

Effects of herbivores on ground flora and nutrient dynamics along Lake Superior's
North Shore Highlands

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Abstract

Impacts due to ungulate herbivores such as moose and white-tailed deer have been of interest to researchers and resource managers for years. Recent studies have begun to suggest the presence of alternative stable states in these systems where the existence of hysteresis could result in significant changes to the understory community that would be costly and time consuming to undo. However, before such assertions can be made, the presence of different states needs to be established. Our study investigated changes to the understory community and nutrient dynamics of twelve paired moose and white-tailed deer exclosure and control plots located along a 95-mile section of the Lake Superior North Shore Highlands. Exclosure ages ranged from 11 to 24 years old. During the summer of 2010, we measured understory and shrub species percent cover, sapling densities, litter depth, and bulk soil composition inside and outside of exclosures at each site. Nitrogen availability was also measured at three sites using resin bags. Browsing significantly affected understory vegetation at all sites except one, as well as ammonium (NH_4) availability and percent of nitrogen and carbon in the mineral soil. The directions of these effects varied by site and seemed to be related to differences in canopy composition, age of exclosure, and relative ungulate population size. Future studies should monitor long-term changes through time, as some trends may be important early on in forest recovery while others do not appear until years later. Although our study design was not able to detect evidence of hysteresis or affirm the presence of alternative stable states, we believe it does suggest evidence of instability and non-linear ecosystem impacts of ungulate herbivory.

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Chapter 1. Introduction

The effects of ungulate herbivory on forest and grassland ecosystems have been studied for many years. Studies have looked at trends in soil composition, nutrient availability, canopy regeneration, shrub composition, and vegetation population growth (Côté et al., 2004; Tremblay et al., 2007). Recently, scientists have also suggested forests subjected to heavy herbivory could be exhibiting alternative stable states (Stromayer and Warren, 1997; Augustine et al., 1998). Such perturbations could produce substantial changes to the forest community that might be costly for forest managers to rectify.

Potential forest alternative stable states

Alternative stable states were first suggested by Lewontin (1969) and Holling (1973) and have continued to be a popular area of debate for ecosystem scientists. Although their existence is generally accepted in many aquatic communities, there has been much speculation but little conclusive research into their presence in terrestrial communities. In particular, current literature for alternative stable states induced by ungulate herbivory is largely theoretical.

A system is generally said to have alternative stable states if one or more parameters of the ecosystem exhibits two discrete equilibria. The two equilibria can be stable equilibria separated by an unstable equilibrium along gradients of values for these parameters, or the two equilibria can exchange stability as threshold values of one or more parameters are crossed (Carpenter, 2001). For instance, the same shallow lake system can be either turbid (algae-dominated) or clear-water (macrophyte and periphyton

dominated) depending on phosphorus availability. At low concentrations of dissolved phosphorus, the lake is likely to be in a clear water state, as algae require high levels of phosphorus to support their fast growth. If phosphorus concentrations increase above a threshold level (e.g. from agricultural runoff), the lake might be shifted into an alternative stable equilibrium where algal growth will increase and shift the lake into a turbid state. If the two equilibria are separated by an unstable equilibrium, the system will exhibit some form of hysteresis, where the necessary perturbation to return a shifted system to its original state is greater than the one that caused it to shift originally. One must then push the parameter across the value for the unstable equilibrium before the system can return to the original stable equilibrium. This is particularly important for managers, as it means accidental state shifts can be difficult and expensive to amend and is the reason why more research is needed to better understand where these alternative stable states exist.

Alternative stable states can occur under a variety of conditions and mechanisms, and in many cases these fast changing, sensitive components may be controlled by other, more slowly changing parameters (Carpenter, 2001). Therefore, the possible state shifts in communities may often be controlled by underlying slow turnover rates, such as plant competition being controlled by soil mineralization rates. The selective grazing by ungulate herbivores on herb species with fewer defenses and higher nutrient contents has been shown to affect ground flora succession through time, with long periods of intensive grazing resulting in a community dominated by grasses and better defended plant species (Augustine and McNaughton, 1998; Strauss and Agrawal, 1999; Tremblay et al., 2007). Because of these differences in plant communities with and without deer, some

researchers have suggested the forests have alternative stable states induced by intensive deer grazing.

Stromayer and Warren (1997) suggest the potential mechanism by which deer may be inducing alternate stable states is by preventing species regeneration long enough to approach localized extinction. Essentially, browsing by deer may suppress seedling stock enough to inhibit canopy restoration after a disturbance, resulting in an important change to the community structure. Based on this and the above-mentioned studies, we can formulate an idea of how a shift in community structure might occur due to ungulate browse damage (Figure 1).

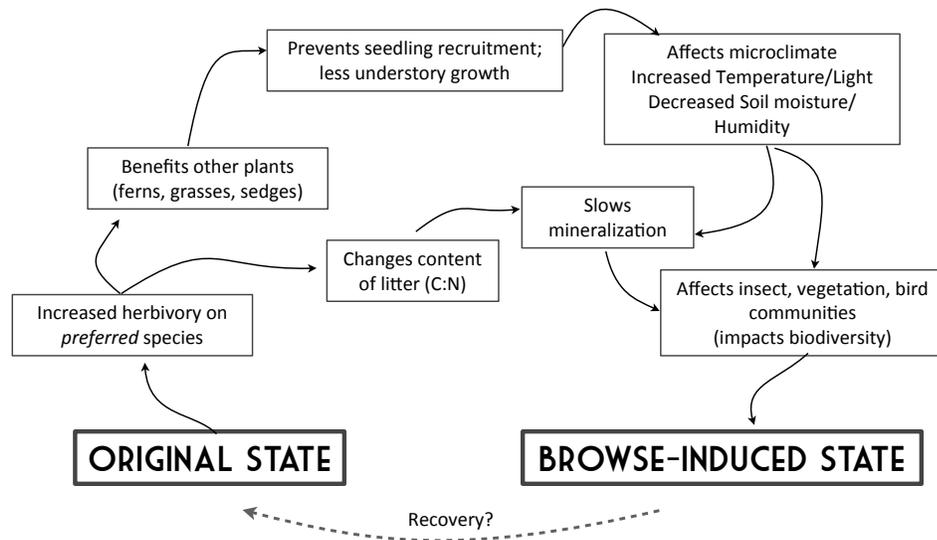


Figure 1. Proposed feedback loop of changes caused by ungulate herbivory to northern temperate forest communities. Based on research summarized by Côté et al. (2004).

For example, increased herbivory on preferred forb species may benefit other plants (e.g. ferns and graminoids) by reducing competition, which can prevent seedling recruitment and lead to less understory growth. Lower understory growth may increase the amount of light reaching the forest floor, increasing soil temperatures, which may

increase mineralization rates, and decreasing soil moisture, which may slow mineralization rates. The changes to the litter layer composition (increased C:N) due to preferred browsing on high-nitrogen species may also contribute to slower mineralization rates (Pastor et al., 1993). The combination of lower nutrient availability and microclimate changes could impact the types of vegetation species able to grow in the area, as well as affecting insect and nesting bird communities. If all of these changes eventually occur they could cause ecosystem instability leading to alternate stable states, the impacts of which could be widespread and potentially long lasting.

Focus of study

Although studies of terrestrial alternative states have been growing in recent years, it is still largely a theoretical area. Part of this is likely due to the difficulty associated with trying to empirically test for hysteresis, the idea that deer browsing can alter the vegetation community to such an extent where simply decreasing the amount of browsing or removing it all together does not allow a return to the pre-browsed state. Tanentzap et al. (2011) suggest there may be a “legacy effect” of herbivore browsing, where canopy regeneration will continue to decline or remain low even after deer numbers are reduced. Given that the rate of forest succession might be well over 300 years, studies testing for hysteresis could be very time consuming and perhaps unrealistic. However, there has not yet been much investigation into how changes in available nitrogen from herbivores may be affecting the understory plant community. If alternative stable states are occurring in forest ecosystems, parameters such as nitrogen concentrations could influence alternate states. This type of a system would have

important implications for herbivore management in protected forests as well as for state reversal once they have already been established. These states could also lead to changes in carbon sequestration and may interact with other factors, such as earthworm invasion, which could further alter forest dynamics.

In order to begin investigating whether or not alternative stable states exist, it is necessary to determine if these ecosystems are in fact exhibiting different states. We decided to study how ungulate herbivores are affecting understory vegetation composition and morphological growth as well as nutrient dynamics in an attempt to discover different “states.” The second chapter of this manuscript discusses our findings related to understory vegetation composition, species diversity, and morphological changes. The third chapter focuses on impacts related to nutrient availability and soil composition.

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Chapter 2. Effects of herbivores on ground flora composition and morphology

Overview

The effects of ungulate herbivory have been documented in a variety of different community types and regions. However, most studies have focused on impacts to canopy regeneration and have neglected understory herbaceous species composition. We investigated trends in understory species percent cover as well as specific morphological changes in plant species caused by herbivory – including stem length, leaf number, and flowering/fruitlet rate in five preferred browse species. Our 12 study sites consisted of paired control and enclosure plots stretching along a 95-mile section of Minnesota's North Shore of Lake Superior. Within each plot we set up 25 subplots and collected species percent cover data, as well as site characteristics and morphology data. A multiple response permutation procedure (MRPP) was used to determine differences between control and enclosure plot compositions. All sites showed a significant difference in understory composition, although trends varied by site. We also found significant changes in plant morphology, including longer stem or basal leaf lengths, greater leaf numbers, and higher fruiting rates of *Clintonia borealis* and *Streptopus roseus* plants found in enclosures, and lower fruiting rates of *Eurybia macrophylla* in enclosures. Our findings suggest that understory herb species composition is sensitive to herbivory and recovery of this important forest layer may occur along a successional gradient.

Introduction

Ungulate herbivores can cause changes to the ecosystems they live in due to the way they move through the area, selectively graze, and excrete waste. Grazing by moose and deer has been shown to reduce regeneration of sensitive canopy tree species, increase woody undergrowth, alter nutrient dynamics, and increase plant defenses and growth patterns (Côté et al., 2004; Pastor et al., 2006; White, 2012).

The selective grazing by ungulate herbivores on herb species with fewer defenses and higher nutrient contents has been shown to affect ground flora succession through time, with long periods of intensive grazing resulting in a community dominated by grasses and better defended plant species (Augustine and McNaughton, 1998; Blair and Brunett, 1980; Strauss and Agrawal, 1999; Tremblay et al., 2007). Some herb species

have developed chemical or morphological defenses that can help them to “tolerate” or “resist” herbivory. These defenses are often more pronounced in areas with high risk of herbivory (Côté et al., 2004). Those that tolerate some damage due to browsing tend to be species that store extra resources underground, re-grow quickly, or protect their meristems (e.g. grasses, ferns, other graminoids; Augustine and McNaughton, 1998). In areas with long periods of sustained heavy browsing such species are likely to outlast undefended or preferred plants, potentially preventing these other species from re-establishing once the heavy herbivory has been decreased. These differences can select for more tolerant or “resistant” species over time, also potentially changing forest floor litter composition, and subsequently ecosystem-scale nutrient dynamics.

Studies have documented changes in community type due to high deer densities, ranging from decreased species richness (Rooney and Dress, 1997) to decreased understory cover (Hough, 1965). In Pennsylvania, researchers found selective browsing decreased abundance of the shrub *Rubus allegheniensis*, which promotes tree seedling establishment, and increased abundance of the fern *Dennstaedia punctilobula*, which prevents seedling establishment (Horsley and Marquis, 1983). This change in community structure remained after browsing ended as the high density of ferns prevented the establishment of more common but sensitive understory species. Specific community changes are believed to depend largely on the intensity of browsing; lower densities of herbivores increase species diversity by reducing competitive exclusion of herbaceous species (Webb et al., 1956).

The two most common ungulate species in northern mixed-wood and conifer forests around the Great Lakes region are white tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*). However, moose numbers have been declining in recent years and although there is still speculation as to the cause, scientists believe it may be due to loss of habitat as well as increased temperatures and diseases brought on by climate change (Lenarz et al., 2010). After decades of high white-tailed deer population sizes, the Minnesota Department of Natural Resources recently stated it is considering raising its deer population goals across the state (MNDNR, 2012). This could have important implications for forest dynamics (Rooney and Waller, 2003).

In order to assess how northern mixed-wood and conifer forests recover from historical ungulate herbivory, we decided to investigate a variety of ecosystem parameters inside and outside exclosures in the North Shore Highlands region of Minnesota. Exclosure studies have been a popular method among researchers to measure the effects of herbivores on forest ecosystems. However, this method is not without limitations. For most studies, there is little to no data on historical levels of herbivory in the area where the exclosures are constructed, meaning that researchers cannot be certain of how previous site use may be influencing current patterns. Excluding deer from a previously browsed area also means that the area studied is “recovering” from herbivory rather than never being browsed and, most importantly, a fence exclosure creates an artificially low deer abundance level (i.e. no deer) that would likely not be found in natural conditions. While acknowledging these important limitations, constructing fence

exclosures is a relatively inexpensive and manageable method to begin to understand the impacts of herbivores on forest communities.

We hypothesized that vegetation communities would be different between exclosure and control plots, with control plots exhibiting a greater graminoid community and exclosures containing more of the preferred browse species such as *Trillium* species and *Clintonia borealis*. We also expected to find differences in species diversity, richness, and evenness as well as trends specific to individual species. In accordance with previous studies, we believed there would be greater shrub and sapling densities in exclosures. Since deer have been shown to cause morphological changes to the species they browse the most, such as *Trillium* species (Anderson, 1994; Augustine and Frelich, 1998), we also looked at several morphological attributes of plants, such as stem length, leaf number, and flowering for *Aralia nudicaulis*, *Clintonia borealis*, *Eurybia macrophylla*, *Streptopus roseus*, and *Trillium* species. These species were selected for their relatively large abundance in most sites (*A. nudicaulis*, *S. roseus*) as well as their browse sensitivity (*C. borealis*, *Trillium*; Anderson, 1994; Balgooyen and Waller, 1995) or ability to withstand and flourish in disturbed areas (*E. macrophylla*). In addition, we investigated how the species-area curve parameters changed for control and exclosure plots, using the exponent (z) of the species-area curve $S = cA^z$ as a measurement of the rate of encountering new species in adjacent plots and the intercept (c) as a measurement of relative richness in unit area plots (Pastor et al., 1996).

Materials and methods

Study sites

The Minnesota Department of Natural Resources has constructed a number of deer exclosure plots located in parks along Lake Superior's North Shore Highlands ecological subsection, stretching from Duluth to Grand Portage, MN and covering the area within 20-25 miles of the Lake Superior shoreline (Minnesota Department of Natural Resources, 2006). Historically the region's forests were characterized by white pine (*Pinus strobus*) and red pine (*Pinus resinosa*), although logging has replaced much of the original canopy with quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Due to its proximity to the lake, the area tends to remain cooler throughout the summer and experiences milder winters and lower snowpack compared to other locations further inland. This makes the area a preferred wintering yard for white-tailed deer in the region. Mean temperatures for the four main months of the 2010 growing season (May, June, July, and August; the months during which the majority of data collection occurred) ranged from 10.8 °C to 17.8 °C in Grand Marais and 11.6 °C to 19.6 °C in Two Harbors. Total precipitation during this time span was 25.27 cm in Grand Marais and 37.03 cm in Two Harbors (Weather Source, LLC, 2012, unpublished data).

We selected parks in this region with the largest well-maintained exclosures with little or no management interference. These parks included Gooseberry Falls (2 exclosures), Split Rock (1 exclosure), Tettegouche (2 exclosures), and Judge C.R. Magney (3 exclosures) State Parks (Table 1). Sites were distributed across the area,

which we believed would give a fair assessment of understory vegetation characteristic of the North Shore Highlands (Figure 2). The exclosures were situated in a variety of forest canopy types, including northern white cedar (*Thuja occidentalis*)-white pine, white spruce (*Picea glauca*)-white pine, cedar-paper birch, paper birch-quaking aspen, and paper birch-white spruce. Some of these exclosures were set up to improve regeneration of certain canopy species (white pine, white spruce, balsam fir (*Abies balsamea*), northern white cedar, etc.) and therefore have had some treatments to promote seedling establishment, such as planting or soil scarification. Exclosures ranged in age from 9 – 24 years old. We avoided any areas within exclosures that had been subjected to unnatural disturbance (planting or other techniques meant to improve canopy regeneration) in order to focus on potential impacts of herbivore grazing.

Besides the four state park sites, we also sampled in the Encampment Forest, a privately owned area with a conservation easement through the Nature Conservancy designed to protect and restore the surrounding forest. There are four 0.25 ha exclosures within the conservation area that were constructed between 1987 and 2002 and are comparable in condition to the DNR exclosures. The Encampment site is located between Gooseberry Falls State Park and Two Harbors, MN.

Our sites spanned a 95-mile section of the North Shore of Lake Superior, beginning with the Encampment Forest site furthest south and ending with Judge C.R. Magney, 30 miles south of the Canadian border.

Table 1. Exclosure plot descriptions for our 12 study sites located in parks along Minnesota’s North Shore of Lake Superior. Cedar refers to *Thuja occidentalis*, White Pine *Pinus strobus*, Spruce *Picea glauca*, Paper Birch *Betula papyrifera*, and Aspen *Populus tremuloides*.

Location	Exclosure Site	Size (ha)	Year Est.	Cover Type	Notes
Encampment Forest	EnA	0.26	1988	Cedar-White Pine	Natural regeneration; hare exclosure added in 1990
	EnB	0.23	1987	Spruce-Cedar-White Pine	Natural regeneration; hare exclosure added in 1992
	EnF	0.22	1990	Cedar-White Pine	Natural regeneration; hare exclosure added in 1991
	EnM	0.19	2002	Cedar-Paper Birch	Natural regeneration
Gooseberry Falls State Park	G1	10.50	1990	Cedar-Paper Birch-Aspen	Rock raked; planted with white pine and norway spruce
	G2	10.77	1987	Cedar-Paper Birch	Partially bulldozed; rock raked
Judge C.R. Magney State Park	M1	0.14	2000	Paper Birch-Aspen	Natural regeneration
	M2	0.18	2000	Paper Birch-Spruce	Natural regeneration
	M3	0.80	2000	Paper Birch-Spruce	Adjacent to camp site; blow-down in 2009; some brush removed and some white pine planting
Split Rock State Park	SR	1.66	1994	Cedar-Paper Birch	Natural regeneration
Tettegouche State Park	T1	1.34	1996	Paper Birch-Aspen	Natural regeneration
	T2	2.17	2002	Cedar-Paper Birch-Aspen	Natural regeneration

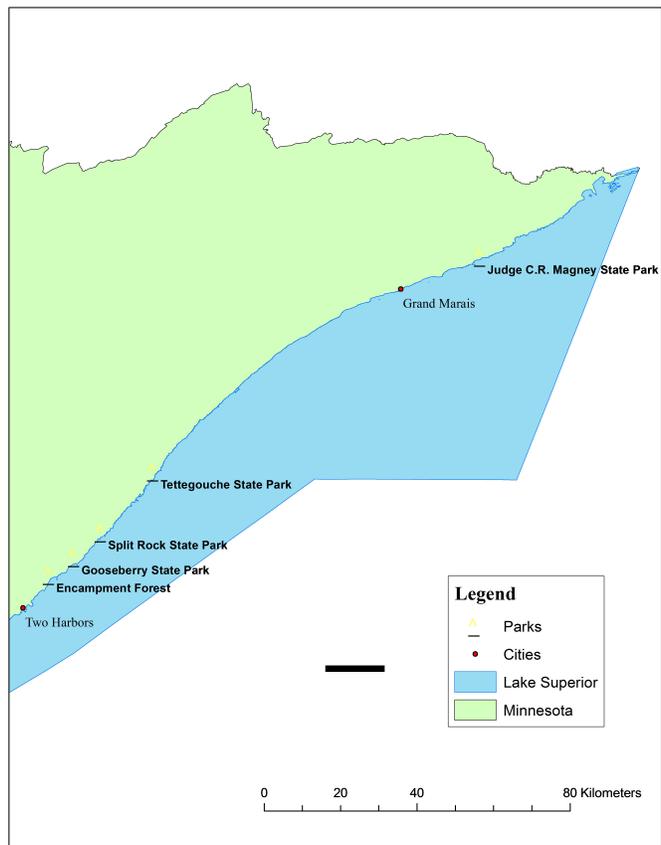


Figure 2. Five study sites located along Minnesota's North Shore region of Lake Superior. Sites include Encampment Forest Association, Gooseberry Falls State Park, Split Rock State Park, Tettegouche State Park and Judge C.R. Magney State Park.

Understory vegetation assessment

Understory species abundance at each site was sampled at the height of the growing season, between late June and August of 2010. At all sites except for those in Judge C.R. Magney State Park, five 50 m transects were set up in both control and enclosure plots, spaced 4-5 m apart. Along each transect, species cover was recorded using the point-intercept method (Mueller-Dombois and Ellenberg, 2003), beginning with the first meter and ending with the 50th for a total of 50 points per transect. The enclosures at Judge C.R. Magney State Park were irregularly shaped which required a 4

transect design ranging in lengths from 16-64 m. However, the same number of point-intercept samples was collected at each plot by adjusting the spacing between samples.

We also set up 1 m radius circular subplots every 8-10 m along each transect, for a total of 25 subplots per plot. Within these subplots, herbaceous species cover-abundance was recorded to the nearest 5% by ocular estimate. Trace amounts of < 1% and 2.5% were also recorded to account for species present but with little cover. Shrub species cover-abundance was measured the same way.

Substrate and soil data were recorded as well. The percent substrate cover was determined at each subplot using the following eight categories: hardwood litter, conifer litter, mixedwood litter, graminoid litter, moss, coarse woody debris, rock, and bare soil. The litter layer, duff and humus layers were measured and mineral soil texture recorded within each subplot using the method described by Richardson and Vepraskas (2000). A 10 cm soil core was also collected from each subplot and brought back to the lab to be analyzed for total carbon and nitrogen concentrations (Chapter 3).

Overstory assessment

A canopy assessment was conducted to determine relative cover between control and exclosure plots as well as across sites. Along the middle and two outer transects within each plot, we recorded the species and diameter at breast height (dbh) for any tree > 10 cm dbh with its center point falling within 3 m of the transect line. In plots that were too small for three transects, the middle and outer transects were still used but the missing distance was completed on the remaining inner transects. The total basal area (BA) of trees within each stand was calculated.

We used the number of trees per species found as well as BA to determine canopy type at each plot, classified by the two most common species (Table 1). We also ranked plots along a forest type gradient, ranging from conifer dominated (1) to hardwood dominated (3). Forest type was determined by calculating the ratio of conifer species' BA to deciduous species' BA in each plot and assigning a value of 1 to 3 (Table 2).

Table 2. Forest type value designations as determined by the ratio of conifer to deciduous BA percentages.

Forest Type	Conifer:Deciduous	Value Assigned
Deciduous	≤ 0.33	3.0
Deciduous-Conifer Mix	0.33 - 0.67	2.5
Even Mix	1.50 - 0.33	2.0
Conifer-Deciduous Mix	1.50 - 3.00	1.5
Conifer	≥ 3.00	1.0

Herbivore pellet assessment

For a relative measure of current herbivore abundance, a standing crop pellet survey was conducted at each site (Marques et al., 2001). This technique allows an approximation of deer and moose densities based on the total number of pellet groups (fecal matter) located in the area. Pellet counts have been increasing in popularity among researchers as they are fairly quick, simple and inexpensive to complete. Although formulas have been developed to translate pellet counts into approximate number of deer based on defecation and pellet group decomposition rates, these calculations frequently come under scrutiny for inaccuracies resulting from these assumed rates and constants. Therefore, we chose to report the raw pellet counts alone as a basic measurement of relative densities between sites.

To measure the number of pellet groups at each site, we used the same transects as in the canopy assessment. Each transect was walked twice, once on either side of the line to improve spotting accuracy. We tallied the number of all pellet groups that contained ≥ 12 pellets, with the center-point of the pellet group lying within 2 m of the line. The total area surveyed per stand was 600 m².

Morphological measurements

At each plot, up to 30 individual plants each of *Aralia nudicaulis*, *Clintonia borealis*, *Eurybia macrophylla*, *Streptopus roseus* and *Trillium* species were measured for morphological differences. Numbers varied by plot due to changes in abundance. Each species was measured for stem height (from base at soil level to apical meristem) and the number of leaves. We also noted if the plant had evidence of flowering or fruiting. For *Clintonia borealis* and *Eurybia macrophylla*, we measured the largest leaf length from base to tip. For *Streptopus roseus* and *Aralia nudicaulis*, which have compound leaves, the number of leaflets was counted.

Statistical analysis

Species-area curves were calculated for each control and exclosure plot by using *PC-ORD v 6* to calculate the expected number of herb species for an increasing number of subplots (McCune and Mefford, 2011). The program does this by finding the mean number of species in 1 subplot, then 2 subplots, 3, 4, and so on, ignoring the spatial distribution of subplots within each control/exclosure. The average expected number of species was then graphed against the number of subplots for each site and fitted to a power function $S = cA^z$ to graph the species-area curve. The intercept (c) and slope (z)

values between control and enclosure plots were then compared using a paired t -test in *JMP Pro v 9.0.2* (SAS Inc., 2012).

Differences in means for individual variables (morphology results, individual species and group percent covers, basal area, c and z values, etc.) between control and enclosure plots were compared using two-sample t -tests assuming unequal variances in *JMP Pro v 9.0.2*. Data were checked for normality with a Shapiro-Wilk test using the null hypothesis that the data are normal and assessed for outliers using a distribution histogram. Results were analyzed between control and enclosure plots at individual sites, and site averages were also compared using paired t -tests. A X^2 test was used to assess categorical responses between control and enclosure plots (i.e. presence and absence of fruits or flowers).

In order to assess possible impacts due to differences caused by environmental gradients such as age of enclosures, forest type, and nitrogen and carbon concentrations in mineral soil, the difference between enclosure and control values were also plotted against gradient data and Pearson product-moment correlation coefficients (r) were computed in *JMP Pro v 9.0.2*.

Vegetation percent cover data were analyzed in *PC-ORD v 6* using species matrices containing herb species alone (93 species) as well as a matrix containing both herb and shrub species (105 species). Species-area curves were calculated for all sites together, then for each control and enclosure plot individually. To avoid a sparse species matrix, species not found in > 5% of all plots (30 plots) were deleted, leaving 33 species in the herbs only matrix and 45 (33 herbs and 12 shrubs) in the herb and shrub matrix.

Matrices were relativized by row so that the proportion of species in each plot summed to one. A detrended correspondence analysis (DCA) was used to compare species percent cover similarity between control and exclosure plots. To compare across all 12 sites, average percent cover of species in control or exclosure plots was used. A multiple response permutation procedure (MRPP) was run to analyze the statistical significance of overall species composition between control and exclosure plots. Matrices were first analyzed with all subplots ($n = 25$) and non-rare species and then assessed for outliers and analyses re-run without subplot outliers, as well as without subplot and species outliers. Since site M2 had a unique species composition compared to the other 11 sites, all analyses were re-run for M2 using its original species.

Results

Overstory

Canopy cover varied between sites as well as between some paired plots (Table 3). The Encampment Forest sites tended to have mostly cedar, white pine, and paper birch in their canopies while sites at Tettegouche and Judge C.R. Magney State Parks tended to have more quaking aspen and paper birch. The Gooseberry and Split Rock State Park sites had mostly cedar and paper birch. Site EnB had a slightly different canopy between the control and exclosure, with more cedar in the control and more white spruce in the exclosure. Sites G1 and T2 had more quaking aspen in their control plots and more cedar in their exclosures. All other sites had similar canopy covers between control and exclosure plots.

Forest type also varied between sites and among control and exclosure plots. Sites EnM, SR, and T1 all had a larger proportion of deciduous species in their exclosure plots while sites G1, M1, M2, M3, and T2 had a larger proportion of deciduous species in their control plots (Table 3). Canopy basal area did not vary across sites ($p = 0.507$, Table 3).

Soil types

Study sites had a range of soil types including loam, clay loam, sandy clay loam, sandy loam and silty clay (Table 3). Soil types were generally similar between control and exclosure plots with the exception of the Encampment Forest sites. Site EnA had more clay loam in the control and loam in the exclosure, site EnB had sandy clay loam in the control and sandy loam in the exclosure, and sites EnF and EnM had loam in their control plots and clay loam in their exclosures.

Pellet counts

The number of pellet groups found varied by site, with site M3 having the highest density (0.39 groups/m²) and the other sites ranging from 0.02 to 0.10 groups/m² (Figure 3).

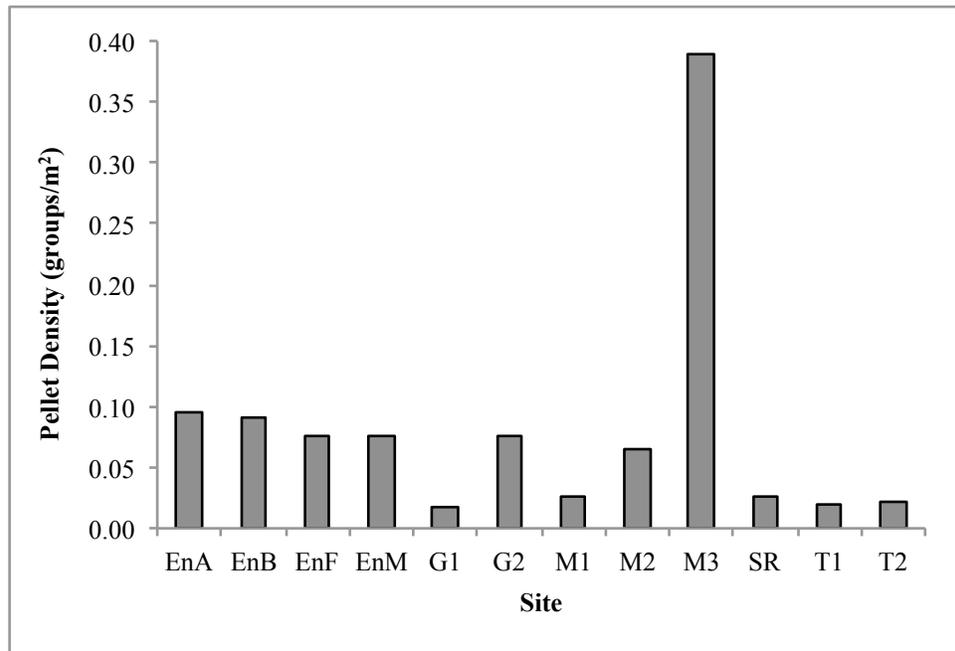


Figure 3. Calculated pellet group density at each site. Numbers reflect pellet groups found in control plots at each site.

Table 3. Site characteristics for the twelve study sites.

Site	Age (years)	Size (ha)	Basal Area (m ² /ha)		Canopy		Forest Type		Soil Texture	
			<i>C</i>	<i>Ex</i>	<i>C</i>	<i>Ex</i>	<i>C</i>	<i>Ex</i>	<i>C</i>	<i>Ex</i>
EnA	23	0.26	32.12	20.84	Cedar-White Pine	Cedar-White Pine	1.0	1.0	Clay Loam	Loam
EnB	24	0.23	20.07	20.09	Cedar-White Pine	Spruce-White Pine	1.0	1.0	Sandy Clay Loam	Sandy Loam
EnF	21	0.22	33.71	30.12	Cedar-White Pine	Cedar-White Pine	1.0	1.0	Loam	Clay Loam
EnM	9	0.19	66.62	38.12	Cedar-Paper Birch	Cedar-Paper Birch	1.0	1.5	Loam	Clay Loam
G1	21	10.50	16.15	33.71	Paper Birch-Aspen	Cedar-Paper Birch	3.0	1.5	Clay Loam	Clay Loam
G2	24	10.77	68.88	70.31	Cedar-Paper Birch	Cedar-Paper Birch	1.0	1.0	Sandy Loam	Sandy Loam
M1	11	0.14	36.76	36.69	Paper Birch-Aspen	Paper Birch-Aspen	3.0	2.0	Silty Clay	Silty Clay
M2	11	0.18	30.82	30.52	Paper Birch-Spruce	Paper Birch-Spruce	2.5	2.0	Sandy Loam	Sandy Loam
M3	11	0.80	39.47	41.98	Paper Birch-Spruce	Paper Birch-Spruce	2.0	1.5	Sandy Loam	Sandy Loam
SR	17	1.66	59.66	56.23	Cedar-Paper Birch	Cedar-Paper Birch	1.5	2.0	Loam	Loam
T1	15	1.34	30.00	25.87	Paper Birch-Aspen	Paper Birch-Aspen	2.5	3.0	Sandy Loam	Sandy Loam
T2	9	2.17	36.36	40.69	Paper Birch-Aspen	Cedar-Paper Birch	3.0	2.0	Loam	Loam

DCA and MRPP

When all sites were included in a single analysis, there were no differences between control and exclosure plots in herb layer species composition (MRPP, $n = 24$, $p = 0.863$) or with the addition of the shrub layer into the species matrix (MRPP, $n = 24$, $p = 0.791$). This is expected, given the range of forest types and exclosure ages across the sites. Sites were separated in species space mostly by their average percent shrub cover, average soil C:N (Chapter 3), and age of exclosure (Figure 4).

There were significant differences in herb species coverage between individually paired control and exclosure plots ($p < 0.05$ for sites EnA, EnF, EnM, G1, M1, M2, SR, T1; $p < 0.1$ for EnB and G2). When row outliers were removed, then herb layer composition in control and exclosure plots at M3 were significantly different ($p = 0.094$), as well as when both row and species outliers removed ($p = 0.038$). Species composition was not significantly different between control and exclosure sites at T2 ($p = 0.161$). Except for sites T2 ($p = 0.417$) and G2 ($p = 0.372$), control and exclosure plots also had significantly different species composition when shrub cover was included ($p < 0.05$). Control and exclosure plots at site M3 were significantly different after both row and species outliers were removed ($p = 0.049$). The relative weight of individual species on DCA axes differed by site with no visible pattern.

greater in older and younger exclosures (~11 years and 24 years), but was greater in controls for middle-aged plots ($p = 0.021$, $R^2 = 0.58$, Figure 5). Coverage of *Aralia nudicaulis* declined with exclosure age, ($r = -0.584$, $n = 12$, $p = 0.046$, Figure 5). The total coverage of all shrubs also declined with exclosure age ($r = -0.476$, $n = 12$, $p = 0.118$, Figure 5).

Graminoid cover was correlated with a forest type gradient (ranging from conifer dominated to deciduous/hardwood dominated), with more graminoid species in control plots than exclosures at hardwood-dominated sites but fewer under conifer canopies ($r = 0.654$, $n = 12$, $p = 0.021$, Figure 6). Shrubs and graminoid covers declined with pellet group counts, with exclosures having greater percent covers when controls had lower pellet group counts but lower covers when controls had higher counts ($r = -0.489$, $n = 11$, $p = 0.127$; $r = -0.725$, $n = 11$, $p = 0.012$ respectively).

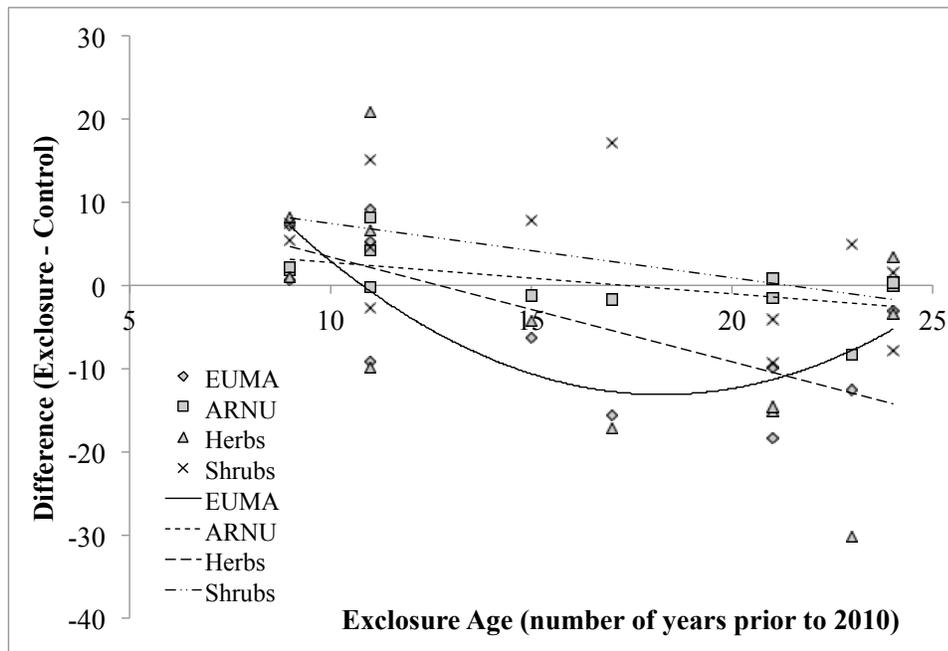


Figure 5. Difference between exclusion and control herb species and group covers along an exclusion age gradient. EUMA = *Eurybia macrophylla*, $R^2 = 0.58$, $p = 0.021$; ARNU = *Aralia nudicalus*, $r = -0.584$, $n = 12$, $p = 0.046$; Herbs $r = -0.466$, $n = 12$, $p = 0.127$; Shrubs $r = -0.476$, $n = 12$, $p = 0.118$.

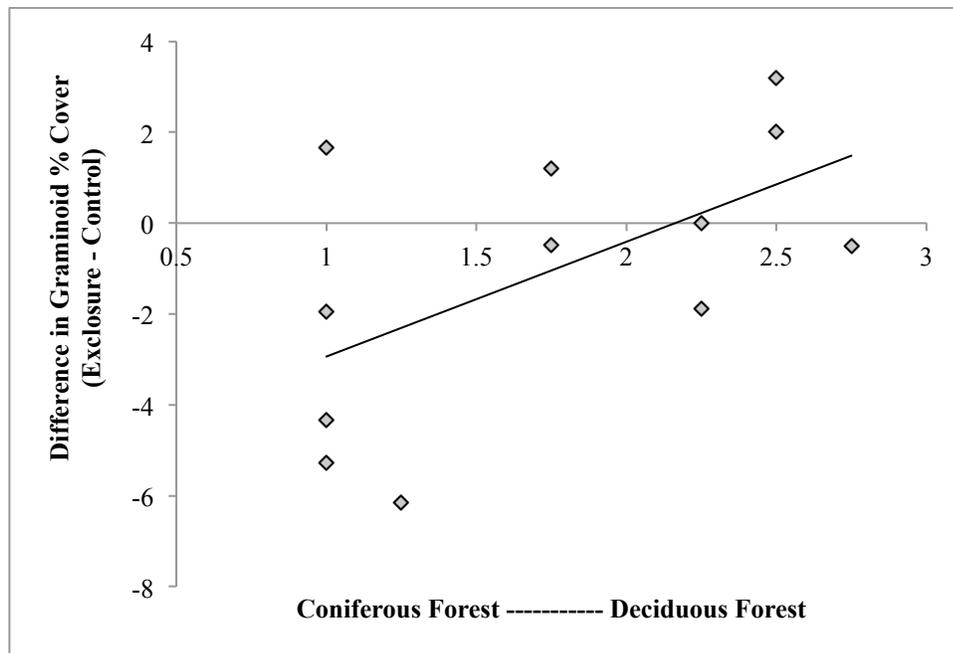


Figure 6. Difference between graminoid cover in exclusion and control plots along a forest type gradient. The x-axis shows a forest type gradient ranging from 1 (conifer dominated) to 3 (deciduous dominated), a scale calculated by the basal area ratio of coniferous to deciduous species at each site (Table 2); $r = 0.654$, $n = 12$, $p = 0.021$.

Sapling regeneration

The total number of saplings found in each plot was higher in exclosures compared with control plots ($p = 0.048$, Figure 7), although differences between exclosures and controls were only significant for sites EnA, EnF, M1, M2, M3, and SR ($p < 0.1$). For sites with *Pinus strobus* saplings, exclosures had a higher average number of saplings than controls ($p = 0.040$). A similar trend was observed for *Abies balsamea* saplings ($p = 0.020$).

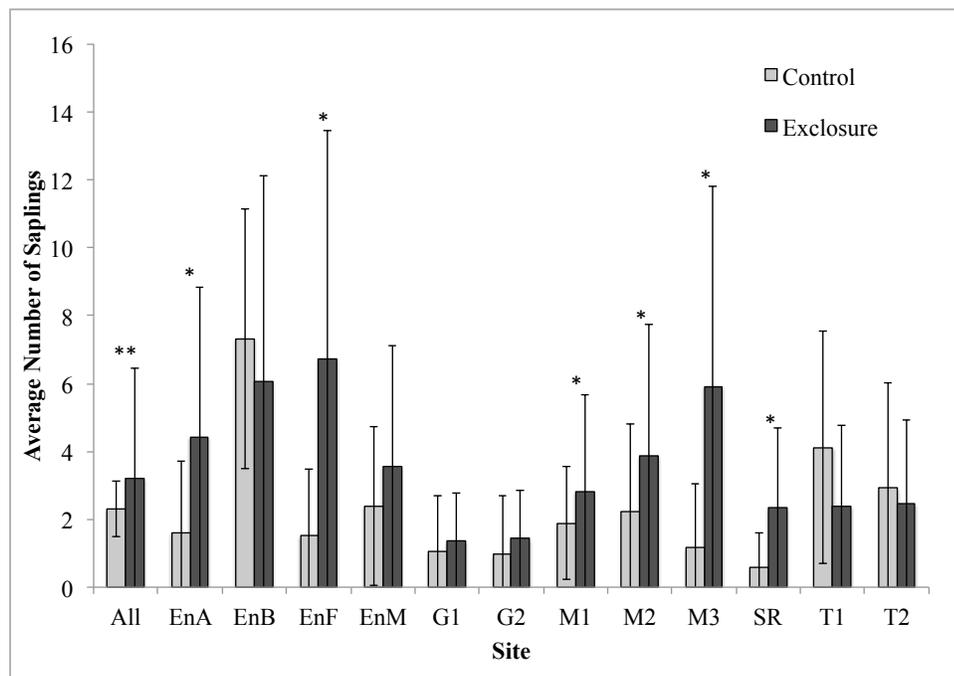


Figure 7. Average number of saplings in control and exclosure plots. Error bars reflect standard deviation. First column, “All” reflects averages across all sites. Differences are significant at $p < 0.1$ are indicated by *, differences significant at $p < 0.05$ are indicated by **.

Species richness, evenness and diversity

Average species evenness was greater among exclosures overall than controls across sites ($p = 0.082$, Table 4). Average species richness and average Shannon Weaver diversity were not significantly different overall between control and exclosures ($p > 0.10$), but did differ within individual sites. Species evenness was also greater in individual exclosure sites compared to controls (significant for sites EnB, EnF, G1, and SR, $p < 0.1$). Species richness was greater in exclosure sites for G1, M1, and M3 but lower in exclosures for sites EnA, EnF, and EnM ($p < 0.05$). Shannon Weaver diversity was generally higher in exclosures (significant for sites EnB, G1, M1, M3, SR, and T1, $p < 0.1$), but was greater in the control for two sites (EnA and EnM, $p < 0.05$).

There was lower species richness in exclosures in conifer forests but higher species richness in exclosure in hardwood forests ($r = 0.595$, $n = 12$, $p = 0.041$). Species richness differences between exclosures and controls declined with pellet group counts ($r = -0.711$, $n = 11$, $p = 0.014$). Shannon Weaver diversity also slightly declined with pellet group counts ($r = -0.513$, $n = 11$, $p = 0.106$).

Table 4. Mean Shannon Weaver diversity, richness, and evenness in control and exclosure plots across sites. * represents $p < 0.1$, ** represents $p < 0.05$.

Site	Shannon Weaver Diversity		Species Richness		Species Evenness	
	Exclosure	Control	Exclosure	Control	Exclosure	Control
All	1.378	1.286	7.139	7.193	0.723*	0.671
EnA	1.262**	1.617	6.160**	9.360	0.673	0.746
EnB	1.769**	1.442	7.708	7.440	0.905**	0.725
EnF	1.740	1.550	7.640**	9.875	0.909**	0.693
EnM	1.288**	1.673	6.400**	8.440	0.701	0.798
G1	1.620**	1.232	11.480**	8.680	0.664*	0.574
G2	1.372	1.330	7.720	7.080	0.670	0.702
M1	1.119**	0.812	6.080**	4.280	0.638	0.548
M2	1.309	1.310	5.440	6.000	0.799	0.752
M3	1.562*	1.404	7.880**	6.920	0.762	0.739
SR	1.686*	1.435	9.080	9.040	0.768**	0.657
T1	1.087*	0.908	6.480	5.880	0.597	0.527
T2	0.724	0.715	3.600	3.320	0.593	0.590

Morphology

Stem lengths of *C. borealis* and *S. roseus* were longer in exclosures compared to controls ($p < 0.05$; Figure 8). *C. borealis* and *S. roseus* had more leaves in exclosures compared with controls ($p < 0.05$; Figure 9). *C. borealis* and *S. roseus* also had a greater proportion of fruit or flowers in exclosures than controls ($p = 0.09$, 0.04 respectively; Figure 10). *E. macrophylla* had a slightly greater proportion of fruiting or flowering plants in control plots ($p = 0.082$).

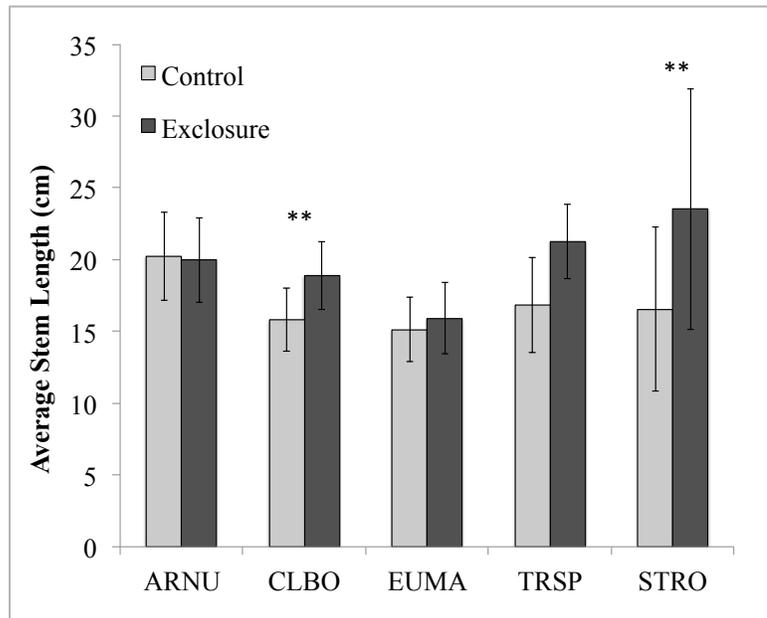


Figure 8. Average stem lengths in control and exclosure plots for individual species. ARNU = *Aralia nudicaulis*, CLBO = *Clintonia borealis*, EUMA = *Eurybia macrophylla*, TRSP = *Trillium* species, STRO = *Streptopus roseus*. Differences significant at $p < 0.05$ indicated by **. Error bars show standard deviation.

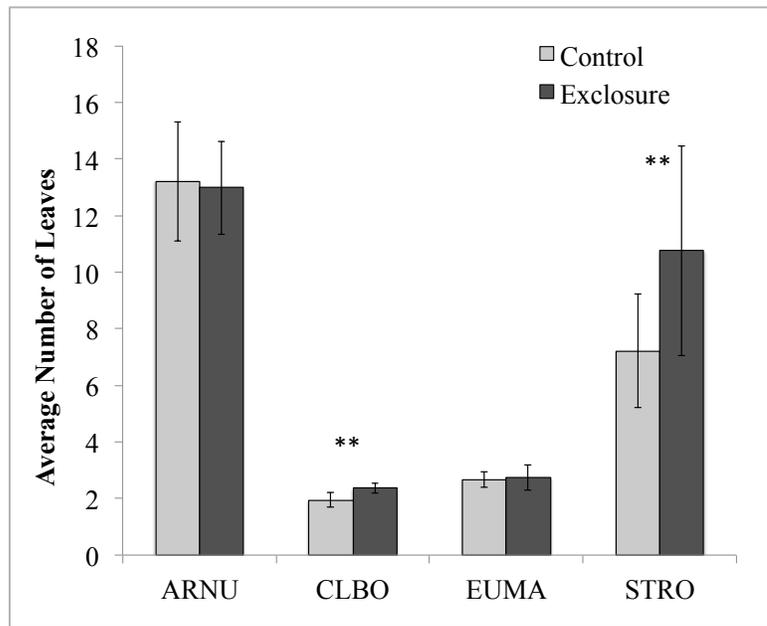


Figure 9. Average number of leaves in control and exclosure plots for individual species. ARNU = *Aralia nudicaulis*, CLBO = *Clintonia borealis*, EUMA = *Eurybia macrophylla*, STRO = *Streptopus roseus*. Differences significant at $p < 0.05$ indicated by **. *Trillium* species not included as all individual plants typically have three leaves. Error bars show standard deviation.

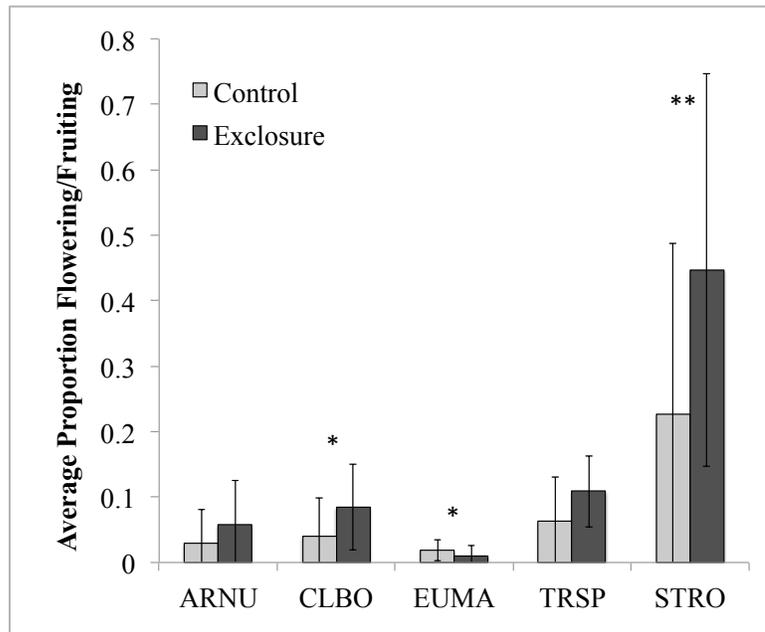


Figure 10. Average proportion of flowering or fruiting plants in control and exclosure plots for individual species. ARNU = *Aralia nudicaulis*, CLBO = *Clintonia borealis*, EUMA = *Eurybia macrophylla*, TRSP = *Trillium* species, STRO = *Streptopus roseus*. Differences significant at $p < 0.05$ indicated by **; differences significant at $p < 0.1$ indicated by *. Error bars show standard deviation.

Species area curves

Values for the intercept of the power function, c , ranged from 3.4 to 12.0 for the control sites and from 4.0 to 14.0 for the exclosure, showing a slightly higher range in the exclosure. The average c value (8.48) was not different between the control and exclosure sites ($p = 0.992$; Figure 11). Values were greater in exclosures with deciduous canopies but higher in controls at sites with conifer dominated canopies ($r = 0.570$, $n = 12$, $p = 0.053$, Figure 12).

Values for the slope of the power function, z , ranged from 0.15 to 0.48 for the control and 0.16 to 0.52 for the exclosure, again showing a slightly higher range in the exclosure. The averages for the control (0.37) and for the exclosure (0.38) were not significantly different ($p = 0.55$; Figure 13). However, most z values were greater in the

exclosure plot compared to control. Differences between exclosure and control values did not show a linear or polynomial correlation to exclosure age or forest type.

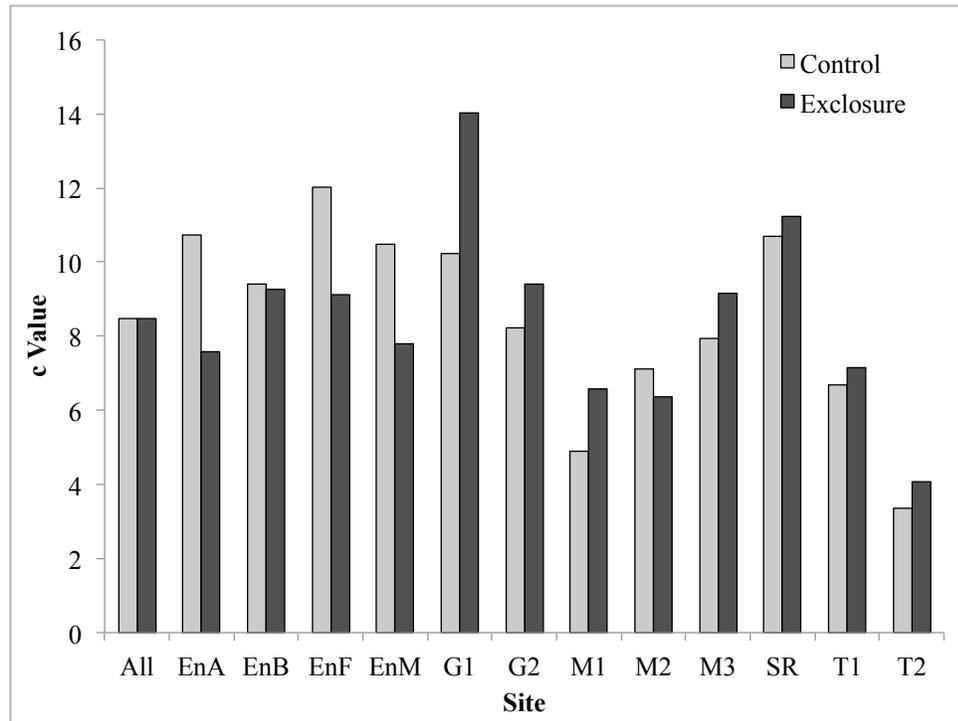


Figure 11. Calculated species area curve c values in control and exclosure plots. First column, “All” reflects averages across all sites.

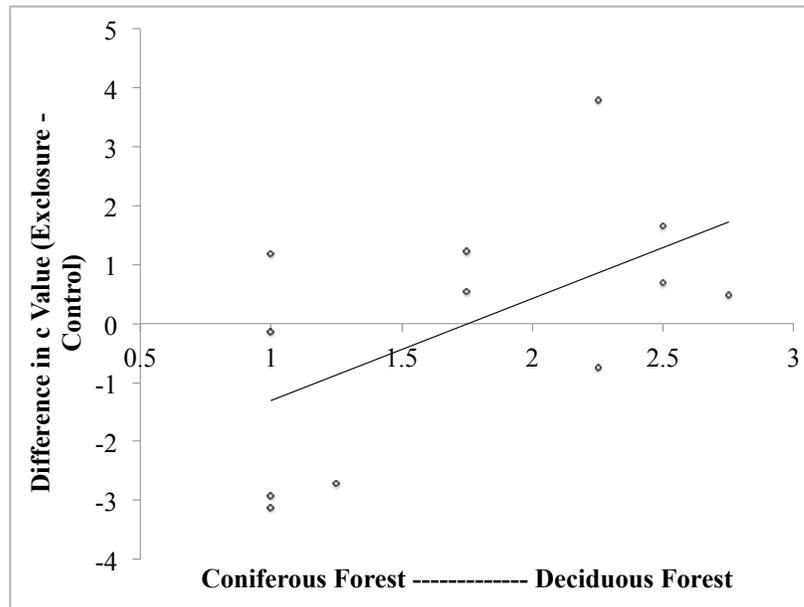


Figure 12. Difference between calculated c values in exclosure and control plots along a forest type gradient. The x-axis shows a forest type gradient ranging from 1 (conifer dominated) to 3 (deciduous dominated), a scale calculated by the basal area ratio of coniferous to deciduous species at each site (Table 2); $r = 0.570$, $n = 12$, $p = 0.053$.

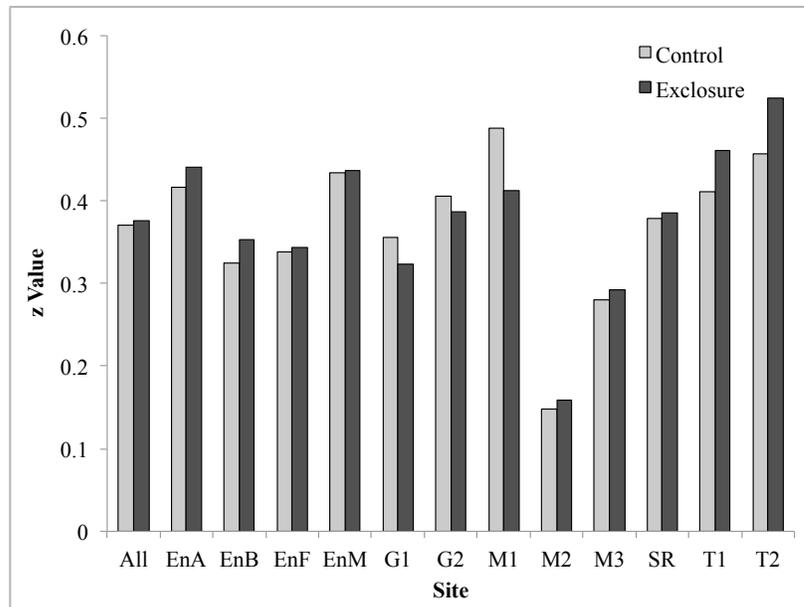


Figure 13. Calculated species area curve z values in control and exclosure plots. First column, “All” reflects averages across all sites.

Discussion

The results of our study supported our hypothesis that understory vegetation composition is consistently different between control and exclosure plots, with the exception of site T2. *C. borealis* was found consistently more in exclosure sites, along with greater sapling regeneration. *P. aquilinum* generally had greater coverage in control plots. However, the behavior of other differences varied considerably between sites. Some of the changes can be accounted for by environmental gradients – such as age of exclosure and forest cover. Species richness and diversity also varied by site and were correlated with environmental gradients. In general, species richness was higher in exclosures for hardwood sites and areas with low pellet group counts. The amount of shrubs also varied by age, with a higher percent in young exclosures but lower percentages in older exclosures, which might suggest a succession to how forests recover from historical herbivory. The general amount of shrub or herb species found in an exclosure at a designated point in time may depend on how long the area has been protected. Some responses may show a decline through time, while others may have a nonlinear response. This may explain why some previous studies have found conflicting results – they were investigating responses at different points along the successional timeline.

We also found strong trends in the way species morphology changes in response to herbivory and the conditions of the recovering forest, such as shorter stem lengths, fewer leaves, and producing fewer fruits and flowers. The methods of our study do not allow for us to tease apart whether these changes are due to plants inside exclosure

requiring less defenses, a response to the increased shade conditions from greater woody growth, or a combination of the two factors. However, Rooney (1997) found that *Maianthemum canadense*, another preferred browse species of white-tailed deer, had longer stem lengths and density as well as a higher number of flowering shoots in an area protected from browsing compared to plants accessible to deer. This study had more similar microclimates between browsed and un-browsed areas, and the author attributed the results to white-tailed deer browsing habits alone.

Our results support the work of previous studies that have found significant effects of ungulate herbivory on vegetation composition and morphology. In particular, Horsley et al. (2003) found that the percent cover of ferns and graminoids increased along with increasing deer browse, and that effects on vegetation were evident at deer population densities much lower than those commonly found in northern forests. Tremblay et al. (2007) found that deer browsing at high population densities reduced viability and success of balsam fir seedlings, but at very low deer densities seedling mortality was also impeded by woody overgrowth. In our sites, graminoid and shrub percent cover, species richness, and species diversity all declined with deer population densities.

Interestingly, our research suggests there is a pattern to forest succession after the pressures of ungulate herbivory are removed, which may explain why our results varied by site. The speed of this succession could be influenced by a variety of factors as well including local seed stock, ground cover, and dominant species. Due to local extirpation of species by heavy browsing through time, it may also be the case that individual sites

never truly “recover” from browse damage even if ungulate herbivores are not allowed to return. For instance, Tanentzap et al. (2011) found that canopy tree species regeneration continued to decline even after herbivory pressure was reduced, suggesting that preventing browse damage alone (either through deer population reduction or exclosure creation) may not be sufficient to return the community to a pre-browse state. Essentially, active restoration may be required and the amount of energy and effort may be much larger than that needed to prevent extensive herbivore damage from the beginning.

Pastor et al. (1996) determined that the species area curve parameters c and z could be used as relative measures of local and landscape species richness, respectively. We did not find significantly different parameter values inside and outside of exclosure plots, but there was a correlation between local richness and percent shrub cover, where richness decreased with increasing shrub cover. This suggests large areas of shrub cover – more commonly found without large herbivores present – may have fewer species per unit area.

The patterns we found appear to depend on the type of forest and relative density of herbivores, indicating the need to use a whole-system assessment of herbivore damage to truly understand impacts. Our finding of consistently different understory compositions between control and exclosure plots as well as age and forest type gradients suggests that ungulate herbivores are influencing vegetation communities. Also, the potential for legacy effects or continued changes after reduction in herbivory indicates that ungulate herbivores could be creating alternative stable states in these systems.

Future research should attempt to monitor forest recovery over time in more similar environments to better determine succession after herbivory. Researchers could return to the same control and exclosure plots over a time interval (between every 1 to 5 years) and record species percent cover, thereby tracking composition through time. The same might be done to determine if plant morphology recovers through time or changes occur quickly after the threat of browsing is removed.

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Chapter 3. Effects of herbivores on available nitrogen and soil C and N

concentrations

Overview

Ungulate herbivores have been known to affect soil nutrient dynamics through selective grazing as well as nitrogen egestion. In most studies, areas subjected to heavy historical browsing have been shown to have depressed nitrogen mineralization and mineral soil C:N ratios. In this study, we investigate changes in litter layer depth, nitrogen mineralization, and mineral soil composition between control and exclosure plots along the North Shore Highlands of Lake Superior. At 12 sites of varying ages and canopy composition, we measured litter layer depth and total carbon and total nitrogen inside and outside exclosures. We measured available nitrogen (NH_4 and NO_3) at six of these sites using ion exchange resin bags. We found higher NH_4 concentrations at 2 control sites, but total carbon and total nitrogen did not show a consistent pattern of variation between exclosures and controls. These discrepancies may correlate with underlying environmental gradients, such as exclosure age, forest type or herbivore population densities.

Introduction

Although the visibly large changes in forests due to ungulate herbivory seem to come from browse damage, deer and moose can have many secondary effects on forest processes as well, including altering nutrient dynamics. Herbivores can influence nitrogen (N) availability in different ways, by adding readily available N to the soil through excretion and egestion (Floate, 1970; Ruess and McNaughton, 1987; Hobbs, 1996) and by changing the forest floor litter composition through selective browsing (Pastor et al., 1993). Northern hardwood and conifer forests are home to two important ungulate herbivores, moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). These populations can fluctuate either according to natural cycles or by anthropogenic management. As these populations change through time, the amount of N recycled to the environment is likely to change as well, potentially affecting the vegetation community.

A significant amount of research has been conducted on how large herbivores affect N cycling (Hobbs, 1996; Pastor and Danell, 2003; Pastor et al., 2006). Nitrogen in urine and feces is often in the form of soluble ammonium and urea - both of which are easily converted within weeks of deposition to the plant-needed form of nitrate. Therefore, N added to the environment through animal excretion or egestion may be important for N flux as it may be more readily available than N recycled through decomposition (Doak, 1952). However, studies have also shown that the preferential grazing by moose and deer can change the nutrient composition of litter returned to the forest floor, decreasing N mineralization (Pastor et al., 1993). Ungulates tend to browse on nitrogen-rich species, mostly hardwoods and herbs, while leaving the less palatable lignin (and therefore carbon) rich vegetation untouched. This may result in a forest floor litter layer with a much higher carbon to nitrogen (C:N) content, potentially slowing net N mineralization (Bryant and Chapin, 1986; Pastor et al., 1988; Pastor and Naimon, 1992).

Pastor et al. (1993) found that excluding moose from an area resulted in higher N mineralization, providing evidence that suggests herbivores do influence local N cycles and primary productivity. A study by Knops et al. (2000) also found soil N was lower in areas with higher deer densities while deer exclosures had higher N availability, largely due to an increase in abundance of the nitrogen-fixing legume, *Lathyrus venosus*. In boreal forest systems, browsing decreases fine root production and increases root turnover rates, likely affecting nutrient dynamics (Ruess et al., 1998). In particular, fewer

ectomycorrhizal infections in heavily browsed plants may magnify nutrient intake deficiencies (Rossow et al., 1997).

In this chapter we investigate how ungulate herbivores influence nitrogen and carbon cycles in order to better understand their influence in northern hardwood and conifer forests. We hypothesized that we would find a deeper litter layer inside the exclosures, along with more available N and a lower mineral soil C:N ratio. We expected that similar trends would be evident in all exclosures. We also assessed the relationship between N mineralization and deer density, as expressed by pellet counts. Finally, we examined the relationship between species area curves (calculated in Chapter 2) and soil characteristics to assess the impact of changing nutrient composition on species richness. A study by Hutchinson et al. (1999) supported evidence of a link between below ground process (nitrogen mineralization) and above ground biodiversity, with greater herbaceous species richness in areas with higher nitrogen availability. Therefore, we expected to find a positive relationship between nitrogen availability and species area curve *c* values, a measure of relative richness (Pastor et al., 1996).

Materials and methods

Study sites

This study used the same exclosure sites as described in Chapter 2 above and Table 1. These twelve exclosure sites located along the North Shore region of Lake Superior were selected based on limited management disturbance and well-maintained fences.

Total carbon and nitrogen measurements

One 10 cm soil core sample was taken from each of the 25 subplots at the same time vegetation data was collected (summer 2010) using a 2.25 cm diameter soil probe. The litter layer was scraped away from the sampling site prior to sampling, so that only mineral soil was included. Core samples were stored at -18 °C until they could be later dried in a laboratory oven at 60 °C for at least 48 hours. Once dried, samples were ground using a mortar and pestle and placed into separate paper envelopes. Samples were later combined in equal parts by transect for a total of 5 mixed samples per plot. Composite samples of 10-15 µm were analyzed for total C and N (as a percentage of dry mass) using a Thermo Scientific FLASH EA™ 1112 Elemental Analyzer.

Soil inorganic nitrogen measurements

The relative availability of inorganic N at each plot was measured using ion exchange resin (Binkley and Matson, 1983). Resin bags were prepared in the lab by placing 8 g of mixed-bead resin into a nylon mesh pouch sealed with zip ties and nylon string. Two bags were buried 10 cm deep along each transect ($n = 10$), using a random number generator to determine two locations along each line. Due to irregularly sized enclosures within Judge C.R. Magney State Park, a third bag was randomly placed along 2 lines in each plot. Dates of bag placement were May 18, 2010 (Encampment Forest), May 20, 2010 (Gooseberry Falls State Park), and June 3, 2010 (Judge C.R. Magney State Park). Resin bags were collected on October 14, 2010 (Gooseberry and Encampment), and October 15, 2010 (Magney). These were stored in separate plastic bags at 1.6 °C until they could be extracted in the lab.

We used a double extraction method to reclaim mineralized nitrogen from the resin. Bags were first washed in the lab using distilled water, dried in an oven at 60 °C for at least 48 hours, then the mineralized N was extracted using two rinses of 1M KCl (1 g resin / 15 mL) and vacuum filtration. Samples were analyzed for ammonium (NH₄⁺) and nitrate (NO₃⁻) using a Technicon autoanalyzer.

Statistical analysis

Differences in plot-level means for individual variables (cation availability, soil composition, etc.) between control and exclosure plots were compared using two-sample *t*-tests assuming unequal variances in *JMP Pro v 9.0.2* (SAS Inc., 2012). Data were checked for normality with a Shapiro-Wilk test using the null hypothesis that the data are normal and assessed for outliers using a distribution histogram. Results were analyzed between overall control and exclosure plots ($n = 12$) at individual sites, and individual site averages were also compared using a paired *t*-test ($n = 25$).

Species area curves

Slope and intercept values for species area curves calculated in Chapter 2 were regressed against resin and mineral soil results.

Results

Changes in litter depth

Overall, exclosures had approximately a 50% deeper litter layer than control plots ($p = < 0.001$, Figure 14). Ten of twelve individual sites had a significantly greater litter layer depth in their exclosures than control plots ($p < 0.05$; $p < 0.10$ for EnB and M3).

Litter depth was not significantly different between exclosures and controls in sites T2 and EnM ($p = 0.90, 0.10$ respectively).

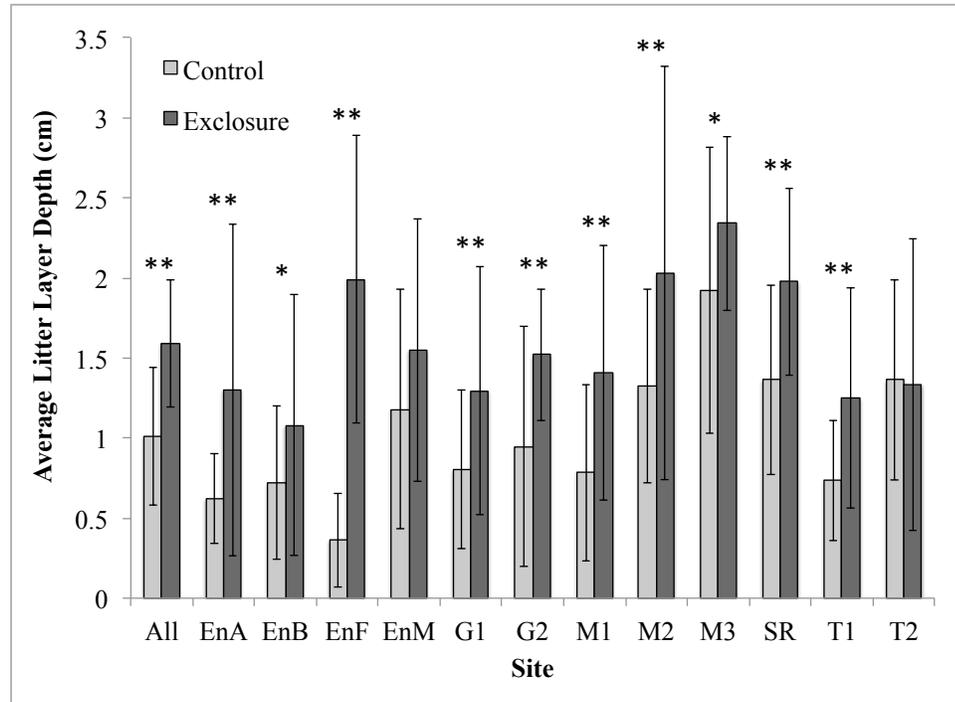


Figure 14. Average litter layer depth in control and exclosure plots. Error bars reflect standard deviations. "All" column is an average of all 12 control and 12 exclosure site values. Differences significant at $p < 0.05$ indicated by **; differences significant at $p < 0.1$ indicated by *.

Changes in available nitrogen

Available nitrogen showed few significant differences between exclosures and controls. NH_4 concentrations were significantly higher in controls at sites M1 and M2 ($p < 0.1$). NH_4 was higher, but not significant, in exclosures EnF and G1 ($p < 0.18$; Table 5). NO_3 did not differ between exclosures and controls, except for a weak increase in the exclosure at site M2 ($p = 0.14$). Total N availability also did not differ between exclosures and controls, although site EnF had a weakly elevated amount in the exclosure ($p = 0.14$).

Table 5. Nitrogen availability results for control and exclosure plots tested. Site "All" shows averages of the averages for all controls and exclosures; * represents a significant difference at $p < 0.1$, ** represents a significant difference at $p < 0.05$.

Site	NO ₃ (ug/g)		NH ₄ (ug/g)		Total N (ug/g)	
	<i>Control</i>	<i>Exclosure</i>	<i>Control</i>	<i>Exclosure</i>	<i>Control</i>	<i>Exclosure</i>
All	22.34	22.38	69.51	63.03	91.85	85.41
EnA	22.22	22.82	51.39	46.97	73.61	69.79
EnF	11.68	16.69	45.76	92.91	57.44	109.60
G1	25.29	20.60	51.69	75.16	76.98	95.77
G2	40.15	17.73	90.95	67.61	131.09	85.34
M1	14.11	25.18	95.44*	54.33	109.55	79.50
M2	20.55	31.23	81.86**	41.23	102.41	72.47

Mineral soil

C and N concentration also varied by site but with no consistent difference between exclosures and controls. Average total carbon was greater in the exclosure at G2 ($p = 0.07$), but greater in the control plots at EnM and T2 ($p < 0.05$; Table 6). Average total nitrogen was greater in the exclosure at site G2 ($p = 0.02$), and higher in the control at site EnM ($p = 0.01$). The C:N ratio was higher in site EnM's exclosure ($p = 0.06$), and higher in the control plot at site T2 ($p = 0.005$).

Table 6. Average total soil carbon and nitrogen results for control and exclosure plots. “All” represents the average of all site averages for control and exclosures ($n = 12$); * represents $p < 0.1$, ** represents $p < 0.05$.

Site	Carbon (% of dry mass)		Nitrogen (% of dry mass)		Average C:N	
	<i>Control</i>	<i>Exclosure</i>	<i>Control</i>	<i>Exclosure</i>	<i>Control</i>	<i>Exclosure</i>
All	9.28	9.38	0.42	0.44	22.82	21.73
EnA	5.91	4.95	0.26	0.23	22.64	21.98
EnB	5.32	4.10	0.22	0.18	24.79	22.35
EnF	6.77	6.60	0.33	0.29	20.70	22.61
EnM	13.35**	10.55	0.64**	0.47	20.81*	22.75
G1	7.56	8.19	0.35	0.39	21.50	21.05
G2	4.42*	6.15	0.22**	0.32	21.36	19.31
M1	5.05	5.46	0.25	0.26	20.46	22.34
M2	20.74	21.07	0.67	0.75	30.83	28.36
M3	14.38	15.33	0.58	0.64	24.53	25.01
SR	10.60	13.03	0.49	0.57	21.71	22.55
T1	7.16	8.08	0.36	0.39	19.71	20.82
T2	11.58**	9.01	0.67	0.81	17.43**	11.63

Total carbon varied parabolically with exclosure age, where younger and older exclosures had lower total carbon and middle-aged exclosures had a greater total carbon ($R^2 = 0.58$, $p = 0.032$; Figure 15). Average total nitrogen declined with number of pellet groups found (pellet group methods and results discussed in Chapter 2), with areas with the largest amount of pellet groups having the lowest soil nitrogen ($r = -0.502$, $n = 11$, $p = 0.116$; Figure 16). Neither carbon, nitrogen, nor C:N had linear or parabolic correlations with forest type ($p > 0.15$).

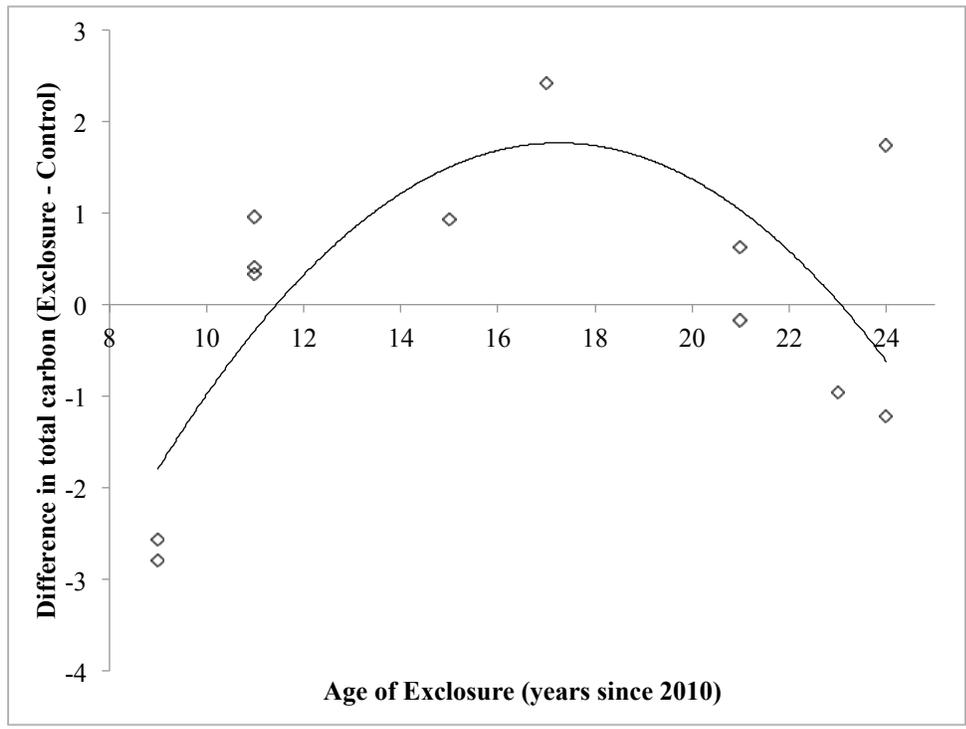


Figure 15. Average difference in total carbon (% of dry mass) between enclosure and control plots along an enclosure age gradient; $R^2 = 0.58$, $p = 0.032$.

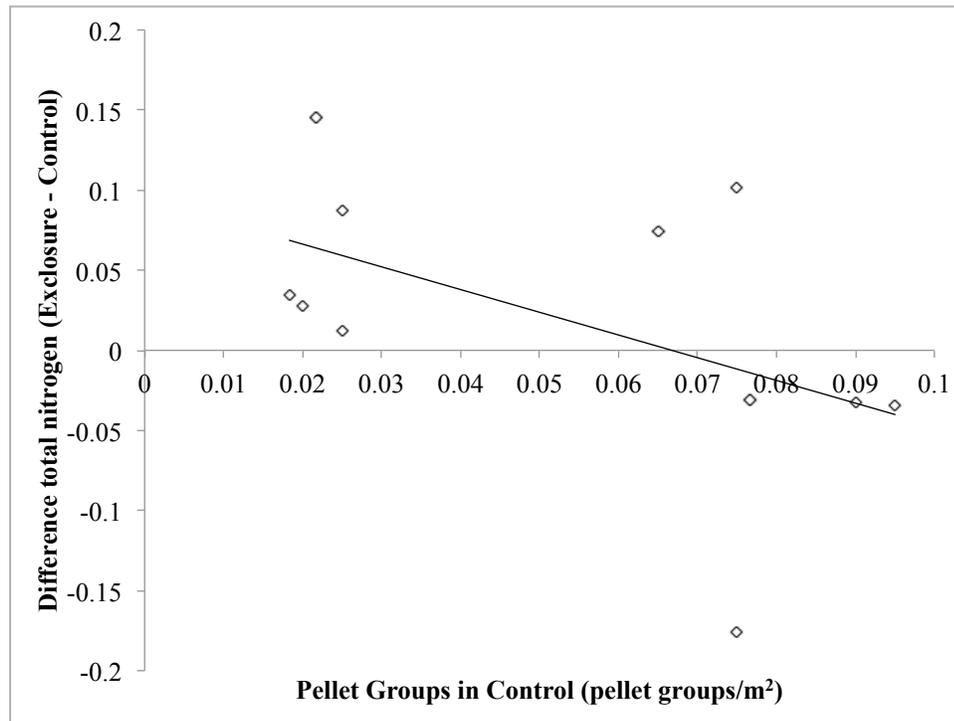


Figure 16. Average difference in total nitrogen (% of dry mass) between exclosure and control plots along a pellet group density gradient. Pellet group density represents a relative measure of deer population size, with areas with a larger pellet density assumed to have a larger deer population size. Site M3 excluded from gradient as an outlier due to a much larger pellet group density; $r = -0.502$, $n = 11$, $p = 0.116$.

Species area curves

Differences between exclosure and control c values were directly correlated with average total nitrogen, with exclosure having higher total nitrogen also had higher c values than their control plots ($r = 0.586$, $n = 12$, $p = 0.045$; Figure 17). Individual z values increased with average total carbon ($r = -0.642$, $n = 12$, $p = 0.001$; Figure 18). Site z values declined with soil C:N ratios, with exclosures having a greater C:N value generally having a lower z value than their control plots ($r = -0.489$, $n = 12$, $p = 0.107$; Figure 19).

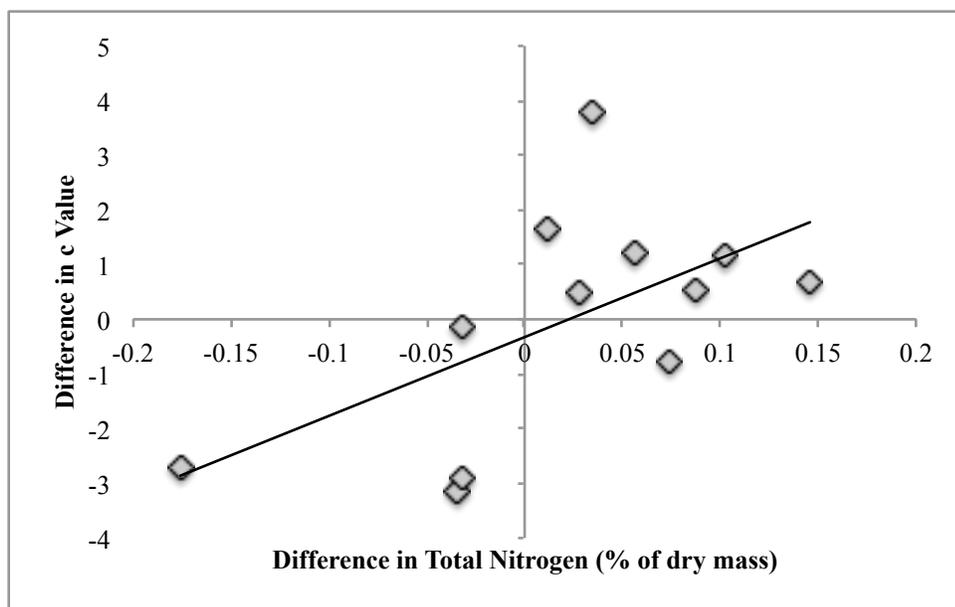


Figure 17. Relationship of the average difference in species area curve c values compared to the average difference in total nitrogen in enclosure and control plots. Positive values on either axis represent a greater value in the enclosure; $r = 0.586$, $n = 12$, $p = 0.045$.

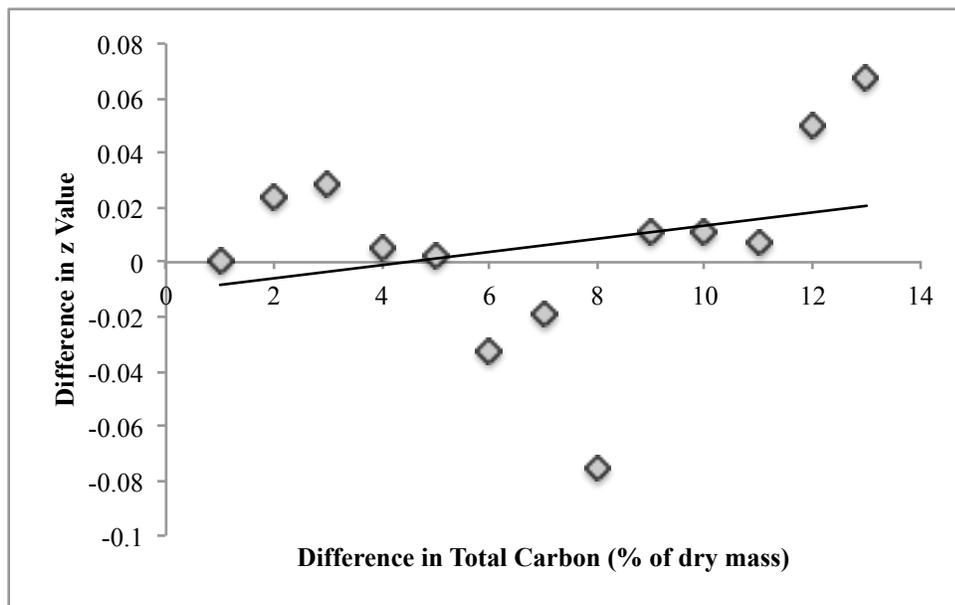


Figure 18. Relationship of the average difference in species area curve z values compared to the average difference in total carbon in enclosure and control plots. Positive values on either axis represent a greater value in the enclosure; $r = -0.642$, $n = 12$, $p = 0.001$.

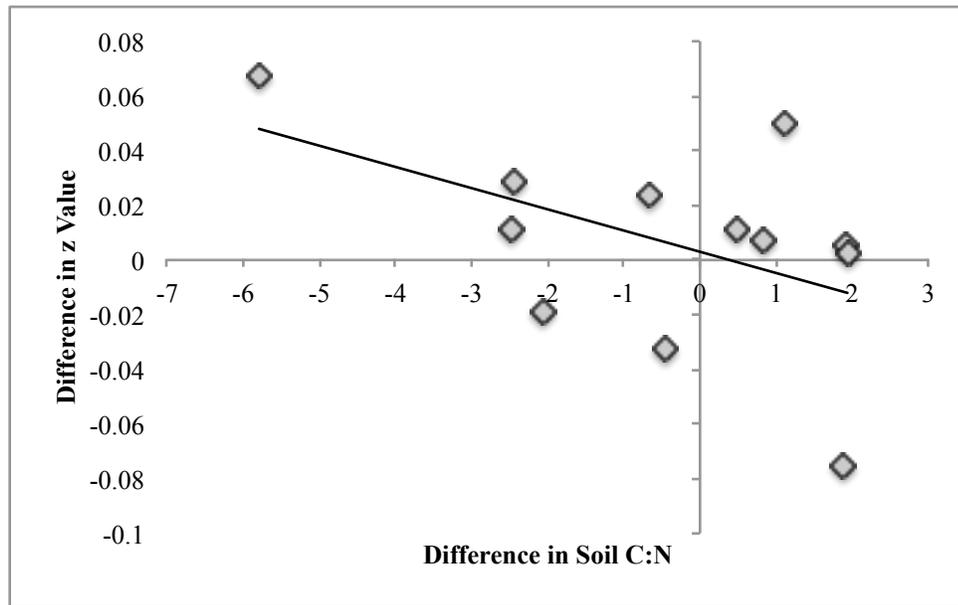


Figure 19. Relationship of the average difference in species area curve z values compared to the average difference in soil carbon to nitrogen ratios in exclosure and control plots. Positive values on either axis represent a greater value in the exclosure; $r = -0.489$, $n = 12$, $p = 0.107$.

Discussion

Our results supported the hypothesis that litter depth would be greater inside exclosures. The results for available nitrogen did show differences between controls and exclosures, however these trends varied by site. These differences may be due to exclosure age differences, although with only three sites measured it is difficult to determine any significant changes through time. Mineral soil differences also varied by site and were correlated with exclosure age and pellet group counts, with total carbon lower in younger and older exclosures and greatest in middle-aged exclosures. This seems to suggest that there may be an initial lag-time before soil carbon increases (correlated with more shrub cover in exclosures), then a decrease through time along with decreasing shrub cover.

Interestingly, we did not find any correlation between differences in total nitrogen and forest canopy types but we did find a correlation between total nitrogen and relative deer densities. Sites with fewer pellet counts tended to have a greater total nitrogen in their exclosures while sites with more deer tended to have greater total nitrogen in their control plots. This may indicate a threshold for deer population size effects, where lower populations could have opposite effects on the forest than larger population sizes. For instance, at larger population sizes the amount of nitrogen inputs from egestion of fecal pellets may offset the reduction in nitrogen mineralization from herbivore induced litter layer changes, resulting in higher soil nitrogen. Previous studies have found evidence that ungulate pellets do increase nitrogen mineralization, although the researchers suggest that the increase would be less than the ultimate decrease in mineralization rate due to selective browsing (Pastor et al., 1993).

The parabolic trends found in our study also disagree with Horsley et al. (2003), who found only linear trends relating deer population sizes to species richness and fern, grass and sedge cover over a 10-year period. This could indicate that quadratic trends require longer than a 10-year period to surface. This implies that herbivory studies should seek to monitor changes over much longer time intervals.

Pastor et al. (2006) found that after 40 years, areas with high rates of browsing will decrease localized nitrogen cycling; our results partially supported this finding. Pastor et al. also suggested that due to patchy browse patterns, some areas might show high browse damage and low nitrogen availability while others will not, potentially resulting in localized extinctions of certain vegetation species. Although we did not

necessarily find “extinctions” in our study, we did find evidence of greatly reduced population sizes, potentially beyond the level of recoverability.

The parameters from the species area curve calculations help to explain how species richness varies at the local and landscape scale. In this study, higher total nitrogen in the enclosure was correlated with higher local species richness, and higher total carbon and C:N in the enclosure was correlated with lower landscape species richness. This suggests the importance of soil nutrient dynamics in the probability of encountering new species, although perhaps not in an expected way.

Due to the high variability in results across the North Shore Highlands, we would recommend further investigation of these relationships. In particular, studies should look at nutrient dynamics along a forest succession continuum, as our results have suggested there may be a time delay for effects to become evident in the mineral soil. This would mean that further impacts due to changes in mineral soil composition, such as changes in herbaceous species diversity, might take even longer to detect. Knowing how changes occur along a broader timeline may provide park officials with the advance notice needed to make appropriate management decisions.

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Chapter 4. Conclusion

Our study found significant differences between vegetation and nutrient dynamics in control and exclosure plots. The patterns observed were not simple, however. Trends varied by site and seemed to depend on the forest type, age of exclosure, relative deer population size. Some differences may also have been due to unknown variables such as local browse history before exclosure establishment, which could influence community structure and processes. The number of significant differences we found between control and exclosure vegetation may suggest there are different states that exist during and after heavy ungulate browsing. However, without an equal interval of exclosure establishment for a detailed timeline or available baseline data, we are unable to determine whether or not these systems exhibit hysteresis, a characteristic of alternative stable states (Beisner et al., 2003).

We did find evidence that supports sections of the proposed feedback loop in Chapter 1 (Figure 1). Specifically, we found changes in the composition of herbaceous species between areas with and without which suggests that browse activity does influence this forest layer. A number of sites showed increased amounts of ferns and graminoids in the control plots, and we found consistent evidence that the presence of deer reduces seedling recruitment of canopy species. Although our results for soil characteristics varied by site, the variation itself may suggest the ungulate herbivores are affecting the stability of these forest systems. Overall, our research supports the first four steps in our feedback loop, which could indicate some test sites are progressing towards a state change (Figure 20). The differences in species composition and nutrient availability

found between control and exclosure plots also may indicate that recovery from heavy browsing pressure may move very slowly and potentially may never be fully complete.

Current projections for climate change impacts suggest that northern Minnesota forests will face drought along with increasing air temperatures, resulting in the migration of native species northward. With the addition of this stress placed on forest ecosystems, other influential forces may become more pronounced – including those due to herbivory. A modeling study by Didion et al. (2011) suggested the combined impacts of climate change and browsing in a mountain ecosystem might reduce browsing-induced stand basal area reduction, but could also result in very different species composition changes from either impact alone.

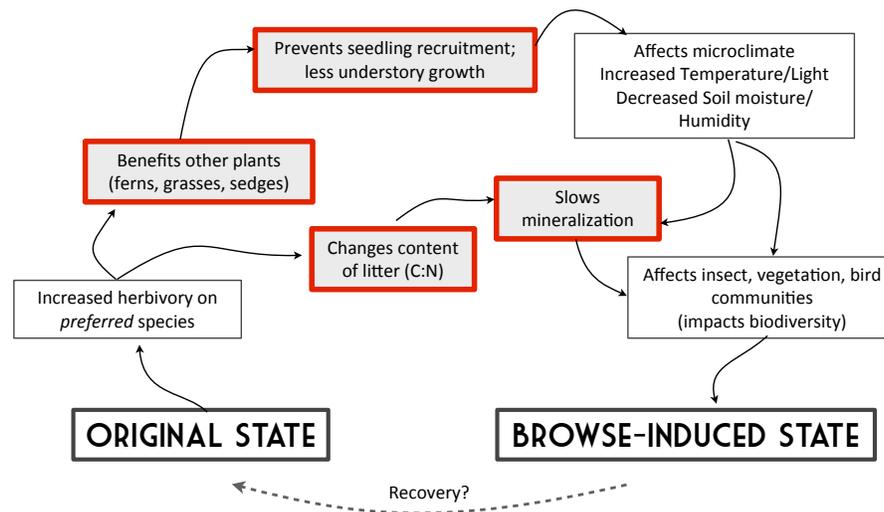


Figure 20. Proposed feedback loop of changes caused by ungulate herbivory to northern temperate forest communities. Based on research summarized by Côté et al. (2004). Red boxes indicate areas of the loop which were supported by research from our study.

This area of research would greatly benefit from future investigation of vegetation and nutrient changes through time, particularly within similar forest types and browse conditions as these appear to be confounding factors. Our study provides evidence of the

possible “legacy effects” caused by heavy browsing pressure and seems to agree with Tanentzap et al. (2011) in that removing herbivore pressure alone did not stop or remedy the negative effects of browsing. In some instances, it appears that effects can continue for years after herbivore removal (e.g. decreasing herbaceous species cover in exclosures over time). Studies attempting to quantify individual forest states with high and low deer densities would also be highly beneficial – providing indicators of an alternative forest community would help forest managers to monitor changes due to deer and moose. In order to determine whether alternative stable states truly exist in these communities, researchers also need to show evidence of hysteresis – which may be difficult in these systems due to forest succession timelines.

With the current projections for climate change already suggesting these ecological systems will undergo significant changes, any source of additional stress could become amplified or its effects altered, especially in systems exhibiting alternative stable states. Therefore it is important that we continue to work at understanding these systems from multiple dimensions concurrently or we may risk misunderstanding dynamic processes that could result in costly and potentially permanent change to North Shore ecosystems.

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