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Persistent, transient, and emergent influences of deer herbivory on canopy gap ground layers, 18 years postdisturbance¹

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Abstract. Through their foraging and habitat selection, white-tailed deer (*Odocoileus virginianus*) can have profound effects on forest plant communities that produce persistent legacy effects. To examine the duration of persistence of potential legacy effects, we investigated the long-term consequences of deer herbivory in plant communities following canopy gap creation in a hemlock–northern hardwood forest in the Upper Peninsula of Michigan. Twenty artificial canopy gaps were created during the winter of 2002–03: seven small gaps (50–150 m²), seven medium gaps (151–250 m²), and six large gaps (251–450 m²). Herbaceous layer communities were sampled within arrays of exclosed and nonexclosed sample plots, established within a few years of gap creation, during the summer of 2020 and compared to a previous study conducted in 2007. Eighteen years following canopy gap creation, herbaceous layer communities exhibited both persistent and transient legacies of deer herbivory. Persistent legacies included similarity of small to large gaps compositionally and low abundance of browse-sensitive species outside of exclosures. Transient patterns included initial high graminoid cover and low cover of trees in the ground layer outside of exclosures and differences in diversity between gap size classes. Some emergent patterns were also observed, including declining floristic quality indices over time but sustained high occurrence of a number of species with moderately high coefficients of conservatism on deer access plots, albeit at low abundance. Differential compositional trajectories emerged based on gap-specific tree species colonization patterns. Our results suggest that through differential foraging patch selection and control of woody regeneration, white-tailed deer may alter or reinforce patterns of dominance depending on initial conditions. These interactions may result in context-specific persistent, transient, and emergent dynamics as plant communities recover from canopy disturbance.

Key words: deer exclosures, floristic quality, hemlock–northern hardwood forests, herbaceous layer, white-tailed deer

The white-tailed deer (*Odocoileus virginianus*) has been described as a keystone herbivore (Waller and Alverson 1997) because of its ability to alter plant communities and trophic interactions (Nuttall *et al.* 2011, Bressette *et al.* 2012, Reed *et al.* 2022). Overabundant deer populations have been associated with regeneration failure of browse-sensitive woody plants (Trumbull *et al.* 1989, Horsely *et al.* 2003), declines in forest herbs and homogenization of forest ground-layer vegetation (Rooney *et al.* 2004, Rooney 2009, Frerker *et al.* 2014, Knauer *et al.* 2023), invasions by exotic species (Gorchov *et al.* 2021), and altered nutrient cycles (Lucas *et al.* 2013, Murray *et al.* 2013). Nevertheless, contex-

tualizing overabundance in forest ecosystems that coevolved with white-tailed deer can be challenging given shifting baselines, changing climatic conditions, seasonal shifts in habitat use, and the influence of landscape and stand structure on habitat use and foraging behavior (Hurley *et al.* 2012).

The patterning of natural and/or anthropogenic disturbances, such as canopy gaps, which increase local forage availability, can have a strong influence on the selection of foraging and bedding sites (Stewart *et al.* 2000, Cromsigt and Kuijper 2011, Tahtinen *et al.* 2014). Habitat selection and seasonality of use can have important implications for ungulate impacts across a range of spatial scales relevant for forest plant communities (Jensen *et al.* 2011). For example, Jensen *et al.* (2011) found that concentrated winter habitat use, if not accompanied by summer use, increased cover and heterogeneity of the herbaceous layer. Also, some recent studies have found that where deer are completely excluded the herbaceous layer may experience declines in smaller-statured herbs and species diversity in response to competitive exclusion by woody plants (Royo *et al.* 2010, Cook-Patton *et al.* 2014, Webster *et al.* 2017). When deer are present, the reduction of the woody

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plant community may benefit herbs at least initially as a result of reduced apparent competition (Cook-Patton *et al.* 2014, Webster *et al.* 2017).

Canopy gaps provide high-resource environments in forested landscapes by increasing light levels, decomposition rates, and moisture availability (Gálhidy *et al.* 2006, Forrester *et al.* 2012). Gap size influences niche partitioning and diversity in forest understories (Kern *et al.* 2013, Bolton and D'Amato 2019, Burton *et al.* 2021). Concentrated foraging within high-resource gap environments can dramatically alter plant community development following disturbance (Cromsigt and Kuijper 2011). As reviewed by Tahtinen *et al.* (2014), the forage maturation hypothesis (see also Stewart *et al.* 2000) would predict that deer should forage disproportionately in small to intermediate-sized gaps where forage is abundant, but low in C:N ratios and secondary plant metabolites.

We investigated herbaceous layer response 18 yr post-gap creation across a range of opening sizes with and without deer exclusion in a hemlock–northern hardwood forest. Experimental gaps were installed during the winter of 2002–03 and exclosures were constructed in 2005. Previous reports on this experiment have shown homogenization of ground-layer plant communities outside of exclosures (Holmes and Webster 2011), altered nitrogen dynamics due to high winter deer use (Tahtinen *et al.* 2014), and shifts in the sapling layer towards browse-tolerant species and confinement of large specimens of browse-sensitive trees to exclosures (VanderMolen and Webster 2021). Herein, we specifically wanted to investigate the persistence of earlier conditions and trends in plant community development following disturbance both in the presence and absence of deer herbivory. We hypothesized that graminoids and shrubs would persist in large gaps but decline in smaller gaps as a result of shading due to lateral crown expansion by gap border trees. Given the sparse nature of regeneration outside of exclosures in some gaps, we hypothesized that we would find differential performance of herbs of various statures inside and outside of exclosures, with small herbs persisting outside of fences and tall palatable herbs more prevalent within. Nevertheless, given the slow recovery of herb layers from herbivory in other studies, we anticipated that general differences in species diversity would persist.

Methods. STUDY SITE. Our study was conducted in a hemlock-hardwood artificial canopy gap study located at the Michigan Technological University Ford Center and Forest (46°37'N, 88°29'W) near Alberta, MI. Geographically situated in the western Upper Peninsula of Michigan, average temperatures range from 17.7 °C in summer to −9.2 °C in winter. Average annual precipitation is 84 cm with a large portion (363 cm) that falls annually as snow in winter months (Arguez *et al.* 2010). Soils in gaps are primarily moderately well-drained cobbly silt loams with a few areas of poorly drained mucky silt loams (Soil Survey Staff 2007). Deer densities are estimated to range from 6.5 deer km^{−2} in the spring to 9.3 deer km^{−2} in the fall (Mayhew 2003).

Artificial canopy gaps were created in the winter months of 2002–03. Canopy and midstory trees were removed from eastern hemlock (*Tsuga canadensis* (L.) Carrière) stands to create 20 canopy gaps: seven small gaps (50–150 m²), seven medium gaps (151–250 m²), and six large gaps (251–450 m²). Gaps were located to favor hemlock and most of the trees removed were hardwoods. A few months after gaps were created (spring of 2003), hardwood advance regeneration (> 1 m tall) and logging slash were removed from gaps to promote regeneration of eastern hemlock. Permanent vegetation sampling 1-m-radius subplots were also established in 2003, 4–12 per gap (depending on gap size) at random distances and azimuths from gap centers. Two years after gap creation (early spring of 2005), one to three randomly selected subplots per gap (depending on gap size) were established as a deer exclusion treatment. Fenced exclosures encircled the 1-m-radius subplots with 15 × 15-cm mesh to a height of 1.52 m.

FIELD DATA COLLECTION. During the summer of 2020 (18 yr after gap creation), we sampled vegetation in all 20 canopy gaps. In each exclosure subplot ($n = 46$) and control subplot ($n = 93$), percentage of cover of each woody and herbaceous species was visually estimated using eight cover classes (0–1%, 2–5%, 6–10%, 11–25%, 26–50%, 51–75%, 76–95%, 96–100%). Our sampling followed the protocol used in 2007 by Holmes and Webster (2011). Nomenclature follows the United States Department of Agriculture Natural Resources Conservation Service PLANTS database (USDA NRCS, 2022), and authorities and common names are provided for all species in Table 1. One exclosure plot collapsed under the

weight of a fallen tree and was removed from sampling. Many plots contained dense regeneration over 2 m tall (see VanderMolen and Webster, 2021); therefore, cover values were recorded for all vegetation at or below 2 m in height and summarized by species. In addition, control and exclosure subplots were averaged to yield one exclosure and control plot per gap.

ANALYTICAL METHODS. To evaluate species composition and compare results to values reported in Holmes and Webster (2011), we generated species richness and Shannon's diversity index rarefaction curves with EcoSim software (Gotelli and Entsminger 2001). As our sampling design contains treatments with differing levels of sampling effort, rarefaction extrapolates richness and diversity values for each treatment along a gradient of sampling intensity, which enables a more standardized comparison (Gotelli and Colwell 2001).

To analyze patterns in floristic quality over time, we calculated the Floristic Quality Index (FQI) for each plot in sampling years 2007 and 2020. The FQI assesses the fidelity of a site to that of a remnant natural community by assigning a coefficient of conservatism (C) to each species then multiplying the mean C of all observed species by the square root of the total observed species (Herman *et al.* 2001):

$$FQI = C\sqrt{n}.$$

We assigned C values according to Herman *et al.* (2001) for Michigan, which range from 0 to 10: a species with a C of 0 could be found in nearly any community type (*i.e.*, *Equisetum arvense* L., or any exotic species), whereas a species with a C of 10 would only be found in presettlement remnant communities (*i.e.*, *Panax quinquefolius* L.). Since we examine abundance by C group elsewhere, we did not adjust FQI by abundance (DeBerry and Perry 2015). To evaluate differences in FQI between treatments and years, we used an analysis of variance (ANOVA) with an alpha level 0.05 in the *STATS* core package of R version 4.1.2 (R Core Team 2021).

To visualize relationships in community composition among treatments, we used a nonmetric multidimensional scaling (NMS) ordination generated in PCORD version 6.22 (McCune and Mefford 2016). In the primary matrix, cover values for a total of 98 observed species were recorded for each of the 40 plots in our study. Environmental

variables included exclosure and gap-size treatments as well as cover values summarized by taxonomic groups and binned C value groups (see Table 1). The ordination was run in autopilot mode with the Sørensen (Bray-Curtis) distance measure for 250 runs of real data and 250 runs of randomized data. Monte Carlo tests were used to determine data dimensionality. Pearson and Kendall correlations were used to examine the relationship of grouped cover values to ordination axes. To compare how similar control and exclosure plots were within a given gap, we calculated mean Euclidian distance between paired plots.

To examine potential compositional differences between groups (gap size and exclosure treatments), we conducted pairwise comparisons with a permutational multivariate analysis of variance (PERMANOVA) and two-way agglomerative cluster analysis (McCune and Grace 2002). For PERMANOVA, we used the "adonis2" function in the "vegan" package (Oksanen *et al.* 2022) in R 4.1.2 (R Core Team 2021) with 999 permutations and a term for treatment interaction. A separate comparison was performed with the "pairwise-Adonis" package (Arbizu 2017) to compare within-treatment gap size pairs using the Bonferroni method to determine significant differences. The PERMANOVA and two-way cluster analysis were conducted with Sørensen (Bray-Curtis) as the distance measure and species data relativized by column (species) maximum (McCune and Mefford 2016). A flexible beta was used for the cluster analysis and results are shown as a dendrogram scaled by distance between groups (McCune and Grace 2002). The cluster analysis was performed in PCORD version 6.22 (McCune and Mefford 2016).

Results. DIVERSITY AND FLORISTIC QUALITY. Rarefaction curves for both Shannon's diversity index (H') and species richness (S) indicated that exclosures and controls accumulated species at a similar rate with increasing sampling effort (Fig. 1). At comparable levels of sampling, these metrics were similar for both treatments. In terms of gap size, medium-sized gaps tended to be more diverse (particularly H') than smaller and larger gaps across deer exclusion treatments (Fig. 1). No clear pattern with opening size was observed for S other than a slight tendency for large gap control plots to accumulate more species. Comparing our results to

Table 1. Mean percentage of herbaceous cover of species in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. Cover values were summarized by coefficient of conservatism (C), gap size, and exclosure treatments. C ranges from 0 to 10 and indicates an estimation of how likely a species would occur at a site relatively unchanged from pre-European settlement conditions (i.e., *Panax quinquefolius* L., American ginseng, is assigned a C of 10, and *Equisetum arvense* L., field horsetail, or any exotic species, is assigned a C of 0).

| USDA code | Latin name | Common name | Taxonomic Group | Small gaps | | Medium gaps | | Large gaps | |
|-----------|--|------------------------|--------------------------------------|------------|-----------|-------------|-----------|------------|-----------|
| | | | | Control | Exclosure | Control | Exclosure | Control | Exclosure |
| C = 0 | | | | | | | | | |
| CIPA6 | <i>Cirsium palustre</i> (L.) Scop. | Marsh thistle | Exotic | 0.25 | 0 | 0 | 0 | 0.12 | 0 |
| DIAC2 | <i>Dichanthelium acuminatum</i> (Sw.) Gould & C.A. Clark | Tapered rosette grass | Graminoid | 0 | 0 | 0 | 0 | 0.07 | 0.19 |
| EPHE | <i>Epipactis helleborine</i> (L.) Crantz | Broadleaf helleborine | Exotic | 0 | 0 | 0 | 0 | 0.02 | 0 |
| EQAR | <i>Equisetum arvense</i> L. | Field horsetail | Cryptogram | 0.29 | 0.82 | 0.51 | 0.33 | 2.36 | 2.19 |
| GATE2 | <i>Galeopsis tetrahit</i> L. | Brittlesstem hemnettle | Exotic | 0.25 | 0.29 | 0.04 | 0 | 0.46 | 0.07 |
| HIAU | <i>Hieracium aurantiacum</i> L. | Orange hawkweed | Exotic | 0 | 0 | 1.18 | 0.57 | 4.52 | 3.11 |
| HICA10 | <i>Hieracium caespitosum</i> Dumort. | Meadow hawkweed | Exotic | 0 | 0 | 0 | 0 | 1.98 | 2.11 |
| HIP2 | <i>Hieracium piloselloides</i> Vill. | Tall hawkweed | Exotic | 0 | 0 | 0.12 | 0 | 0 | 0 |
| HYPE | <i>Hypericum perforatum</i> L. | Common St. Johnswort | Exotic | 0 | 0 | 0.01 | 0.17 | 0 | 0 |
| LACO3 | <i>Lapsana communis</i> L. | Common nipplewort | Exotic | 0.02 | 0.04 | 0.02 | 0.04 | 0.11 | 0.29 |
| MYSY | <i>Myosotis sylvatica</i> Ehrh. | Woodland forget-me-not | Exotic | 0.29 | 0 | 0 | 0 | 0.65 | 0.29 |
| PLMA2 | <i>Plantago major</i> L. | Common plantain | Exotic | 0 | 0 | 0 | 0 | 0 | 0.02 |
| PTAQ | <i>Pteridium aquilinum</i> (L.) Kuhn | Western brackenfern | Cryptogram | 0 | 0 | 9.49 | 4.37 | 0 | 0 |
| RAAC3 | <i>Ranunculus acris</i> L. | Tall buttercup | Exotic | 0 | 0 | 0.02 | 0 | 0 | 0.03 |
| TAOF | <i>Taraxacum officinale</i> F.H. Wigg. | Common dandelion | Exotic | 0 | 0 | 0 | 0.02 | 0.03 | 0 |
| VEOF2 | <i>Veronica officinalis</i> L. | Common gypsyweed | Exotic | 1.72 | 0.21 | 2.63 | 2.85 | 5.95 | 3.35 |
| VESE | <i>Veronica serpyllifolia</i> L. | Thymeleaf speedwell | Exotic | 0 | 0 | 0.04 | 0 | 0 | 0 |
| C = 1 | | | | | | | | | |
| ACRU | <i>Acer rubrum</i> L. | Red maple | Tree | 10.15 | 13.07 | 11.96 | 14.6 | 1.35 | 7.79 |
| GECA7 | <i>Geum canadense</i> Jacq. | White avens | Forb (> 30.5 ≤ 91.5 cm) ¹ | 0 | 0 | 0.02 | 0 | 0.27 | 0 |
| RUAL | <i>Rubus allegheniensis</i> Porter | Allegheny blackberry | Shrub | 0.29 | 0 | 7.37 | 6.35 | 1.35 | 0.19 |
| SADI | <i>Salix discolor</i> Muhl. | Pussy willow | Shrub | 0 | 0 | 0 | 0 | 0.02 | 0.75 |
| C = 2 | | | | | | | | | |
| CACO7 | <i>Carex communis</i> L.H. Bailey | Fibrousroot sedge | Graminoid | 0.17 | 0.07 | 0 | 0 | 0 | 0 |
| CARA8 | <i>Carex radiata</i> (Wahlenb.) Small | Eastern star sedge | Graminoid | 0 | 0 | 0 | 0 | 0.15 | 0 |
| LACA | <i>Lactuca canadensis</i> L. | Canada lettuce | Forb (> 91.5 cm) ¹ | 0 | 0 | 0 | 0.04 | 0.23 | 0 |
| ONSE | <i>Onoclea sensibilis</i> L. | Sensitive fern | Cryptogram | 3.3 | 0 | 0.12 | 0.04 | 4.79 | 5.13 |
| PRSE2 | <i>Prunus serotina</i> Ehrh. | Black cherry | Tree | 1.86 | 0.04 | 0.28 | 0.38 | 2.72 | 2.11 |
| PRVI | <i>Prunus virginiana</i> L. | Chokecherry | Shrub | 0 | 0 | 0.02 | 1.81 | 0.06 | 0 |
| RUID | <i>Rubus idaeus</i> L. | American red raspberry | Shrub | 2.16 | 2.71 | 4.12 | 0.67 | 7.61 | 2.74 |

Table 1. Continued.

| USDA code | Latin name | Common name | Taxonomic Group | Small gaps | | Medium gaps | | Large gaps | |
|-----------|--|--------------------------|--------------------------------------|------------|-----------|-------------|-----------|------------|-----------|
| | | | | Control | Exclosure | Control | Exclosure | Control | Exclosure |
| C = 3 | | | | | | | | | |
| ABBA | <i>Abies balsamea</i> (L.) Mill. | Balsam fir | Tree | 2.69 | 1.18 | 13.59 | 10.19 | 1.01 | 2.58 |
| CAAR3 | <i>Carex arctata</i> Boott ex Hook. | Drooping woodland sedge | Graminoid | 2.29 | 0.5 | 2.74 | 0.42 | 4.02 | 0.39 |
| CAGY4 | <i>Carex gynandra</i> Schwein. | Nodding sedge | Graminoid | 0.15 | 1.79 | 0.7 | 0.57 | 0.6 | 0.31 |
| CAIN12 | <i>Carex intumescens</i> Rudge | Greater bladder sedge | Graminoid | 0 | 0 | 0 | 0 | 0.46 | 0 |
| CALE11 | <i>Carex leptoneuria</i> (Fernald) Fernald | Nerveless woodland sedge | Graminoid | 0.17 | 0 | 0 | 0 | 0 | 0 |
| CAPR9 | <i>Carex projecta</i> Mack. | Necklace sedge | Graminoid | 0 | 0 | 0.17 | 0 | 0 | 0.33 |
| GEAL3 | <i>Geum aleppicum</i> Jacq. | Yellow avens | Forb (> 91.5 cm) ¹ | 0 | 0 | 0 | 0 | 0.33 | 0 |
| JUEF | <i>Juncus effusus</i> L. | Common rush | Graminoid | 0 | 0.04 | 0 | 0 | 0 | 0 |
| MAST | <i>Matteuccia struthiopteris</i> (L.) Todaro | Ostrich fern | Cryptogram | 4.34 | 2.71 | 0 | 0 | 0 | 0.33 |
| PIGL | <i>Picea glauca</i> (Moench) Voss | White spruce | Tree | 0.86 | 0 | 0.41 | 0.63 | 0 | 0.19 |
| POCI | <i>Polygonum ciliode</i> Michx. | Fringed black bindweed | Vine | 0.17 | 0 | 0.02 | 0 | 0.14 | 0.29 |
| SARA2 | <i>Sambucus racemosa</i> L. | Red elderberry | Shrub | 0.7 | 6.75 | 0.12 | 6.29 | 0.18 | 3.4 |
| C = 4 | | | | | | | | | |
| ATFI | <i>Athyrium filix-femina</i> (L.) Roth | Common ladyfern | Cryptogram | 9.68 | 8.25 | 4.78 | 2.48 | 11.37 | 9.54 |
| CASC13 | <i>Carex scabrata</i> Schwein. | Eastern rough sedge | Graminoid | 0.02 | 0 | 0 | 0 | 0.01 | 0.15 |
| CAS18 | <i>Carex stricta</i> Lam. | Upright sedge | Graminoid | 0 | 0 | 0 | 0 | 0.27 | 0.33 |
| EUMA27 | <i>Eurybia macrophylla</i> (L.) Cass. | Bigleaf aster | Forb (> 91.5 cm) ¹ | 0 | 0.86 | 3.03 | 2.06 | 0.23 | 0 |
| GATR3 | <i>Galium triflorum</i> Michx. | Fragrant bedstraw | Forb (> 30.5 ≤ 91.5 cm) ¹ | 0 | 0 | 0 | 0 | 0.12 | 0 |
| MACA4 | <i>Maianthemum canadense</i> Desf. | Canada mayflower | Forb (Liliopsida) | 9.95 | 5.73 | 5.99 | 3.43 | 4.1 | 1.6 |
| POGR4 | <i>Populus grandidentata</i> Michx. | Bigtooth aspen | Tree | 0 | 0 | 0 | 0.25 | 0 | 0 |
| THOC2 | <i>Thuja occidentalis</i> L. | Arborvitae | Tree | 0.02 | 0.07 | 0.16 | 0.6 | 0 | 0 |
| C = 5 | | | | | | | | | |
| ACSA3 | <i>Acer saccharum</i> Marshall | Sugar maple | Tree | 37.83 | 53.95 | 27.36 | 32.95 | 40.16 | 41.25 |
| AGPE | <i>Agrostis perennans</i> (Walter) Tuck. | Upland bentgrass | Graminoid | 0 | 0 | 0.02 | 0 | 0 | 0 |
| ANQU | <i>Anemone quinquefolia</i> L. | Wood anemone | Forb (≤ 30.5 cm) ¹ | 0.02 | 0 | 0 | 0 | 0 | 0 |
| ARNU2 | <i>Aralia nudicaulis</i> L. | Wild sarsaparilla | Forb (> 30.5 ≤ 91.5 cm) ¹ | 1.52 | 1.87 | 2.17 | 1.52 | 3.48 | 1.49 |
| ARTR | <i>Arisaema triphyllum</i> (L.) Schott | Jack in the pulpit | Forb (> 30.5 ≤ 91.5 cm) ¹ | 0.04 | 0.04 | 0.27 | 0 | 0.06 | 1.69 |
| CADI10 | <i>Cardamine diphylla</i> (Michx.) Alph. Wood | Crinkleroot | Forb (> 30.5 ≤ 91.5 cm) ¹ | 0.02 | 0.04 | 0 | 0 | 0 | 0 |
| CAOR5 | <i>Carex ormostachya</i> Wiegand | Necklace spike sedge | Graminoid | 0 | 0 | 0 | 0 | 0.06 | 0 |
| CLBO3 | <i>Clintonia borealis</i> (Aiton) Raf. | Bluebead | Forb (Liliopsida) | 3.13 | 12.04 | 9.38 | 25.02 | 1.63 | 2.4 |
| COAL2 | <i>Cornus alternifolia</i> L. f. | Alternateleaf dogwood | Shrub | 0.64 | 0 | 0 | 2.71 | 0 | 0 |
| COCO6 | <i>Corylus cornuta</i> Marshall | Beaked hazelnut | Shrub | 2 | 0 | 0.12 | 0.08 | 0 | 0 |
| DRCA11 | <i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs | Spinulose woodfern | Cryptogram | 9.86 | 10.85 | 7.95 | 9.5 | 14.63 | 15.51 |
| GYDR | <i>Gymnocarpium dryopteris</i> (L.) Newman | Western oakfern | Cryptogram | 1.7 | 2.43 | 0.14 | 0 | 2.48 | 1.5 |

Table 1. Continued.

| USDA code | Latin name | Common name | Taxonomic Group | Small gaps | | Medium gaps | | Large gaps | |
|-----------|---|-----------------------------------|--|------------|-----------|-------------|-----------|------------|-----------|
| | | | | Control | Exclosure | Control | Exclosure | Control | Exclosure |
| LOCA7 | <i>Lonicera canadensis</i> W. Bartram ex Marshall | American fly honeysuckle | Shrub | 5.69 | 1.68 | 0.86 | 6.38 | 1.5 | 1.78 |
| LYAN2 | <i>Lycopodium annotinum</i> L. | Stiff clubmoss | Cryptogram | 0 | 0 | 0.12 | 0 | 0 | 0 |
| LYDE | <i>Lycopodium dendroideum</i> Michx. | Tree groundpine | Cryptogram | 0 | 0.07 | 0.6 | 0.74 | 0 | 0 |
| MARA7 | <i>Maianthemum racemosum</i> (L.) Link | Feathery false lily of the valley | Forb (Liliopsida) | 0.5 | 0.82 | 0 | 0.17 | 0.65 | 2.06 |
| MIRE | <i>Mitchella repens</i> L. | Partridgeberry | Forb (≤ 30.5 cm) ¹ | 0.17 | 0 | 0 | 0 | 0 | 0 |
| OSV1 | <i>Ostrya virginiana</i> (Mill.) K. Koch | Hophornbeam | Tree | 9.39 | 1.32 | 7.13 | 1.49 | 3.99 | 0.44 |
| PHCO24 | <i>Phegopteris connectilis</i> (Michx.) Watt | Long beechfern | Cryptogram | 3.6 | 3.86 | 1.3 | 0.42 | 1.6 | 1.04 |
| POP4 | <i>Polygonatum pubescens</i> (Willd.) Pursh | Hairy Solomon's seal | Forb (Liliopsida) | 0.31 | 0.02 | 0.02 | 0.2 | 0.21 | 0 |
| SACA13 | <i>Sanguinaria canadensis</i> L. | Bloodroot | Forb (≤ 30.5 cm) ¹ | 0 | 0 | 0 | 0 | 0.06 | 0.03 |
| SCLA2 | <i>Scutellaria lateriflora</i> L. | Blue skullcap | Forb ($> 30.5 \leq 91.5$ cm) ² | 0 | 0 | 0 | 0 | 0.15 | 0 |
| TACA7 | <i>Taxus canadensis</i> Marshall | Canada yew | Shrub | 0 | 0 | 0.02 | 0 | 0 | 0 |
| TIAM | <i>Tilia americana</i> L. | American basswood | Tree | 0.02 | 1.18 | 0.32 | 5.79 | 1.79 | 2.47 |
| TRBO2 | <i>Trientalis borealis</i> Raf. | Starflower | Forb (≤ 30.5 cm) ¹ | 3.17 | 1.9 | 4 | 2.58 | 1.32 | 0 |
| TRCE | <i>Trillium cernuum</i> L. | Whip-poor-will flower | Forb (Liliopsida) | 0 | 0.25 | 0 | 0.19 | 0.06 | 0 |
| TRGR4 | <i>Trillium grandiflorum</i> (Michx.) Salisb. | White trillium | Forb (Liliopsida) | 0 | 0 | 0.12 | 0 | 0.09 | 0 |
| TSCA | <i>Tsuga canadensis</i> (L.) Carrière | Eastern hemlock | Tree | 0.55 | 0.11 | 1.37 | 9.5 | 0.33 | 3.07 |
| C = 6 | | | | | | | | | |
| FEOC | <i>Festuca occidentalis</i> Hook. | Western fescue | Graminoid | 0.17 | 0 | 0 | 0 | 0 | 0 |
| FRNI | <i>Fraxinus nigra</i> Marshall | Black ash | Tree | 1.33 | 0.82 | 0 | 1.29 | 1.41 | 0.02 |
| ORAS | <i>Oryzopsis asperifolia</i> Michx. | Roughleaf ricegrass | Graminoid | 0.05 | 0.5 | 0.62 | 0.08 | 0.26 | 0 |
| OSCL2 | <i>Osmunda claytoniana</i> L. | Interrupted fern | Cryptogram | 0 | 0 | 0.04 | 0.61 | 4.51 | 0.24 |
| PYEL | <i>Pyrola elliptica</i> Nutt. | Waxflower shinleaf | Forb (≤ 30.5 cm) ¹ | 0 | 0 | 0 | 0 | 0 | 0.17 |
| RAPE2 | <i>Ranunculus pensylvanicus</i> L. f. | Pennsylvania buttercup | Forb ($> 30.5 \leq 91.5$ cm) ¹ | 0 | 0 | 0 | 0 | 0.06 | 0 |
| RIAM2 | <i>Ribes americanum</i> Mill. | American black currant | Shrub | 0 | 0 | 0.29 | 0 | 0 | 0 |
| C = 7 | | | | | | | | | |
| BEAL2 | <i>Betula alleghaniensis</i> Britton | Yellow birch | Tree | 0.75 | 2.96 | 2.11 | 14.7 | 4.24 | 11.08 |
| BRER2 | <i>Brachyelytrum erectum</i> (Schreb. ex Spreng.) P. Beauv. | Bearded shorthusk | Graminoid | 0.71 | 0.86 | 0.53 | 0.77 | 0.13 | 0.69 |
| OXMO | <i>Oxalis montana</i> Raf. | Mountain woodsorrel | Forb (≤ 30.5 cm) ² | 0.18 | 0.29 | 0.12 | 0.02 | 0.78 | 0.96 |
| C = 8 | | | | | | | | | |
| ADBI | <i>Adenocaulon bicolor</i> Hook. | American trailplant | Forb ($> 30.5 \leq 91.5$ cm) ³ | 0.02 | 0.25 | 0.12 | 0 | 0 | 0 |
| C = 9 | | | | | | | | | |
| POAL3 | <i>Poa alsodes</i> A. Gray | Grove bluegrass | Graminoid | 0.02 | 0 | 0 | 0 | 0 | 0 |

Table 1. Continued.

| USDA code | Latin name | Common name | Taxonomic Group | Small gaps | | Medium gaps | | Large gaps | |
|-----------------|------------------------------|-------------------|-------------------------------|------------|-----------|-------------|-----------|------------|-----------|
| | | | | Control | Exclosure | Control | Exclosure | Control | Exclosure |
| C not available | | | | | | | | | |
| CAREX | <i>Carex</i> L. | Sedge | Graminoid | 1.28 | 0.56 | 2.2 | 1.43 | 1.1 | 0.69 |
| EPILO | <i>Epilobium</i> L. | Willowherb | Forb (> 91.5 cm) ¹ | 0.04 | 0 | 0.02 | 0 | 0 | 0.67 |
| HIERA | <i>Hieracium</i> L. | Hawkweed | Exotic | 1.4 | 0.5 | 3.39 | 0.93 | 1.2 | 0.19 |
| JUNCU | <i>Juncus</i> L. | Rush | Graminoid | 0 | 0 | 0 | 0 | 0.01 | 0 |
| SALIX | <i>Salix</i> L. | Willow | Shrub | 0 | 1.14 | 0 | 0.02 | 0 | 0.03 |
| SOLID | <i>Solidago</i> L. | Goldenrod | Forb (> 91.5 cm) ⁴ | 0.06 | 0 | 0.3 | 0.24 | 0.41 | 0.06 |
| SYMPH4 | <i>Symphoricarichum</i> Nees | Aster | Forb (> 91.5 cm) ¹ | 0.61 | 0.29 | 0.5 | 0.11 | 0.4 | 0.1 |
| UNKGRA | unknown graminoid | Unknown graminoid | Graminoid | 0.12 | 0 | 0.32 | 0 | 0.12 | 0 |
| VIOLA | <i>Viola</i> L. | Violet | Forb (≤ 30.5 cm) ² | 0.17 | 0 | 0.02 | 0 | 0 | 0 |

¹ (Black and Judziewicz, 2009)
² (Newcomb, 1989)
³ (Patterson *et al.*, 1985)
⁴ (Hilty, 2020)

data from 2007, it appears that all treatments experienced a modest but consistent decline in H' and S (see fig. 4 in Holmes and Webster 2011). Unlike diversity metrics, clear differences between treatments were observed for FQI values. During both sampling periods, FQI was significantly greater within control plots regardless of opening size ($P = 0.003$; Fig. 2). FQI also displayed a consistent and significant decline across all treatments between the 2007 and 2020 sampling periods ($P = 0.003$; Fig. 2). These differences in FQI, however, only capture the number of conservative species, not their individual dominance within the community. The highest coverages of species with high coefficients of conservatism, individually and in aggregate, were typically observed within exclosures, especially in small and medium gaps (Fig. 3). Therefore, while deer access may be associated with a greater number of moderately conservative species in the herbaceous layer, deer exclusion is associated with greater dominance (cover) of conservative species in the community.

TAXONOMIC AND INDIVIDUAL SPECIES RESPONSE. Substantial changes in the representation of growth forms and taxonomic groups were observed between 2007 and 2020. Most notably, the relative percentage of cover of tree seedlings and saplings in the herbaceous layer doubled across nearly all treatment combinations (Fig. 4). These increases were commensurate with large decreases in the relative cover of graminoids and shrubs. A notable increase in the relative cover of cryptograms was also observed within exclosure and control plots in large gaps (Fig. 4). In general, changes in relative cover of different growth forms were similar between exclosures and controls.

Seedlings and saplings of woody plants constituted the largest share of horizontal coverage in the herbaceous layer (Fig. 4; Table 1). The strongest association with exclosures was observed for *Betula alleghaniensis* Briton, which had coverages an order of magnitude higher within exclosures compared to controls. Conversely, *Ostrya virginiana* (Mill.) K. Koch, while also common, had approximately five to nine times greater coverage on control plots compared to exclosures. Shrubs also displayed contrasting patterns, with *Rubus idaeus* L. displaying greater coverage on control plots and *Sambucus racemosa* L. greater coverage within exclosures (Table 1). *Lonicera canadensis* W. Bartram ex Marshall was also locally abundant

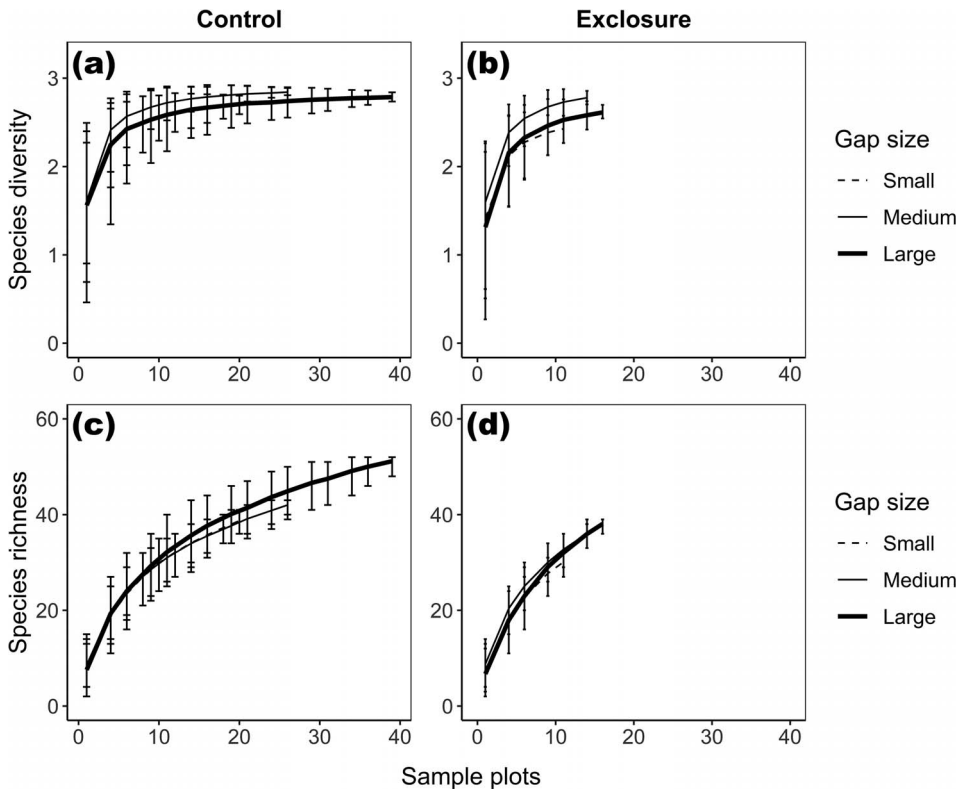


FIG. 1. Rarefaction curves for Shannon's diversity index and species richness in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. Diversity and richness values were summarized for each gap size class (small: 50–150 m², medium: 151–250 m², large: 251–450 m²) and by deer exclosure treatment. Rarefaction extrapolates richness and diversity values along a gradient of sampling intensity to enable a more standardized comparison between treatments with different levels of sampling effort. Error bars represent 95% confidence intervals.

but did not display a consistent trend with deer exclusion across gap sizes. *Acer saccharum* Marshall displayed the highest coverage of any species across all treatment combinations, with mean coverage ranging from 27.4% to 54.0% (Table 1). *Acer saccharum* was somewhat more abundant within exclosures, especially within small gaps. *Acer rubrum* L. was the next most abundant species and displayed a similar tendency of higher coverage within exclosures.

Coverage of ferns was high in both exclosures and controls, with absolute cover of all fern species combined highest on control plots and relative cover somewhat higher on control plots (Fig. 4; Table 1). The two most abundant fern species were *Dryopteris carthusiana* (Vill.) H.P. Fuchs and *Athyrium filix-femina* (L.) Roth, respectively. Collectively, these species averaged about 20% cover in small gaps, 12% cover in medium gaps,

and 25% cover in large gaps (Table 1). They were slightly more abundant on control plots; however, the differences were all within 1%. Of the six other species of ferns observed, only *Phegopteris connectilis* (Michx.) Watt was found across all treatments. Some of the other species were at times locally abundant, but too idiosyncratic in their occurrence to generalize.

Other than woody and fern species, many plants had low absolute percentages of cover (Table 1). A few notable exceptions include consistently high cover of *Clintonia borealis* (Aiton) Raf. within exclosures, where it had approximately two to four times more cover than on control plots. Conversely, the smaller-statured *Maianthemum canadense* Desf. and less conspicuous *Trientalis borealis* Raf. exhibited high coverage on control plots. High coverage on control plots was also observed for *Carex arctata* Boott ex Hook., *Hieracium* spp.,

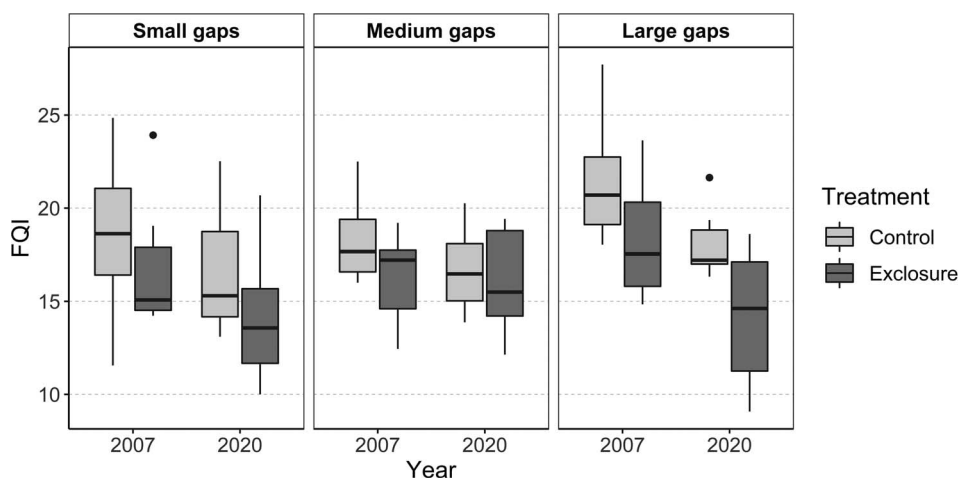


FIG. 2. Box plots of Floristic Quality Index (FQI) distributions for sample plots in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 5 and 18 yr after gap disturbance. FQI values were summarized by gap size, sampling year (2007, 2020) and treatment (deer exclosure and control). FQI assesses the similarity of a site to that of a remnant natural community. Higher values indicate more similarity to communities relatively unchanged from pre-European settlement conditions. Each species in a site (plot) is assigned a coefficient of conservatism (C), and $FQI = C/\sqrt{n}$. Gaps sampled in 2007 were significantly higher in FQI than in 2020 ($F = 9.516$, $df = 1$, $P = 0.003$) and control plots were also significantly higher in FQI than exclosure plots for both sampling periods ($F = 9.786$, $df = 1$, $P = 0.003$). Box plots indicate median (bold horizontal bar), first and third quartiles (horizontal box edges), largest or smallest value no further than 1.5 times the interquartile range (vertical lines extending from box, or “whiskers”), and outliers (dots).

and *Veronica officinalis* L. (the latter two being nonnative exotics).

COMMUNITY COMPOSITION. Our NMS ordination had a three-dimensional solution and final stress of 15.76. It explained 78.5% of the variation in species composition, with Axis 1 explaining the most variation (42.7%), followed by Axis 2 (18.8%) and Axis 3 (17.0%). Percentage of cover of generalist species ($C = 1-2$) displayed a strong positive correlation with Axis 1 ($r = 0.543$; Table 2). Axis 2 was most strongly correlated with cover of cryptograms ($r = -0.510$), followed by moderately conservative species ($C = 3-5$; $r = -0.467$) and exotics ($C = 0$; $r = -0.445$). Medium gaps tended to be associated with regions of the ordination space associated with species with low coefficients of conservatism, whereas small and large gaps were more associated with moderately conservative species and cryptograms (Fig. 5).

Inspection of the ordination plot (Fig. 5) and Euclidian distances between control/exclosure pairs within individual gaps (Appendix Fig. A1) indicated that compositional differences between control and exclosure plots were greatest within large and medium gaps. Permutational multivariate analysis of variance results provided weak evi-

dence of a global exclosure treatment effect ($R^2 = 0.04$, $P = 0.061$; Table 3), but strong evidence of a gap size effect on species composition ($R^2 = 0.08$, $P = 0.002$; Table 3), especially between medium and large gap sizes ($R^2 = 0.078$, adjusted $P = 0.012$; Table 3). Differences were better described with a two-way cluster analysis (chaining = 2.2%; Appendix Fig. A2). Three main groups emerged: (1) *A. rubrum*-dominated exclosures; (2) mixed *Acer*, rich herb controls; and (3) *A. saccharum*-dominated exclosures. Group 1 included some gaps of each size class and was 70% exclosures. Group 2 was mostly controls (74%) but included a few exclosures (26%), and Group 3 was 70% exclosures. From these groups emerged five relatively distinct subgroups: (1.1) *A. rubrum*-dominated exclosures (some of each size class); (1.2) *Abies balsamea* (L.) Mill. and *Tilia americana* L. medium gaps; (2.1) medium gaps dominated by herbs; (2.2) large and small gap controls with mixed *Acer* spp., *Tsuga canadensis*, and *A. balsamea*; and (3.0) *A. saccharum*-dominated exclosures with sparse herbs.

Discussion. Eighteen years following canopy gap creation, herbaceous layer communities ex-

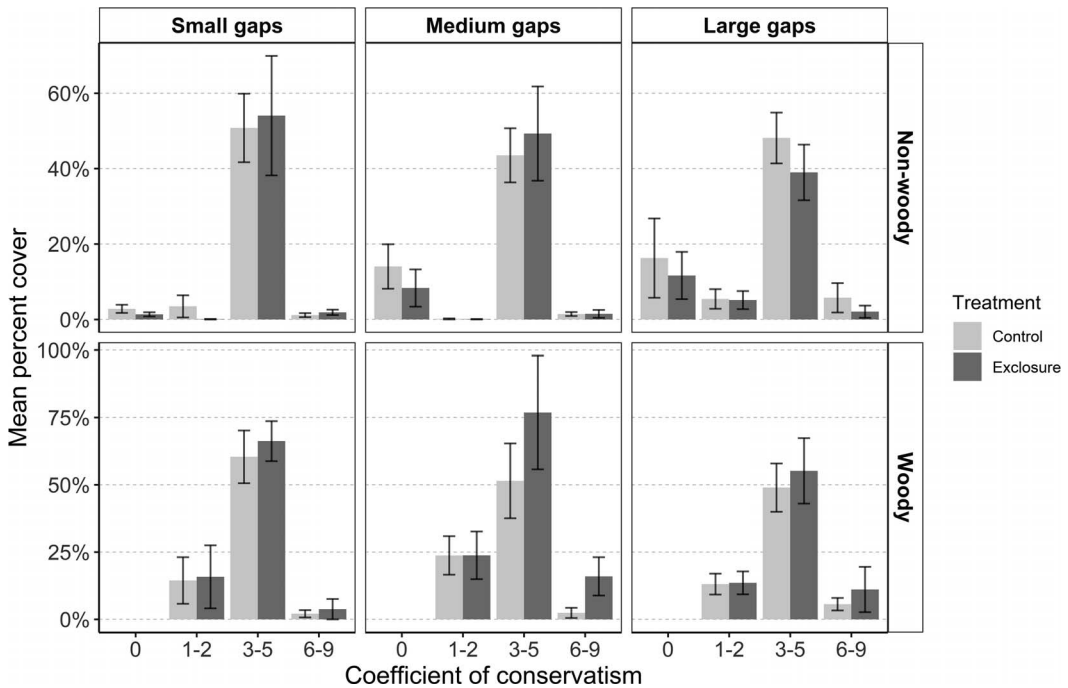


FIG. 3. Mean \pm standard error of herbaceous percentage of cover of species in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. Percentage of cover values were summarized by binned coefficients of conservatism (C), gap size and exclosure treatments, and woody/nonwoody status. C ranges from 0 to 10 and indicates an estimation of how likely a species would occur at a site relatively unchanged from pre-European settlement conditions (i.e., *Panax quinquefolius* L., American ginseng, is assigned a C of 10, and *Equisetum arvense* L., field horsetail, or any exotic species, is assigned a C of 0). See Table 1 for observed species grouped by C values. Note difference of scale between plot panel rows.

hibited both persistent and transient legacies of deer herbivory. Persistent legacies included similarity of small to large gaps compositionally and low abundance of browse-sensitive species outside of exclosures. Transient patterns included initial high graminoid cover and low cover of trees in the ground layer outside of exclosures and differences in diversity between gap size classes. Some emergent patterns were also observed including declining FQI over time, but sustained high occurrence of a number of moderately conservative species on deer access plots. This latter trend supports the hypothesis that by reducing the abundance of more competitive species and woody plants, deer may create opportunities for the persistence of less-competitive herbaceous species (Royo *et al.* 2010, Cook-Patton *et al.* 2014), albeit at low abundance. Similarly, differential trajectories emerged based on gap-specific tree species colonization patterns.

One of the key findings of Holmes and Webster (2011) was that herbivory was associated with

greater similarity among ground layer communities across gap size classes five growing seasons following gap creation. After 18 growing seasons, this pattern has generally persisted for large and small gaps. Only 33% and 43% of large and small gap controls, respectively, clustered out with their paired exclosures. Controls in these gaps tended to have low cover but high frequency of moderately conservative species and high cover of ferns. Tree species were common in the ground layer, but no one species appeared to dominate based on percentage of cover. A concurrent regeneration survey by VanderMolen and Webster (2021) found that *A. saccharum* was common across treatments in the sapling layer and *O. virginiana* was among the tallest trees outside of deer exclosures. Lower numbers of tall saplings outside of exclosures (VanderMolen and Webster 2021) may, at least in part, explain the greater abundance of species in the ground layer of control plots. Interestingly, medium gap exclosures and controls tended to cluster together (71% of the time), suggesting

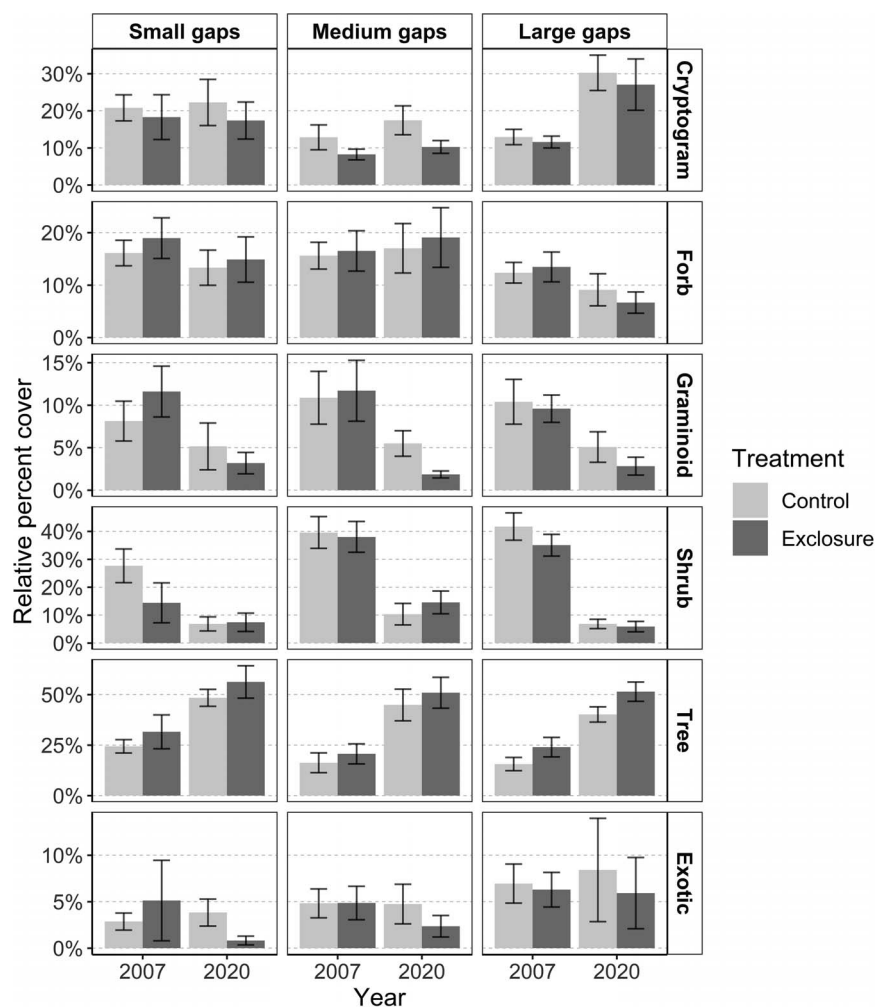


FIG. 4. Mean \pm standard error relative percentage of cover of species in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. Relative percentage of cover values were grouped by taxonomic level (see Table 1) and summarized by gap size, sampling year (2007, 2020), and deer exclosure treatment. Relative cover values are proportional to the total observed cover at the plot level. Note difference of scale between plot panel rows.

some convergence in the ground layer of these openings. This may be the result of differential use of different size openings by foraging deer (Cromsigt and Kuijper 2011, Tahtinen *et al.* 2014) and/or differences in resource availability and productivity between gaps of different sizes (Gálhidy *et al.* 2006, Burton *et al.* 2014, Burton *et al.* 2021).

Another persistent legacy of deer herbivory was the low coverage of browse-sensitive species outside of deer exclosures. For example, *C. borealis*, which has been used as an indicator of overbrowsing in the region (Balgooeyen and Waller 1995, Kraft *et al.* 2004), exhibited two to four times higher cover within exclosures. Similarly, *B. alleghaniensis* had coverages an order of magnitude higher within exclosures compared to controls. *Betula alleghaniensis* is a preferred browse species (Bradshaw and Waller 2016). Recent work by VanderMolen and Webster (2021) in these gaps found that tall regeneration of this species was restricted to exclosures. Similar results were also reported by Burton *et al.* (2021) for gaps in northern Wisconsin.

We observed patterns of community dominance consistent with those observed early in many gap-

Table 2. Correlations of plotted vectors with nonmetric multidimensional scaling (NMS) ordination of herbaceous and woody cover in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. Cover values for species belonging to taxonomic or conservatism groups were summed together at the plot level. Coefficients of conservatism (*C*) range from 0 to 10 and indicate an estimation of how likely a species would occur at a site relatively unchanged from pre-European settlement conditions (*i.e.*, *Panax quinquefolius* L., American ginseng, is assigned a *C* of 10, and *Equisetum arvense* L., field horsetail, or any exotic species, is assigned a *C* of 0). See Table 1 for observed species grouped by *C* values. Many but not all plots contained dense regeneration; therefore, woody regeneration density (stems 100 m⁻²) values were also added as a vector.

| Vector | Axis 1 | | | Axis 2 | | | Axis 3 | | |
|------------------------------------|----------|-----------------------|--------|----------|-----------------------|--------|----------|-----------------------|--------|
| | <i>r</i> | <i>R</i> ² | tau | <i>r</i> | <i>R</i> ² | tau | <i>r</i> | <i>R</i> ² | tau |
| Area (2003) | 0.07 | 0.005 | 0.138 | −0.097 | 0.009 | −0.125 | 0.102 | 0.01 | 0.093 |
| Cryptogram | −0.288 | 0.083 | −0.158 | −0.51 | 0.26 | −0.381 | −0.15 | 0.023 | −0.073 |
| Exotic | 0.149 | 0.022 | 0.089 | −0.4 | 0.16 | −0.34 | 0.503 | 0.253 | 0.325 |
| Forb (Liliopsida) | 0.36 | 0.13 | 0.352 | −0.042 | 0.002 | 0.024 | 0.066 | 0.004 | 0.055 |
| Forb (> 30.5 ≤ 91.5 cm) | 0.114 | 0.013 | 0.138 | −0.278 | 0.077 | −0.231 | −0.13 | 0.017 | −0.083 |
| Forb (≤ 30.5 cm) | 0.37 | 0.137 | 0.271 | −0.094 | 0.009 | −0.061 | −0.104 | 0.011 | −0.042 |
| Forb (> 91.5 cm) | 0.362 | 0.131 | 0.256 | −0.335 | 0.112 | −0.447 | 0.149 | 0.022 | 0.175 |
| Graminoid | 0.117 | 0.014 | 0.175 | −0.084 | 0.007 | −0.04 | 0.407 | 0.165 | 0.224 |
| Shrub | 0.105 | 0.011 | 0.183 | −0.02 | 0 | −0.008 | −0.144 | 0.021 | −0.1 |
| Tree | 0.076 | 0.006 | −0.015 | 0.007 | 0 | 0.023 | −0.664 | 0.441 | −0.554 |
| Vine | 0.081 | 0.007 | 0.124 | −0.084 | 0.007 | −0.124 | −0.172 | 0.029 | −0.045 |
| <i>C</i> = 0 | 0.307 | 0.094 | 0.239 | −0.445 | 0.198 | −0.435 | 0.538 | 0.289 | 0.321 |
| <i>C</i> = 1–2 | 0.543 | 0.295 | 0.483 | 0.291 | 0.084 | 0.095 | 0.08 | 0.006 | 0.149 |
| <i>C</i> = 3–5 | −0.277 | 0.077 | −0.144 | −0.467 | 0.218 | −0.285 | −0.531 | 0.281 | −0.441 |
| <i>C</i> = 6–9 | 0.312 | 0.097 | 0.198 | 0.143 | 0.02 | −0.008 | −0.172 | 0.029 | 0.083 |
| Woody regeneration density (1–2 m) | −0.033 | 0.001 | 0.016 | 0.074 | 0.005 | 0.048 | −0.188 | 0.035 | −0.193 |
| Woody regeneration density (> 2 m) | −0.227 | 0.051 | −0.103 | 0.217 | 0.047 | 0 | −0.117 | 0.014 | −0.19 |

herbivore studies. Most notably, 5 yr postharvest control plots were typified by high graminoid cover and low cover of trees in the ground layer outside of exclosures (Holmes and Webster 2011). This finding is consistent with early results from other studies examining canopy gaps and interactions with ungulate herbivores (Rooney 2009, Burton *et al.* 2021). While these patterns of dominance have been persistent in several studies (Kelemen *et al.* 2012, Knapp *et al.* 2021, VanderMolen *et al.* 2021), they were more transient within our experimental gaps. For example, the relative cover of graminoids decreased across all treatment combinations between 2007 and 2020. While the greatest declines were observed within exclosures, declines on control plots were substantial (~ 50%). These declines, however, were modest compared to declines in the relative cover of shrubs across all treatments, which declined by upwards of 75% on control plots in medium and large gaps. These results were likely influenced by the size range of openings we examined and legacy effects associated with past herbivory. For example, persistent shrub and

graminoid layers have generally been associated with openings larger than those we examined (Kelemen *et al.* 2012, Widen *et al.* 2018, Knapp *et al.* 2021, VanderMolen *et al.* 2021). Our largest openings were similar in size to the smallest classes of openings examined in those studies, a size class where patches of regeneration failure/delay associated with competing vegetation were less frequent (VanderMolen *et al.* 2021). Our range of opening size is more similar to Burton *et al.* (2021) who, 4 yr following gap creation, found similar results to Holmes and Webster (2011), but hypothesized based on species life histories that some near-term effects may be “transient” as species turned over to greater dominance by woody plants and canopy closure exerted greater control over community composition. Our results are consistent with their hypothesis (see also Sabo *et al.* 2019).

Another important factor likely influencing community response is differential use of various sized openings by deer. Tahtinen *et al.* (2014) hypothesized that high winter of use of small gaps at our site by overwintering deer was creating a

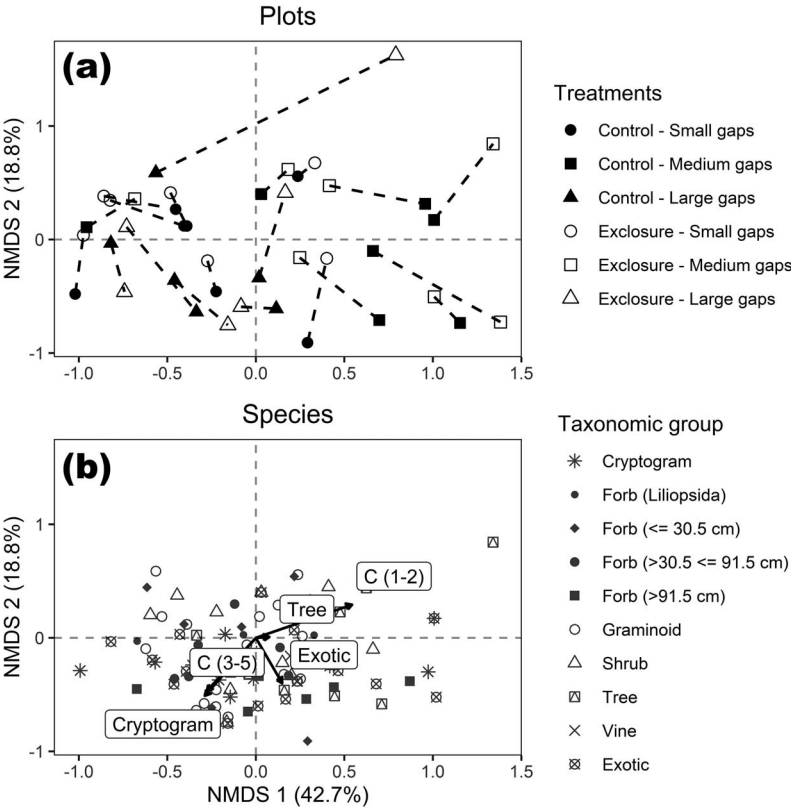


FIG. 5. Nonmetric multidimensional scaling (NMS) ordination plots of (a) sample plots pairs and (b) species with significant plotted vectors in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. Deer exclosure and control treatment paired plots in the same gap are connected by a dotted line representing distance on Axes 1 and 2 (a). Plant species are grouped by taxonomic level (see Table 1) and represented by shape (b). Only significant vectors are plotted as either a taxonomic grouping of species or a group of species in binned coefficients of conservatism (b).

Table 3. Results of a permutational multivariate analysis of variance (PERMANOVA) using distance matrices in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. PERMANOVA tests for differences between groups, in this case treatments, in contrast to the null hypothesis of equivalent group centroids and dispersions. We used the “adonis2” function in the “vegan” package (Oksanen *et al.* 2022) in R 4.1.2 (R Core Team, 2021) and specified the Bray-Curtis dissimilarity method, 999 permutations, and a term for treatment interaction. $\text{Pr}(> F)$ is the probability that observed F is greater than calculated F (when null hypothesis is true) by chance alone. A separate pairwise comparison was performed with the “pairwiseAdonis” package (Arbizu 2017) to compare within-treatment gap sizes where the adjusted P -value used the Bonferroni method to determine significant differences.

| Treatment | df | Sum of squares | Partial R^2 | F value | $\text{Pr}(> F)$ |
|----------------------|----|----------------|---------------|-----------|---------------------|
| Exclosure | 1 | 0.437 | 0.036 | 1.421 | 0.061 |
| Gap size | 2 | 1.034 | 0.084 | 1.681 | 0.002* |
| Exclosure * gap size | 2 | 0.358 | 0.029 | 0.583 | 0.997 |
| Residual | 34 | 10.453 | 0.851 | — | — |
| Total | 39 | 12.282 | 1 | — | — |
| Pairwise comparison | df | Sum of squares | R^2 | F value | Adjusted P -value |
| Medium vs. small | 1 | 0.467 | 0.057 | 1.558 | 0.123 |
| Medium vs. large | 1 | 0.631 | 0.078 | 2.037 | 0.012* |
| Small vs. large | 1 | 0.456 | 0.06 | 1.507 | 0.135 |

* Asterisks denote values at or below a 0.05 probability threshold.

phenomenon similar to a forest “grazing lawn” (for a review, see Cromsigt and Kuijper 2011). The increase in woody plant cover in the ground layer, but limited advancement into the sampling layer (VanderMolen and Webster 2021), is consistent with descriptions of this phenomenon in other forested systems (Kuijper *et al.* 2009). Transient differences in diversity between gap size classes over the 18-yr study period were also consistent with trends in diversity and dominance following canopy gap disturbance generally (Kelemen *et al.* 2012, Bolton and D’Amato 2019, Sabo *et al.* 2019).

The primary emergent pattern we observed was a tendency for deer access plots to sustain higher FQI than exclosures. This pattern was associated with the high occurrence of a number of species with moderate coefficients of conservatism, albeit often at low cover, on deer access *vs.* exclosure plots. Small-statured herbs, such as *M. canadense*, appeared to benefit from reduced competition, especially from woody plants, when deer had access. These findings generally support the hypothesis that herbivory may help maintain species diversity (Cook-Patton *et al.* 2014) by reducing the competitive advantage enjoyed by taller herbs and woody plants in the absence of herbivory (Webster *et al.* 2017). An important caveat, however, in our study was a strong seasonal pattern of deer use in deep snow zones of the northern Lake States (high winter use; Parikh and Webster 2019) that may simultaneously enhance impacts on woody plants while tempering impacts on herbaceous plants. In the northern Lake States, deer migrate upwards of 50 km to areas of dense conifer cover (*e.g.*, *T. canadensis* and *Thuja occidentalis* L.) during the winter in response to deep persistent snow packs (“yarding”) (Verme 1973, Van Deelen *et al.* 1998). Consequently, summer deer use/abundance in *T. canadensis* stands, like the one examined herein, may be substantially lower than in winter, since many of the winter occupants have returned to distal summer ranges. Correspondingly, Jensen *et al.* (2011) observed greater herb layer heterogeneity and cover in relict *T. canadensis* stands with high levels of winter use and a general shift towards dominance by browse-tolerant hardwoods rather than the browse-sensitive *T. canadensis* (Anderson and Loucks 1979). That being said, similar patterns of abundance of small-statured herbs in the presence of deer herbivory have been noted

elsewhere, including a long-term exclosure study in the southern Appalachians (Webster *et al.* 2017) and among spring ephemerals in northern Wisconsin (Burton *et al.* 2021).

Collectively, our results highlight the complex and pervasive influence of white-tailed deer on ground-layer development following disturbance. Through differential foraging patch selection and control of woody regeneration, white-tailed deer may alter or reinforce patterns of dominance depending on initial conditions (see also Augustine *et al.* 1998). These interactions may result in context-specific persistent, transient, and emergent dynamics as plant communities recover from canopy disturbance. Our work reinforces the need for long-term replicated studies in both disturbed and intact forest communities to broaden our view of these dynamics (see Sabo *et al.* 2019, Reed *et al.* 2022, Knauer *et al.* 2023).

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Appendix

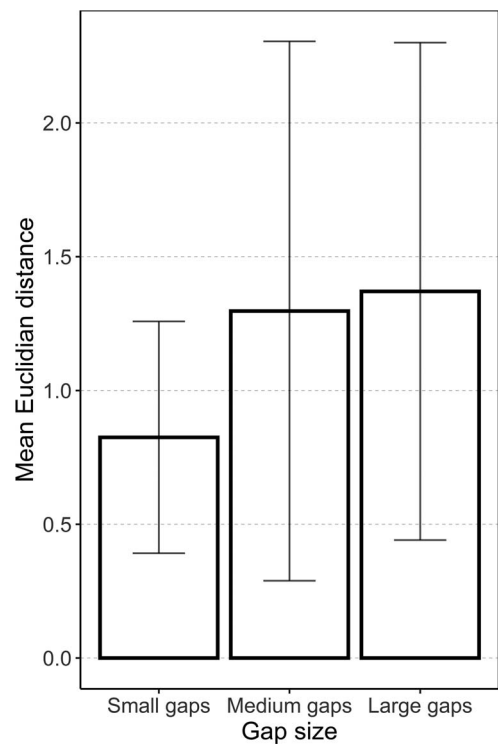


FIG. A1. Mean \pm standard deviation of Euclidean (straight-line) distances between control and deer exclosure treatment plot locations in the three-dimensional ordination space summarized by gap size. Distances are a result of a nonmetric multidimensional scaling (NMS) ordination plot for herbaceous and woody cover in a hemlock-hardwood artificial canopy gap study near Alberta, MI, 18 yr after gap disturbance. Larger distances between plots in the ordination space indicate greater compositional dissimilarity between treatments.

