristics known to influence community composition. In every subplot, we estimated canopy openness (i.e., light transmittance) at 0.3-m and 2-m heights based on measures of photosynthetic photon flux (PPF) under diffuse light conditions (uniformly overcast sky, dusk or dawn), using Onset HOBO pendant loggers (Onset, Bourne, MA, USA). PPF was measured in three quadrats across a north-south transect within every subplot (Fig. 1). To calculate openness, the resulting values were divided by the PPF simultaneously measured by a sensor positioned above the forest overstory adjacent to the study site.

Soil measurements in 2013 included moisture content (SMC), compaction, and relative availability of ammonium and nitrate. SMC, expressed as percent on a volume basis, was measured monthly during the growing season using time-domain reflectometry probes (6 cm length, Delta TH20, Dynamax Inc., Houston, TX), which were inserted into mineral soil, after removal of the duff layer, once in each of the transition north, central north and central south quadrats. No measurements occurred within 24 h of rainfall. In the four corners of the same quadrats, compaction was measured with a hand-held penetrometer (Lang Penetrometer, Inc., Gulf Shores, AL, USA). The relative availability of soil ammonium and nitrate was assessed, near quadrats in the north and south zones of 380-m² subplots of gap and no-harvest treatments, during summer (May through early August) and fall (early August until late October), using ion-exchange membrane probes (Plant Root Simulator, Western Ag Innovations, Saskatoon, Canada).

2.4. Data analysis

To assess the influences of gap creation and deer exclusion on the composition and vertical structure of the understory plant community, we examined change in the horizontal percent cover of groundlayer (herb and short-stature shrub) species and tree seedlings, by height class, in each subplot. We substituted the midpoint percent cover for each species' cover class before calculating the ratio of cover (C) in 2013 to that in 2006 (C_{2013}/C_{2006}) and transforming it using the expression $1/[1 + e^{C_{2013}/C_{2006}(-1)}]$. We used the transformation to make change data positive, which allowed a wider range of statistical analyses. Groundlayer species were grouped according to growth form and/or native range (Table A.1). Rare tree species ($< 7\%$ cover in any plot in 2006 or 2013) that were not analyzed individually were divided into shade-tolerant and less-tolerant groups based on Niinemets and Valladares (2006) (Table A.1). For saplings, we calculated change by subplot, over seven years (2006–2013), in (1) BA and stem density in each of the three DBH classes, (2) species richness (number of species);

and, for use in multivariate analyses, (3) BA by species (across all three DBH classes) after transformation ($1/[1 + e^{C_{2013}/C_{2006}(-1)}]$).

Prior to multivariate analyses, we deleted data for species that occurred in less than 5% of our subplots in each height class, resulting in 128 groundlayer variables, 29 tree (and arborescent shrub) seedling variables, and 18 species for the sapling dataset. We employed PERMANOVA, using Euclidean distance and 100 permutations, to test the significance of differences in vegetation change among deer exclusion and gap treatments. To test if treatment groups differed significantly in community dispersion change (change in β -diversity), or distance to group centroids, we employed PERMDISP (Anderson, 2004), using Euclidean distance and 999 permutation tests.

We also used non-metric multidimensional scaling (NMDS) to explore the influences of treatments on the composition of groundlayer and understory tree communities. Due to the nature of our change data transformation, we used Euclidean distance to calculate the dissimilarity matrices for species change. Then, environmental vectors (gap size as a continuous variable, deer converted to a binary variable, and pre-treatment overstory BA), normalized between 0 and 1, were fit to the ordination results. When an environmental variable was significantly correlated with NMDS axis scores ($P < 0.1$), we overlaid its linear vector onto the two-dimensional ordination of species composition data.

Finally, we used analysis of variance (ANOVA), including fixed-effect and mixed models, to further test the significance of observed changes in the abundance of individual species and species groups, and the species richness of several groups, in response to treatments. To account for the nested, unbalanced design, where gap plots contained all three gap sizes while no-harvest subplots were isolated in separate plots, we first tested each gap size separately against the no-harvest control, with overstory and fence treatments, and pre-treatment overstory BA, as predictors of sapling abundance. For groundlayer vegetation and seedling responses, overstory and fence treatments, pre-treatment overstory BA and height class were fixed effects, and plot was a random effect. We then assessed the significance of relationships between change and gap size using mixed models with plot (and subplot for groundlayer vegetation and seedling data) as a random effect, and gap size, fence treatment and pre-treatment BA (and height for groundlayer vegetation and seedling data) as fixed effects. Adopting the same model structures as those used for sapling data, we also tested the significance of treatment effects on environmental factors, at seven years post-treatment (2013), using separate ANOVAs for openness (at 0.3 m and 2.0 m heights), availabilities of soil nitrate and ammonium summed across the season, compaction and SMC (averaged across the summer), with overstory and fence treatments as the predictors. Response variables were transformed when necessary to reduce heteroscedasticity.

Parametric statistics were conducted in JMP Pro 11. Multivariate statistics were performed in R v. 3.2.2 and Vegan package 2.0–10 (Oksanen et al., 2013). The overall sample size was 40 subplots and 20 plots, unless otherwise noted, with $n = 5$ plots for each of the four gap \times fence treatments.

3. Results

3.1. Sapling community change

Overall composition of the sapling community responded to the overstory and fence treatments. PERMANOVA tests of the sapling community found differences among gap size ($F_{1,39} = 15.0$, $P < 0.05$) and fence ($F_{1,39} = 12.3$, $P < 0.05$) treatments and their interaction ($F_{1,39} = 7.1$, $P < 0.05$). PERMDISP showed that gap and fence treatments both affected the distance to sapling change centroids (model $F_{7,32} = 6.0$, $P < 0.001$). Permutated pairwise comparisons differed between 15 of the 26 possible pairs, and, notably, no-harvest subplots differed from 50-m² gap subplots only within exclosures (Fig. A.2).

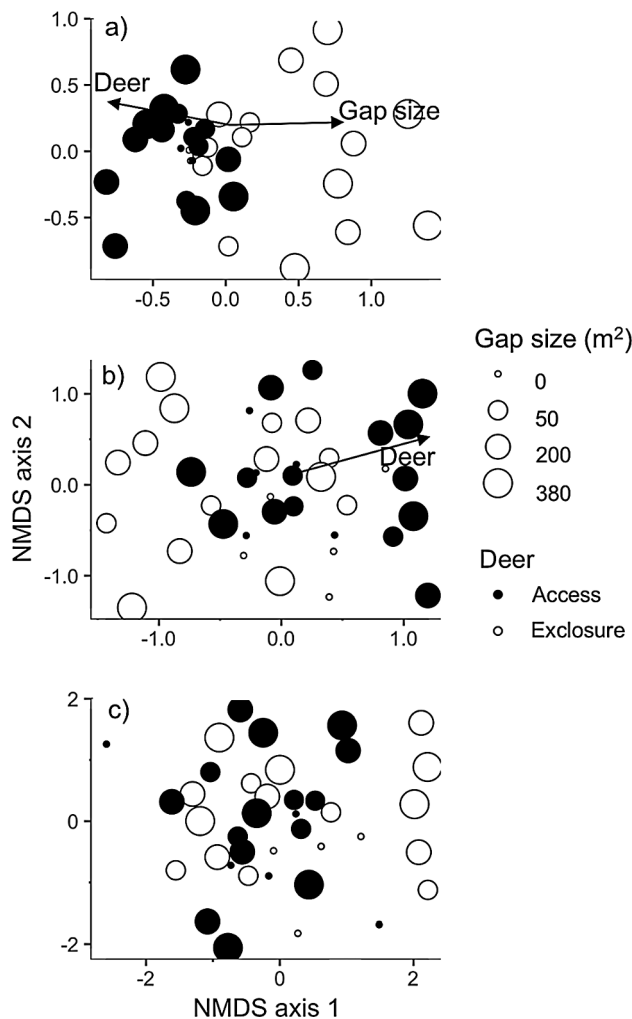


Fig. 2. NMDS of all 40 subplots for transformed change ($1/[1 + e^{C_{2013}/C_{2006} \cdot (-1)}]$) of a) BA of saplings ($0.5 \text{ cm} \leq \text{DBH} < 5 \text{ cm}$, stress = 0.16), b) percent cover of tree and arborescent shrub seedlings by height class (stress = 0.26), and c) percent cover of herbs and short-stature shrubs by height class (stress = 0.25). Vector overlays show significant environmental variables (gap size [as a continuous variable: 0, 50, 200, 380 m²] and deer [converted to a binary variable: exclusion = 0, deer access = 1] treatments, but not pre-treatment overstory basal area [BA]) that correlate with vegetation composition axes, with deer access and increasing gap size having nearly opposite effects on the sapling community.

NMDS (stress = 0.16, dimensions = 2, Fig. 2a, Table A.2) again showed that sapling composition change varied with overstory ($P < 0.05$) and deer ($P < 0.001$) treatments, but pre-treatment overstory BA did not affect sapling abundance.

Gap size had a positive effect on species richness in the sapling/arborescent shrub community (Fig. 3a, Tables A.3 and A.4), and it was amplified with deer exclusion. Three species of saplings/arborescent shrubs, *Betula alleghaniensis*, *Sambucus racemosa* and *Cornus alternifolia*, were observed in 50-m² gaps but were absent in no-harvest plots and were not found in any plot prior to treatment. In the 200-m² and 380-m² gaps, these species were joined by three others—*Prunus virginiana*, *P. pensylvanica* and *Corylus cornuta*—which, again, were absent from no-harvest plots and all plots prior to treatment.

Changes in overall sapling density (across all DBH classes) did not differ between 50-m² gaps and no-harvest plots, or between fence treatments (model $P = 0.77$). The overall number of saplings did increase in 200-m² relative to controls ($P \leq 0.05$) and 380-m² gaps ($P = 0.001$). There were more saplings in exclusion v. deer-access areas

in 380-m² gaps, but not in the no-harvest plots ($P = 0.03$ for gap \times fence interaction). Across all treatments and species, sapling density increased most in D_1 compared to D_2 and D_3 (318 v. -65 and 68 stems ha⁻¹, respectively). Therefore, most density results include only the smallest DBH class (D_1).

ANOVAs of change in D_1 sapling abundance (Tables A.3 and A.4, Fig. 4) also revealed treatment effects on individual species and/or species groups. In 200 m² gaps compared to no-harvest controls, the density of arborescent shrubs, *Ostrya virginiana*, rare tolerant trees and *Fraxinus americana* increased. In 380 m² gaps v. controls, arborescent shrubs and *Fraxinus americana* were again greater, as well as *Carya cordiformis* and *Acer saccharum*. Densities of *O. virginiana* increased more in deer access plots while *C. cordiformis* and *A. saccharum* increased more inside exclosures. Comparing the three gap sizes, the density of D_1 arborescent shrubs, *Ulmus* spp. and rare less-tolerants increased with gap size, with rare less-tolerants growing primarily inside exclosures.

3.2. Change in the tree seedling community

PERMANOVA tests indicated that the tree seedling community responded to overstory ($F_{1,39} = 4.3$, $P \leq 0.05$) and fence ($F_{1,39} = 1.6$, $P \leq 0.05$) treatments. NMDS also detected a fence treatment difference ($P \leq 0.05$, stress = 0.25, dimensions = 2, Fig. 2b, Table A.2). However, neither fence nor overstory treatment affected the distance to centroids of tree seedling change (model $F_{7,32} = 0.8$, $P = 0.6$, PERMDISP).

Gap creation increased the richness of the seedling community and the cover of several species, particularly in taller height classes (Fig. 3b, Fig. A.1, Tables A.5 and A.6). The fence treatment alone did not affect change in tree and arborescent shrub species richness or abundances, but its interactions with gap and with height were significant in several cases (Fig. 5, Tables A.5 and A.6). For instance, the cover of rare less-tolerants in the tallest height class increased more within 380-m² gaps inside fences compared to no-harvest, deer-access areas.

3.3. Change in the herb and short-stature shrub community

PERMANOVA indicated that the herb and short-stature shrub (groundlayer) community was affected by gap size ($F_{1,39} = 2.2$, $P \leq 0.01$), but not by fence or pre-treatment overstory BA. PERMDISP results for groundlayer composition change showed that overstory and fence treatments did not differ in distance to centroids. Likewise, treatments and pre-treatment BA were not significant environmental overlays for the NMDS of overall groundlayer community change (stress = 0.25, Fig. 2c, Table A.2).

Across the experiment, average richness of groundlayer species increased through time from 24.8 to 31.7 species (Fig. 3). The most pronounced effect was on richness of short-stature shrubs, which increased with gap size and, as gap size increased, especially in taller height (h) classes. For example, in h_3 , the number of species rose from none pre-treatment to an average of 1.2, 1.4, 2.2 and 2.1 species per subplot in 0, 50, 200 and 380-m² subplots, respectively, in 2013 (Table A.6). Exotic herb richness increased significantly through time in gaps, changing by an average of 0, 0.3, 0.7, and 0.8 species in 0, 50, 200 and 380-m² subplots, respectively (Fig. 3, Table A.6). Moreover, change was more pronounced in plots with higher pre-treatment overstory BA (Table A.6).

Abundance of short-stature shrubs and native and exotic forbs varied with treatments (Fig. 6, Fig. A.1, Tables A.5 and A.6). Similar to richness, positive changes in cover of short-stature shrubs and exotic forbs typically increased with gap size. Compared with no-harvest controls, native forb cover was significantly greater in 50-m² and 200-m² gaps but not 380-m² gaps. The increase was greatest in 50-m² gaps inside exclosures within h_2 (6 v. 2.1% in 50-m² gaps v. no-harvest controls), but the fence treatment was only significant as an interaction term with height.

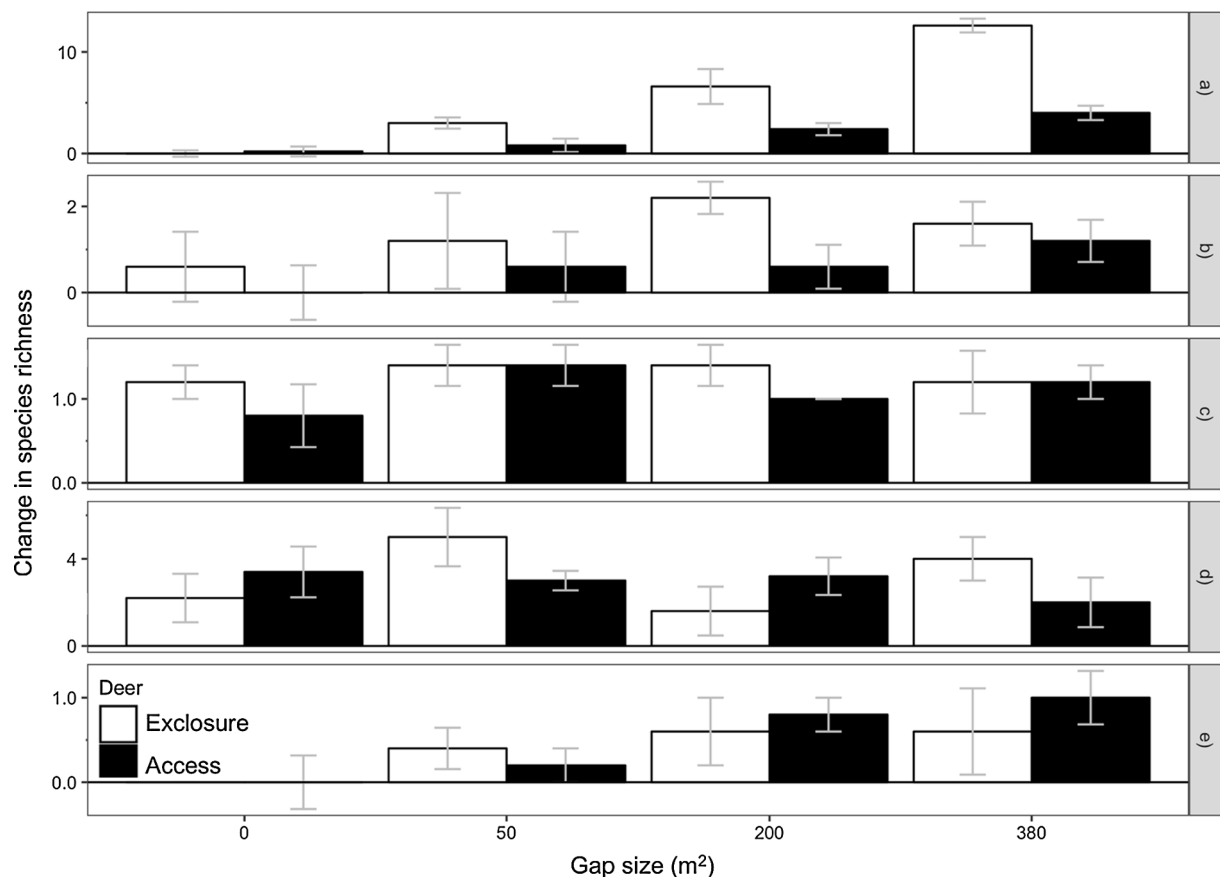


Fig. 3. Change in species richness of a) saplings, b) tree and arborescent shrub seedlings, c) short-stature shrubs, d) native forbs, and e) exotic forbs. Values are averages (with standard errors) across $n = 5$ plots, for each gap size (0–380 m²) and fence treatment (exclosure and deer access).

3.4. Change in the environment

Canopy openness at 0.3 m was greater in 50-m² gaps (Fig. A.3) than no-harvest plots, particularly inside exclosures (8.5 v. 13.4% in exclosures with no-harvest v. 50-m² gaps, respectively, interaction $P \leq 0.05$). No environmental variables differed between 200-m² gaps and no-harvest plots in either fence treatment. In 380-m² gap v. no-harvest models, canopy openness at 2 m was greater in gaps (21.2 v. 11.1%, respectively, $P \leq 0.01$, Fig. A.3). In our mixed models with plot as a random effect and fence, gap size and fence \times gap as fixed effects, canopy openness at 0.3 m was higher inside exclosures compared to deer-access areas (13.0 v. 9.5%, $P \leq 0.05$). Soil compaction, SMC and the availabilities of nitrate and ammonium did not differ across treatments ($P > 0.07$, Figs A.4 – A.6).

4. Discussion

Seven years after treatment, effects of canopy gaps and deer exclusion were evident, and the effects were most pronounced when treatments were combined. Differences among treatments were greater for saplings and tree seedlings than for groundlayer species. Our hypothesis that the abundance of a broad suite of species would increase nearly a decade after overstory disturbance in fenced areas was generally supported for woody species, but herbs showed little response.

Community-level tests all agreed that gap creation and deer exclusion brought about sapling compositional change and that they had similar, compounding effects. Our observation that deer exclusion led to greater numbers of saplings and higher tree species richness contributes to the large body of literature documenting the detrimental effects of overabundant deer on the regeneration of ecologically and economically important tree species as well as on non-timber

arborescent species that are rarely examined. In no-harvest plots, we saw little difference in sapling community dynamics between fence treatments, likely due to the dearth of regeneration opportunities in lower light environments. This study provides additional evidence that inconsistencies in the effectiveness of exclosures to increase species diversity across studies could be due to the confounding influences of variation in overstory structure (Wright et al., 2012; Sabo et al., 2017).

Several lines of evidence supported our hypothesis that deer pressure reduces community responses to gaps, similar to other reports from northern temperate forests (e.g., Holmes and Webster, 2011; Nuttle et al., 2013). Deer browsing of species such as *Carya cordiformis* can negate growth responses that gap theory (e.g., Runkle, 1981; Kneeshaw and Prévost, 2007) predicts from increased availabilities of light and soil resources. Our tests provide evidence that inconsistencies across studies in the effectiveness of gaps to increase species diversity could be because of the confounding effects of variable deer abundance (Kern et al., 2017).

Our results expand temporally on a previous study at the same site that examined growth of tagged trees four years after gap creation and deer exclusion (Forrester et al., 2014). Short-term deer effects were limited to preferential browsing on sprouts of certain species and gaps conferred no consistent advantage to less shade-tolerant species. After three additional years, we see that ingrowth into the sapling layer leads to a shift in patterns and differences among treatments, with increases of richness in gaps and fences being driven by less-tolerant species. This highlights the value of longer-term studies that allow for lag times, due to germination and growth, before regeneration reaches the sapling stage. Continued tracking of saplings at our site is necessary to uncover how many of these gap exploiters will persist through the stem exclusion phase, or be out-competed by shade-tolerant advance regeneration. Given that *Acer saccharum* increased more than any other species in no-

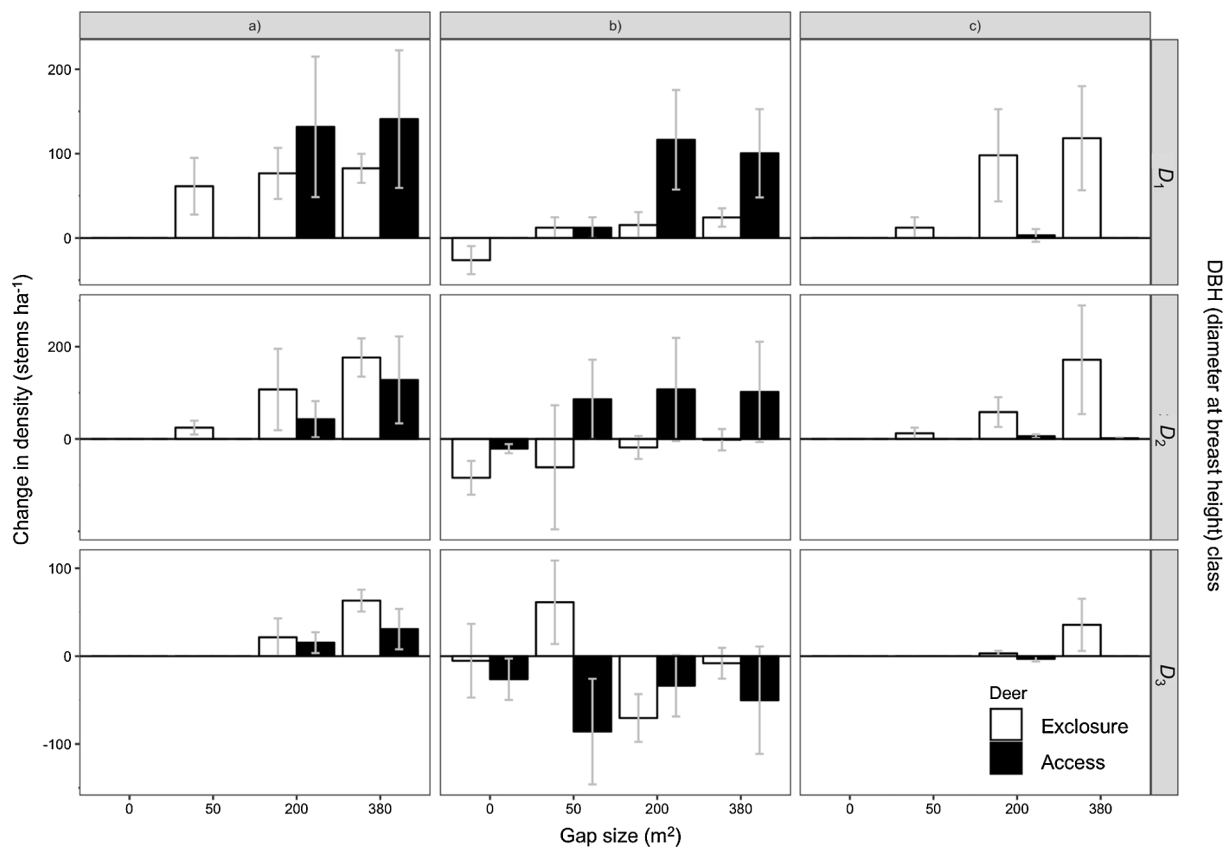


Fig. 4. Change in sapling density (stems ha⁻¹) of a) arborescent shrubs, b) *Ostrya virginiana*, and c) rare less-tolerants, averaged across plots for a given DBH class (“1” = 0.5 cm ≤ D₁ < 1.0 cm, “2” = 1.0 cm ≤ D₂ < 2.5 cm, “3” = 2.5 cm ≤ D₃ < 5.0 cm). Values are averages (with standard errors) across n = 5 plots, for each gap size (0–380 m²) and fence treatment (exclosure and deer access).

harvest plots but contributed proportionally less to compositional shifts with time as gap size increased, sizable gaps may reverse “maple-ization” (Neuendorf et al., 2007) in favor of more diverse forests.

Compared to that of saplings, change in the composition of the tree seedling community by year seven responded similarly, but less dramatically, to gap creation and deer exclusion. As we mentioned, some advance regeneration has grown out of the seedling layer into the sapling class. Shorter-stature seedlings and sprouts might have been less responsive to gap creation if competitors usurped the pulses in light availability and soil resources that may accompany canopy disturbance (Scharenbroch and Bockheim, 2007). In support, we found scant differences in environmental variables by seven years post-treatment. Regarding the lack of response to exclusion, young trees may be protected from herbivory by snow pack in the winter (Allison, 1990; Gill, 1992) or by tall understory species during the growing season (Gill, 1992). To the contrary, however, observations in white pine plantations under natural forest canopies showed reduced browse incidence as stems increased from ground-level to above 150 cm (Saunders and Puettmann, 1999).

Unlike the arborescent components, the groundlayer community showed weak responses to deer exclusion and overstory condition at seven years post-treatment. Notable exceptions include exotic forb richness, native forb cover and short stature shrub cover and height changes, all of which were generally enhanced with gap size. At one, two and three years post-treatment in the same experiment, Burton et al. (2014) also examined the response of the understory community to gap creation (but not to deer exclusion). In the short-term, they found that the richness and productivity of graminoids and shrubs increased with gap size. Differences in methods (Burton et al., 2014) preclude direct comparisons, but partial divergences between these studies provide evidence for the transience of some groundlayer

responses. This contrasts with the strong community differences that were found following gap creation in a 13-year experiment (Kern et al., 2014). In their study, however, the pre-treatment forest matrix was thinned rather than closed canopy, and researchers analyzed quadrat-level data at different locations within their gaps (similar to Burton et al., 2014) rather than considering the overall gap effect, as we did.

In agreement with our study, Kern et al. (2014) did not find community-level effects of deer exclusion on groundlayer composition after four years. It is possible that we are premature in expecting community-level summer herb responses to deer exclusion after only seven years and that the increases in native forb height inside exclosures may be an early stage of expansion of these species. Other researchers have noted slow recovery of groundlayer species following deer population reduction (e.g., Webster et al., 2005; Tanentzap et al., 2012; Habeck and Schultz, 2015), with possible explanations including legacy effects of historic conditions that limit recovery (Royo et al., 2010a, b; Nuttle et al., 2014; Thomas-Van Gundy et al., 2014; Pendergast et al., 2016). Alternatively, the lack of a pronounced response by herbs may relate to the relatively low deer density in this area. Landscape-level estimates of 8–12 deer km⁻² (Robert Rolley, personal communication) were just above the threshold suggested for maintaining forest diversity (Horsley et al., 2003; Tremblay et al., 2006).

Consistent with the groundlayer community response, we saw little effect of treatments on environmental variables measured in 2013. This was surprising, as most studies of temperate forest gaps show differences in openness, which is typically measured at a height of 1 m (e.g., Beckage et al., 2000; Royo et al., 2010a, b; Burton et al., 2014). Light availability at 0.3 m did increase temporarily at our site following gap creation (according to significant differences with treatment detected in 2009, Burton et al. unpublished data), as did light availability at 1 m, and SMC (Burton et al., 2014). By year seven, however, we no longer

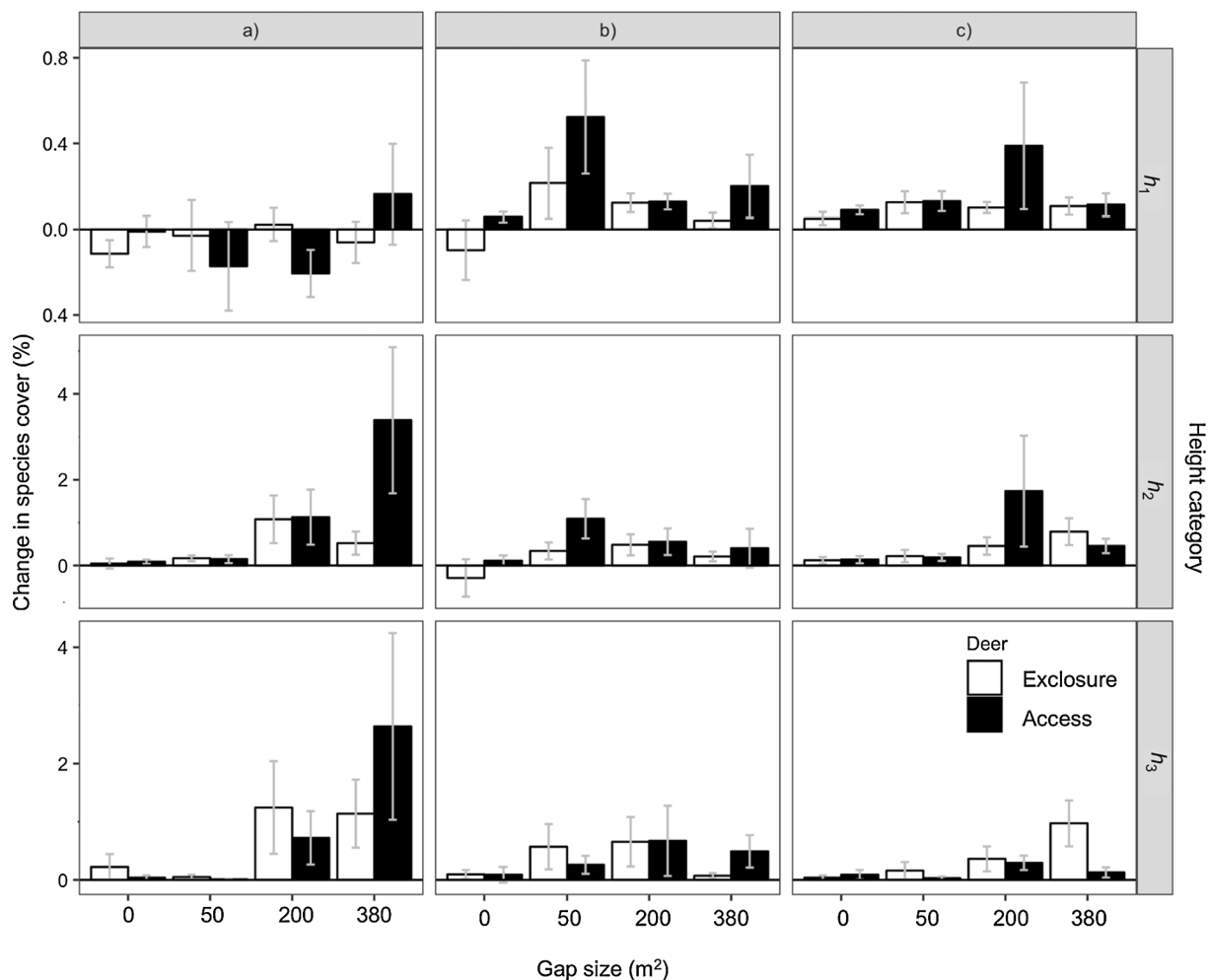


Fig. 5. Change in percent cover of tree seedlings for a) arborescent shrubs, b) *Ostrya virginiana*, and c) rare less-tolerants. Values are averages (with standard errors) across $n = 5$ plots, for each and height category ($0 < h_1 < 30$ cm, $30 \leq h_2 < 100$ cm and $100 \leq h_3 < 140$ cm), gap size (0 – 380 m²) and fence treatment (exclosure = 0, deer access = 1).

observed consistent treatment-mediated modifications of environmental conditions. Here, we show that increased vegetation density nearly negated increases in light availability at 0.3 m due to gap creation. Similar to our study, light profiles by height (0.2–5 m) and with time following selection harvest (1–13 years) in northern hardwood forests of Quebec demonstrated a pulse in light availability until approximately 7 years post-harvest (Beaudet et al., 2004). Low levels of light reaching the forest floor by seven years post-treatment likely reduced opportunities for germination and survival of sun-loving species in response to overstory disturbance at our site, similar to seedling responses under dense shrub cover in the southern Appalachians (Beckage et al., 2000).

In addition to fleeting environmental differences resulting from our treatments, conditions prior to the experiment, or disturbance legacies (Johnstone et al., 2016), may also have affected our outcomes. Pre-treatment overstory BA tempered the manner in which gap creation influenced understory species. Negative relationships with pre-treatment BA were synergistic with gap creation, providing open conditions for longer time periods to encourage short-stature shrub, *Carya cordiformis* and *Fraxinus americana* abundance. Positive correlations with pre-treatment BA, in conjunction with positive gap effects, may indicate that more dramatic shifts in the overstory environment led to greater change in sapling and exotic forb richness, as well *Ostrya virginiana* cover. The spatial distributions of pre-treatment overstory trees, and subsequent coarse woody debris following gap creation, likely influenced microsite environments that drove composition (similar to Bače

et al., 2015). Future researchers may want to consider finer-scale changes in the understory community against detailed pre- and post-treatment environmental maps. Such studies may serve as a bridge between highly controlled experiments conducted in artificial environments and projects, like ours, that attempt to closely mimic natural and management-scale processes.

5. Conclusions and management implications

While most studies focus on tree regeneration or understory species alone, our more holistic view of the forest plant community allowed us to demonstrate how different components respond to the same drivers. Prior to treatment, some less tolerant saplings (e.g., *Carya cordiformis* and *Fraxinus americana*) were likely already well-established seedlings that were able to quickly capitalize on gap creation and lack of deer herbivory. Tree seedlings measured seven years post-treatment could have been very small or even nonexistent at the time of gap creation. Shorter-stature trees, shrubs and herbs that showed strong responses to canopy gaps initially (Burton et al., 2014) may be less responsive at year seven due to denser sapling layers intercepting gap-mediated resource additions. By continuing to follow these plots, we have the opportunity to learn if the herb community is merely slow at responding to deer exclusion, if additional disturbances are necessary for persistent responses to gap creation, or if these treatments are most effective for shifting tree communities.

Overall, our results do suggest that gap dynamics help to reverse

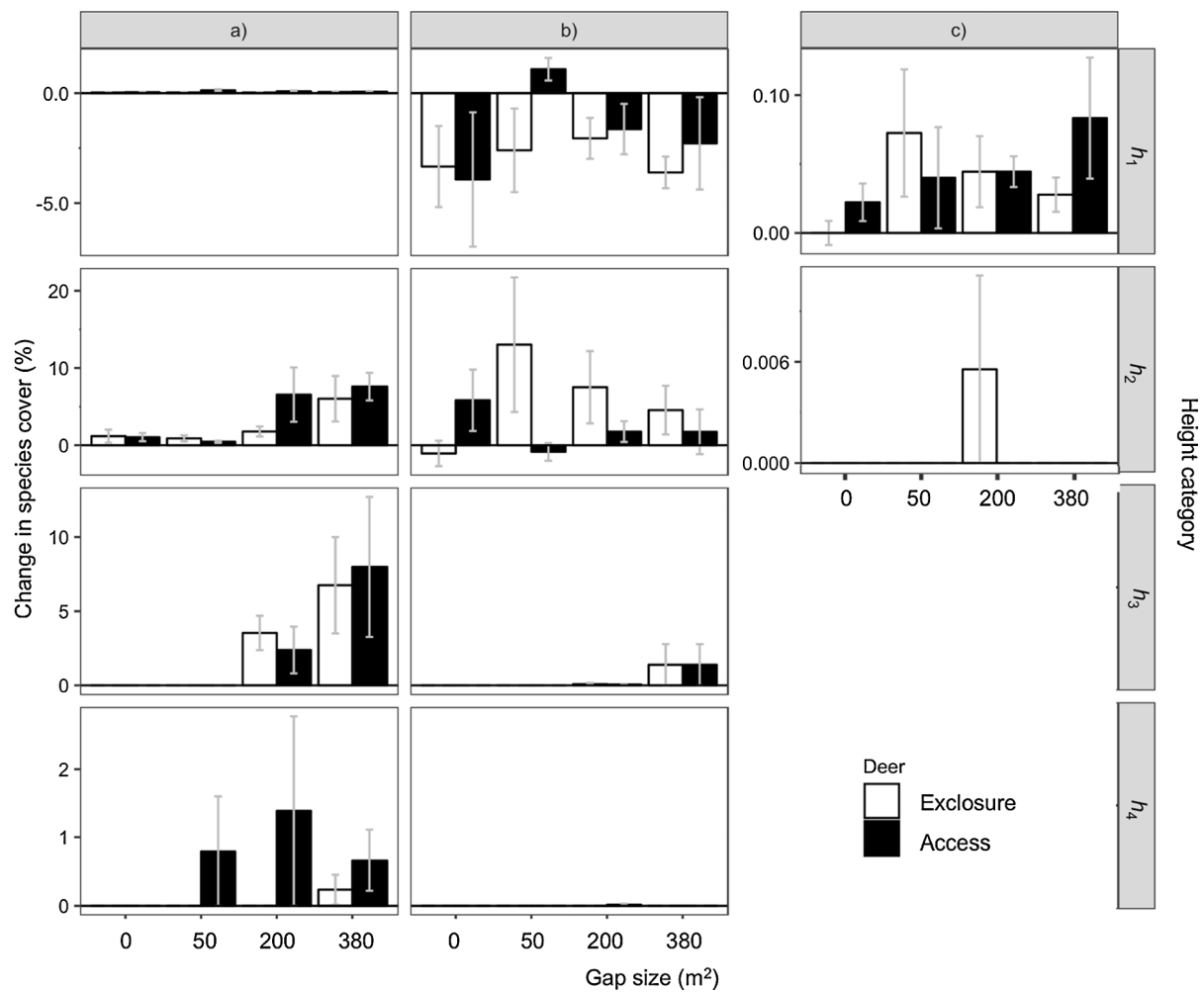


Fig. 6. Change in percent cover of a) short-stature shrubs, b) native forbs, and c) exotic forbs. Values are averages (with standard errors) across $n = 5$ plots, for each height category ($0 < h_1 < 30$ cm, $30 \leq h_2 < 100$ cm, $100 \leq h_3 < 140$ cm, and $h_4 > 140$ cm), gap size (0 – 380 m²) and fence treatment (exclosure and deer access). Panels are absent when there were no data for a specific group and height combination.

biotic homogenization by allowing less-tolerant species to regenerate (Yamamoto, 2000). Single-tree selection, which is commonly practiced in northern hardwood forests, yields canopy openings similar to our experiment's smallest gap size, 50 m². Small gaps encouraged the establishment and growth of only a few more species relative to unharvested plots, indicating low utility for increasing diversity. By adjusting management regimes towards small-group selection (similar to our 380 m² gaps), foresters may disadvantage shade-tolerant species such as *Ostrya virginiana* and *Acer saccharum*, and encourage less-tolerant trees and shrubs. Further diversifying vertical and horizontal forest structure to better simulate the range of characteristics in natural gaps (e.g., creating tip-up mounds or additional retention of coarse woody debris and snags) could further enhance community heterogeneity (Yamamoto, 2000; Kern et al., 2017). Exotic forbs also benefited from gap creation in our study, however. This finding serves as a reminder to be vigilant about monitoring for problematic invaders before and after logging operations.

The long-term success of diversifying the overstory is difficult to extrapolate from sapling data. Regional modeling efforts, however, indicate that controlling tall individuals of less-desirable species could influence gap capture (Cole and Lorimer, 2005; Webster and Lorimer, 2005; Hanson et al., 2011). Canopy recruitment may prove fickle due to climate (e.g., Poznanovic et al., 2013), pests including emerald ash borer (e.g., Kashian and Witter, 2011) and the complex contributing to hickory decline (Juzwik et al., 2008), or other site conditions (Kern

et al., 2013, 2017). Competitive exclusion of tree seedlings by shrubs is a management concern in some areas (e.g., Royo and Carson, 2006; Kern et al., 2012, 2013) but we found increases in the richness and cover of both groups with gap size (similar to Falk et al., 2010). While operationally challenging, treatments that include a diversity of gap sizes may be optimal for promoting species diversity in the short-term, until more widespread studies can better account for confounding site variables that result in different responses to canopy openings.

To further improve the likelihood of forest communities benefiting from gap creation, managers need to consider deer herbivory. The potential for diminishing non-preferred browse species such as *O. virginiana*, increasing overall sapling richness, BA and density, or conserving species of special concern may be worth the investment in stand-level deer management. Dramatically increasing the size of gaps for patch cut treatments may stimulate a protective shrub layer to foster palatable, shade-intolerant species (Walters et al., 2016), although this method needs considerable testing at a broad range of sites prior to widespread use. There are several examples of private and public organizations partnering to balance white-tailed deer herd populations despite frequently competing interests by hunters and land managers (e.g., deer management assistance programs run by natural resource agencies in several states including Arkansas, Kentucky, Louisiana, Mississippi, Pennsylvania and Virginia, and a deer cooperative with a broad group of stakeholders [Stout et al. 2013]). Where such options are not yet viable, foresters may opt to install commercial scale

enclosures to achieve similar results (e.g., Pennsylvania Bureau of Forestry, 2013). As additional collaborations form, we have the potential to discover unexpected management opportunities to address multiple drivers of forest homogenization simultaneously at operational scales in order to restore ecosystem functions.

Acknowledgements

Site access was granted by the Flambeau River State Forest. Funding was provided by USDA CSREES National Research Initiative (Grant No. 2006-55101-17060), the McIntire-Stennis Program, Pittman-Robertson Funds, and Wisconsin DNR Division of Forestry and WI DNR Bureau of Integrated Science Services. Tera Lewandowski provided the soil nutrient data. Many field assistants and students contributed to data collection including, in 2013, Rachel Kueler, Paige Ruppel, Emily Lannoye, Holly Henriksen, Jay Osvatic and Donnie Radcliffe.

Authors' Contributions

AS and PJ collected 2013 data. JB collected 2006 data. AS and EK analyzed data and wrote manuscript. JF and DM designed and managed the experiment. All authors provided substantial edits to the manuscript and gave final approval for publication.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.11.004>.

References

- Allison, T.D., 1990. The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). I. Direct effect on pollen, ovule, and seed production. *Oecologia* 83, 523–529.
- Anderson, M.J., 2004. PERMDISP: a FORTRAN Computer Program for Permutational Analysis of Multivariate Dispersions (for any two-factor ANOVA design) Using Permutation Tests. University of Auckland, New Zealand, Department of Statistics.
- Anderson, R.C., 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecol. Appl.* 4, 104–109.
- Anderson, R.C., Loucks, O.L., 1979. White-tailed deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *J. Appl. Ecol.* 16, 855–861.
- Bačre, R., Svoboda, M., Janda, P., Morrissey, R.C., Wild, J., Clear, J.L., Čada, V., Donato, D.C., 2015. Legacy of pre-disturbance spatial pattern determines early structural diversity following severe disturbance in montane spruce forests. *PLoS ONE* 10, e0139214.
- Balgooyan, C.P., Waller, D.M., 1995. The use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin, USA. *Nat. Areas J.* 15, 308–318.
- Beaudet, M., Messier, C., Leduc, A., 2004. Understorey light profiles in temperate deciduous forests: recovery process following selection cutting. *J. Ecol.* 92, 328–338.
- Beckage, B., Clark, J.S., Clinton, B.D., Haines, B.L., 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understoreys. *Can. J. For. Res.* 30, 1617–1631.
- Burton, J.I., Mladenoff, D.J., Forrester, J.A., Clayton, M.K., 2014. Experimentally linking disturbance, resources and productivity to diversity in forest ground-layer plant communities. *J. Ecol.* 201, 1634–1648.
- Cole, W.G., Lorimer, C.G., 2005. Probabilities of small-gap capture by sugar maple saplings based on height and crown growth data from felled trees. *Can. J. For. Res.* 35, 643–655.
- Collins, B.S., Dunne, K.P., Pickett, S.T.A., 1985. Responses of forest herbs to canopy gaps. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press Inc, Orlando, FL, pp. 218–234.
- Dyer, J.H., Gower, S.T., Forrester, J.A., Lorimer, C.G., Mladenoff, D.J., Burton, J.I., 2010. Effects of selective tree harvests on aboveground biomass and net primary productivity of a second-growth northern hardwood forest. *Can. J. For. Res.* 40, 2360–2369.
- Falk, K.J., Elliot, K.A., Burke, D.M., Nol, E., 2010. Early seedling response to group selection harvesting in a northern hardwood forest. *Forest Chron.* 86, 100–109.
- Fletcher, J.D., McShea, W.J., Shipley, L.A., Shumway, D., 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Nat. Areas J.* 21, 172–176.
- Forrester, J.A., Lorimer, C.G., Dyer, J.H., Gower, S.T., Mladenoff, D.J., 2014. Response of tree regeneration to experimental gap creation and deer herbivory in north temperate forests. *For. Ecol. Manage.* 329, 137–147.
- Frerker, K., Sabo, A., Waller, D., 2014. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. *PLoS ONE* 9, e115843.
- Gasser, D., Messier, C., Beaudet, M., Lechowicz, M.J., 2010. Sugar maple and yellow birch regeneration in response to canopy opening, liming and vegetation control in a temperate deciduous forest of Quebec. *For. Ecol. Manage.* 259, 2006–2014.
- Gauch Jr., H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, UK.
- Gill, R.M.A., 1992. A review of damage by mammals in north temperate forests: 1. Deer. *Forestry* 65, 145–169.
- Goetsch, C., Wigg, J., Royo, A.A., Ristau, T., Carson, W.P., 2011. Chronic over browsing and biodiversity collapse in a forest understorey in Pennsylvania: results from a 60-year-old deer exclusion plot. *J. Torrey Bot. Soc.* 138, 220–224.
- Goodburn, J.M., 1996. Comparison of forest habitat structure and composition in old-growth and managed northern hardwoods in Wisconsin and Michigan. MS thesis. University of Wisconsin-Madison.
- Habeck, C.W., Schultz, A.K., 2015. Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. *AoB Plants* 7. <https://doi.org/10.1093/aobpla/plv119>.
- Hanson, J.J., Lorimer, C.G., Halpin, C.R., 2011. Predicting long-term sapling dynamics and canopy recruitment in northern hardwood forests. *Can. J. Forest.* 41, 903–919.
- Holmes, S.A., Webster, C.R., 2011. Herbivore-induced expansion of generalist species as a driver of homogenization in post-disturbance plant communities. *Plant Ecol.* 212, 753–768.
- Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13, 98–118.
- Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L.W., Schoennagel, T., Turner, M.G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14, 369–378.
- Juzwik, J., Haugen, L., Park, J.-H., Moore, M., 2008. Fungi associated with stem cankers and coincidental scolytid beetles on declining hickory in the upper midwest. In: Jacobs, Douglass, F., Michler, Charles H. (Eds.), *Proceedings, 16th Central Hardwood Forest Conference*, 2008 April 8–9; West Lafayette, IN. Gen. Tech. Rep. NRS-P-24, pp. 476–482.
- Kain, M., Battaglia, L., Royo, A., Carson, W.P., 2011. Over-browsing in Pennsylvania creates a depauperate forest dominated by an understorey tree: results from a 60-year-old deer enclosure. *J. Torrey Bot. Soc.* 138, 322–326.
- Kashian, D.M., Witter, J.A., 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on south-eastern Michigan landscapes. *For. Ecol. Manage.* 261, 480–488.
- Kern, C.C., Amato, A.W., Strong, T.F., 2013. Diversifying the composition and structure of managed, late-successional forests with harvest gaps: what is the optimal gap size? *For. Ecol. Manage.* 304, 110–120.
- Kern, C.C., Burton, J.I., Raymond, P., D'Amato, A.W., Keeton, W.S., Royo, A.A., Walters, M.B., Webster, C.R., Willis, J.L., 2017. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry* 90, 4–17.
- Kern, C.C., Montgomery, R.A., Reich, P.B., Strong, T.F., 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. *Forest Sci.* 60, 335–344.
- Kern, C.C., Reich, P.B., Montgomery, R.A., Strong, T.F., 2012. Do deer and shrubs over-ride canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? *For. Ecol. Manage.* 267, 134–143.
- Kneeshaw, D.D., Prévost, M., 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. *Can. J. For. Res.* 37, 1534–1544.
- Kobe, R.K., Pacala, S.W., Silander Jr, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5, 517–532.
- McClure, J.W., Lee, T.D., 1993. Small-scale disturbance in a northern hardwoods forest: effects on tree species abundance and distribution. *Can. J. For. Res.* 23, 1347–1360.
- McKinney, K.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453.
- Miller, S.G., Bratton, S.P., Hadidian, J., 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. *Nat. Areas J.* 12, 67–74.
- Moore, M.R., Vankat, J.L., 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. *Am. Midl. Nat.* 115, 336–347.
- Neuendorf, J.K., Nagel, L.M., Webster, C.R., Janowiak, M.K., 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. *North. J. Appl. For.* 24, 197–202.
- Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience* 58, 123–138.
- Nuttall, T., Ristau, T.E., Royo, A.A., 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. *J. Ecol.* 102, 221–228.
- Nuttall, T., Royo, A.A., Adams, M.B., Carson, W.P., 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecol. Monogr.* 83, 3–17.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. *vegan: Community Ecology Package*. R package version 2.0-7.
- Pendergast, T.H., Hanlon, S.M., Long, Z.M., Royo, A., Carson, W.P., 2016. The legacy of deer overabundance: long-term delays in herbaceous understorey recovery. *Can. J. For. Res.* 46, 362–369.
- Pennsylvania Bureau of Forestry, 2013. White-tailed deer plan 2013–2018. http://www.docs.dcnr.pa.gov/cs/groups/public/documents/document/dcnr_20027101.pdf.
- Poznanovic, S.K., Webster, C.R., Bump, J.K., 2013. Maintaining mid-tolerant tree species

- with uneven-aged forest management: 9-year results from a novel group-selection experiment. *Forestry* 86, 555–567.
- Raymond, P., Munson, A.D., Ruel, J.-C., Coates, K.D., 2006. Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood white pine stands. *Can. J. For. Res.* 36, 639–651.
- Rogers, D.A., Rooney, T.P., Hawbaker, T.J., Radeloff, V.C., Waller, D.M., 2009. Paying the extinction debt in southern Wisconsin forest understories. *Conserv. Biol.* 23, 1497–1506.
- Rooney, T.P., 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74, 201–208.
- Rooney, T.P., 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecol.* 202, 102–111.
- Rooney, T.P., Solheim, S.L., Waller, D.M., 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. *For. Ecol. Manage.* 163, 119–130.
- Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* 36, 1345–1362.
- Royo, A.A., Collins, R., Adams, M.B., Kirschbaum, C., Carson, W.P., 2010a. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91, 93–105.
- Royo, A.A., Stout, S.L., deCalesta, D.S., Pierson, T.G., 2010b. Restoring forest herb communities through landscape-level deer herd reductions: is recovery limited by legacy effects? *Biol. Conserv.* 143, 2425–2434.
- Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62, 1041–1051.
- Sabo, A.E., Freker, K.L., Waller, D.M., Kruger, E.L., 2017. Deer-mediated changes in environment compound the direct impacts of herbivory on understory plant communities. *J. Ecol.* 105, 1386–1398.
- Saunders, M.R., Puettmann, K.J., 1999. Effects of overstory and understory competition and simulated herbivory on growth and survival of white pine seedlings. *Can. J. For. Res.* 29, 536–546.
- Scharenbroch, B.C., Bockheim, J.G., 2007. Impacts of forest gaps on soil properties and process in old growth northern hardwood-hemlock forests. *Plant Soil* 294, 219–233.
- Schatz, J.D., Forrester, J.A., Mladenoff, D.J., 2012. Spatial patterns of soil surface C flux in experimental canopy gaps. *Ecosystems* 15, 616–623.
- Scheller, R.M., Mladenoff, D.J., 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecol. Appl.* 12, 1329–1343.
- Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern U.S. Great Lakes forests due to land use. *Landscape Ecol.* 22, 1089–1103.
- Schumacher, H.B., Carson, W.P., 2013. Biotic homogenization of the sapling layer in 19 late-successional and old-growth forest stands in Pennsylvania. *J. Torrey Bot. Soc.* 140, 313–328.
- Seymour, R.S., White, A.S., deMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America – evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manage.* 155, 357–367.
- Shotola, S.J., Weaver, G.T., Robertson, P.A., Ashby, W.C., 1992. Sugar maple invasion of an old-growth oak-hickory forest in southwestern Illinois. *Am. Midl. Nat.* 127, 125–138.
- Smith, K.J., Keeton, W.S., Twery, M.J., Tobi, D.R., 2008. Understory plant responses to uneven-aged forestry alternatives in northern hardwood–conifer forests. *Can. J. For. Res.* 38, 1303–1318.
- Stearns, F., Likens, G.E., 2002. One hundred years of recovery of a pine forest in northern Wisconsin. *Am. Midl. Nat.* 148, 2–19.
- Stout, S.L., Royo, A.A., deCalesta, D.S., McAleese, K., Finley, J.C., 2013. The Kinzua Quality Deer Cooperative: can adaptive management and local stakeholder engagement sustain reduced impact of ungulate browsers in forest systems? *Boreal Environ. Res.* 18, 50–64.
- Tanentzap, A.J., Kirby, K.J., Goldberg, E., 2012. Slow responses of ecosystems to reductions in deer (Cervidae) populations and strategies for achieving recovery. *For. Ecol. Manage.* 264, 159–166.
- Thomas-Van Gundy, M., Rentch, J., Adams, M.B., Carson, W., 2014. Reversing legacy effects in the understory of an oak-dominated forest. *Can. J. For. Res.* 44, 350–364.
- Tremblay, J.P., Huot, J., Potvin, F., 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. *Oecologia* 150, 78–88.
- Van Deelen, T.R., Pregitzer, K.S., Haufler, J.B., 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. *Am. Midl. Nat.* 135, 181–194.
- Waller, D.M., Alverson, W.S., 1997. The white-tailed deer: a keystone herbivore. *Wildl. Soc. Bull.* 25, 217–226.
- Walters, M.B., Farinosi, E.J., Willis, J.L., Gottschalk, K.W., 2016. Managing for diversity: harvest gap size drives complex light, vegetation, and deer herbivory impacts on tree seedlings. *Ecosphere* 7, e01397. <https://doi.org/10.1002/ecs2.1397>.
- Webster, C.R., Jenkins, M.A., Rock, J.H., 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biol. Conserv.* 125, 297–307.
- Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of less-tolerant tree species: a retrospective approach. *Ecol. Appl.* 15, 1245–1262.
- Wiegmann, S.M., Waller, D.M., 2006. Fifty years of change in northern upland forest understories: Identity and traits of “winner” and “loser” plant species. *Biol. Conserv.* 129, 109–123.
- Wright, D.M., Tanentzap, A.J., Flores, O., Husheer, S.W., Duncan, R.P., Wiser, S.K., Coomes, D.A., 2012. Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. *Biol. Conserv.* 153, 64–71.
- Yamamoto, S.-I., 2000. Forest gap dynamics and tree regeneration. *J. Forest Res.* 5, 223–229.