



Comparing and Evaluating Methods Used to Assess the Impacts of Ungulate Browsing in the Great Lakes Network National Parks

Natural Resource Technical Report NPS/GLKN/NRTR—2013/680



ON THE COVER

Clockwise from top left: groundlayer sampling in an area of low deer density; browsed woody plant; browsed herbaceous plant; forest understory in an area of high deer density.

Photographs taken by NPS Great Lakes Network field crew.



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Abstract

Ungulate browsing affects many plant species, shifting patterns of relative abundance, plant community diversity, and ecosystem processes. Although we know that ungulates have many impacts, we lack consistent, widespread, and standard methods to monitor and assess them. We also lack a monitoring network that would allow us to track and compare regional impacts. The Great Lakes Network Office (GLN) of the National Park Service is in an ideal situation to address these issues. The GLN identified white-tailed deer as an important vertebrate that could threaten the health of Great Lakes forests. To supplement their permanent vegetation monitoring program, the GLN monitors deer and moose browse on woody and herbaceous plants in each of nine national parks in the region. We used data from these surveys to investigate (1) how best to simplify sampling methods to make them more efficient, (2) different scales of relationships among patterns of browsing across species and sites (with the goal of inferring efficient and reliable indicators of ungulate impacts on woody species), and (3) relationships between these patterns of woody browse and local site impacts on understory species. Our findings suggest that the GLN can reduce the sample size for monitoring woody plant browse while retaining high reliability. The woody browse data reveal clear preferences by ungulates among species, but these vary across the region and with local community composition. Ungulate impacts in the understory are correlated with woody browse impacts and also vary according to local ecological conditions. To move toward a more efficient and accurate composite indicator of overall ungulate impacts, we constructed and compared models that include varying specificities and amounts of data. One combines data on woody plant browsing with data on the abundance of specific understory species to infer overall levels of threat from ungulate browsing. These modes of analysis and combined models should improve our ability to monitor the impacts of ungulate browsing, particularly if such methods can be expanded and standardized across the region.

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Introduction

The overabundance of white-tailed deer (*Odocoileus virginianus* Zimm.) has well-documented negative impacts on forests in the Great Lakes region of the United States. Current deer populations are much higher than historic levels; in Wisconsin alone deer populations have more than tripled since the 1960s and consistently remain higher than goals established by the Department of Natural Resources (Wisconsin DNR 2010). Waller and Alverson (1997) identified white-tailed deer as a keystone herbivore due to their ability to affect the distribution and abundance of many other forest species. High deer densities in the region negatively impact tree regeneration (Rooney and Waller 2003) and significantly affect the growth and reproduction of herbaceous understory species (Augustine and Frelich 1998). It is clear these trends are occurring not only in the Midwest but also in the eastern U.S. where deer populations have been high for quite some time and the trends of decreased regeneration and diversity are even more pronounced (see Augustine and McNaughton 1998, Russell et al. 2001, and Côté et al. 2004 for reviews). Moose (*Alces alces andersoni*) browsing also detrimentally affects woody plant growth and regeneration while drastically altering the succession of forests due to preference and avoidance of particular species (Snyder and Janke 1976, McInnes et al. 1992). Given the potentially serious impacts of ungulate herbivory, it behooves us to monitor levels of browse and consequent changes in species abundances and community composition. Furthermore, we need to establish a baseline to track changes through time, which will allow us to assess the profundity of these effects. Land managers in the National Park Service (NPS) and across the Great Lakes region concur, but lack any consistent, widespread, and standard methods for such monitoring.

Most ungulate browsing studies focus on impacts on tree seedlings and saplings rather than general understory vegetation. While tree regeneration is an economically important issue, understory species make up the majority of stand diversity and provide important habitat for birds and other forest vertebrates (McShea and Rappole 1992, Canterbury et al. 2000, Newson et al. 2011). Further, the understory species targeted by herbivory are often of special conservation concern, such as orchids and other showy wildflowers (Miller et al. 1992). Browse in the understory, however, is hard to detect. Often the whole plant is ripped up, leaving no direct evidence of browse, and instead effects are noticed gradually over time by observed reductions in abundance, height, and number of reproductive individuals (Anderson 1994, Augustine and Frelich 1998, Rooney and Waller 2003, McGraw and Furedi 2005). This creates challenges for conservation managers who wish to detect browse on sensitive understory species but do not have years' worth of site history at their disposal.

While detection and quantification of browse levels on forest structure is a challenge in itself, directly linking the abundance of ungulates to these observed changes is a further challenge. Due to deer mobility, estimates of deer densities in an area are not only costly and labor-intensive, but often times inaccurate (see Waller et al. 2009 for a review of methods). While moose densities are carefully tracked in Isle Royale National Park, it is rare to have an island situation so easily monitored with species confined to a limited area. More recently, efforts have been made to sidestep costly, inaccurate estimates of deer density by assessing ungulate impacts directly from measures of browsing pressure (Kirschbaum and Anacker 2005, Morellet et al. 2007, Latham et al. 2009). Ultimately, it is these impacts on vegetation, rather than the causal factors, that are of interest to forest managers. While some forest monitoring programs have adopted this idea,

implementation has been problematic, with continual refinement of methodology. One of these monitoring programs, administered by the National Park Service Great Lakes Inventory and Monitoring Network, has been monitoring ungulate browse impacts in the upper Midwest since 2007.

The Great Lakes Inventory and Monitoring Network (GLN) is part of the National Park Service's nationwide effort to establish long-term monitoring practices in order to make more scientifically sound management decisions. The GLN is one of 32 designated networks in the country, each charged with identifying "Vital Signs" for monitoring ecosystem health at the regional level. The Network consists of nine national parks, seven of which are associated with Great Lakes freshwater ecosystems and two of which are large, riparian corridors (Figure 1). Collectively, the nine parks exhibit a continuum of forest types ranging from eastern deciduous to northern hardwood to boreal. The GLN identified white-tailed deer as part of a group of "Problem Species" that ranked as the fifth highest priority among 46 Vital Signs identified for monitoring and management (Route and Elias 2005). Subsequently, a sampling protocol was created to measure the impact of this variable in concert with the Network's forest health monitoring protocol (Sanders et al. 2008).



Figure 1. Map of the nine national parks that make up the Great Lakes Inventory and Monitoring Network (<http://science.nature.nps.gov/im/units/GLKN/aboutus.cfm>).

When the GLN sampling protocol was developed in 2006, it was designed to provide high statistical power but required high sampling intensity and significant time and effort (Johnson et

al. 2006). While the tradeoff was sensible for the early phase of the monitoring program, the intervening five years of sampling on now permanently marked monitoring sites provide an opportunity to refine these methods to increase efficiency while sustaining accurate estimates of key parameters. Here, we use the data gathered in the initial round of sampling to identify patterns, relationships among variables, and associated redundancies. We use these to suggest how best to improve and streamline field monitoring methods.

We hypothesize that:

- a) plant species vary in their (i) abundance in the region, (ii) local attractiveness to ungulates, and (iii) susceptibility to and ability to recover from browse. This variation strongly affects a species' usefulness for monitoring browse impacts. Notably, species will lose their effectiveness as indicators as they become scarcer due to browsing;
- b) analyzing different scales of data at the levels of region, park, site, and species will yield varying degrees of information and utility;
- c) species that increase or decrease in abundance in response to browse create opportunities for positive and negative indicators of browsing impacts; and
- d) using path analysis models that incorporate known effects of a site's canopy composition on understory species will improve our ability to identify understory species to use as indicators.

By testing these hypotheses, we aim to: 1) increase the efficiency of browse monitoring practices employed by the GLN in the field, 2) identify trends detected in the woody browse data using both coarse and fine scales of data, and 3) attempt to solve the problem of linking understory impacts to woody browse observations when time is of the essence and deer and moose density data are not available.

Methods

Under the Inventory and Monitoring Program, National Park Service personnel completed plot establishment and the initial sampling round during the 2007-2011 growing seasons. A given park was sampled during only one of those years, and between one and three parks were sampled each year,. At the time of this report, only three of the parks had been sampled using the full and consistent browse survey methodology described here. For this reason, we only present and analyze data from these three parks. In particular, for this report we draw on field data gathered during the growing seasons in 2009 and 2010 from permanent monitoring sites established at Sleeping Bear Dunes National Lakeshore (SLBE), Pictured Rocks National Lakeshore (PIRO) and Isle Royale National Park (ISRO).

Sleeping Bear Dunes National Lakeshore is situated along the northeastern shore of Lake Michigan and comprises 169 km of Lake Michigan shoreline and inland forests dominated by American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.). Although eastern deciduous forests predominate, there are also significant inclusions of pine (*Pinus* sp. L.) forests on coarse textured soils. The park contains two islands in Lake Michigan. South Manitou Island has had deer only intermittently and for limited times. North Manitou Island has a more dramatic history. Here, deer were introduced in 1938, maintained at artificially high levels by supplemental feeding, then largely eradicated in the 1980s following acquisition by the National Park Service. This island now supports an estimated 0.77-1.2 deer/km² (2-3 deer/mile²; Sanders and Grochowski 2010).

Pictured Rocks National Lakeshore is located on the south shore of Lake Superior in Michigan's Upper Peninsula. This area marks a transition between eastern deciduous and northern hardwood forest types, which is controlled by both an east-west moisture gradient and a north-south temperature gradient driven by Lake Superior. In addition, large inclusions of coarse textured soils support *Pinus* spp. stands, resulting in a mosaic of hardwood and coniferous stands within the park.

Isle Royale National Park is a 72 km-long archipelago situated in northwestern Lake Superior and consists of one main island and over 400 smaller islands. This park is within the northern hardwood-boreal forest transition zone and encompasses large amounts of both biomes. The eastern third of the island has shallow soils and is dominated by balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss). Here, a large number of bays and inlets allow Lake Superior to moderate land temperatures, promoting boreal forests. On the western third of the island, sugar maple-yellow birch (*Betula alleghaniensis* Britton) and white cedar (*Thuja occidentalis* L.) forests form a mosaic across the landscape. Thicker, glacial derived soils predominate on the western side. This, coupled with higher elevations and a larger, cohesive landmass, promotes northern hardwood forests. While Isle Royale does not support deer, there is a significant moose population of interest in our present browse survey.

The Great Lakes Network's vegetation monitoring program sampled a total of 161 sites among the three parks (SLBE: 50 sites, PIRO: 59 sites, and ISRO: 52 sites). Within each park, site locations were randomly selected using a generalized random-tessellation stratified design (Stevens and Olsen, 2004). Vegetation was sampled using the Hybrid plot sampling design (see

Johnson et al. 2006) to characterize forest over- and understory vegetation and the environment at each site. This design encompasses aspects of both the U.S. Forest Service Forest Inventory and Analysis (FIA) plot (USDA 2005) and the Plant Ecology Laboratory plot developed and employed by Curtis (1959) in the upper Midwest in the 1950s and 1960s. The Hybrid plot was developed to include within plot replication and a large sampling area, while facilitating sample collection efficiency (Johnson 2006). Here, we rely on the data collected on the abundance (frequency) of understory species and estimates of browsing on woody species.

Each site's understory vegetation was characterized using 1 m² quadrats spaced every 5 m along each of three 50 m transect lines (30 quadrats total; Figure 2). Within each quadrat, the presence and identity of all herbaceous and shrubby species were recorded as well as the identity and number of tree seedlings. Among other measures, this allows for computation of the frequency of all herbaceous species across the 30 quadrats. In addition, field workers searched for three herbaceous species at each park previously identified as suitable local indicators of ungulate browsing based on deer preference (or avoidance) as determined in prior studies. These species are referred to as indirect-indicators because direct evidence of browsing is usually not evident by looking at the plant. Rather, over time these species display a reduction in height or lower rates of reproduction. For any such species present in a quadrat, workers scored the number of individuals present, how many were browsed, how many were reproductive, and the maximum height of that indicator species within the quadrat.

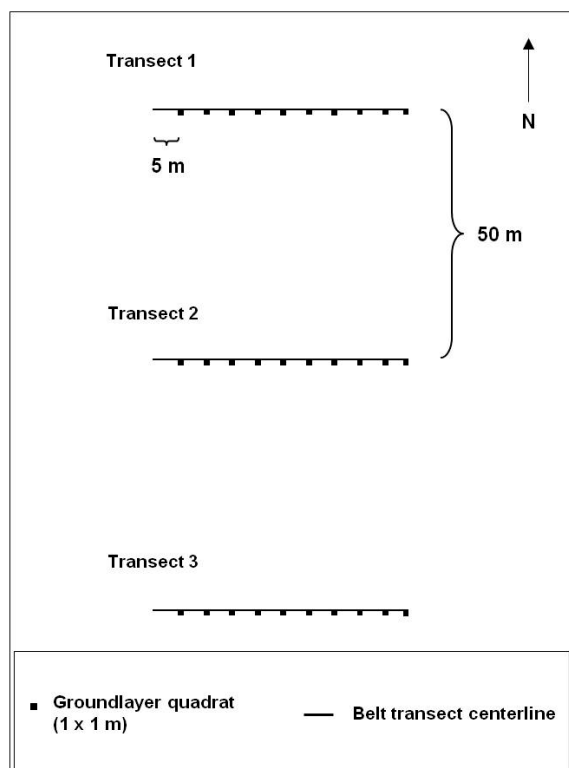


Figure 2. Diagram of understory sampling design at GLN permanent monitoring sites.

To quantify browsing levels on woody species, workers established 68 pairs of concentric browse circles, evenly distributed along the three east-west vegetation transects as well as four north-south transects flanking the ends of these (Figure 3). Centers for the paired circles were established every 5 m along these transects. The smaller circle (2m^2) had a radius of 0.80 m while the larger circle (4m^2) had a radius of 1.12 m. Within these, workers scored the presence and identity of all woody species between 0.2 and 1.8 m in height (defining the "molar zone") and noted whether branches of each species had been browsed. At Isle Royale, the molar zone was extended to 2.0 m to reflect the height of moose.

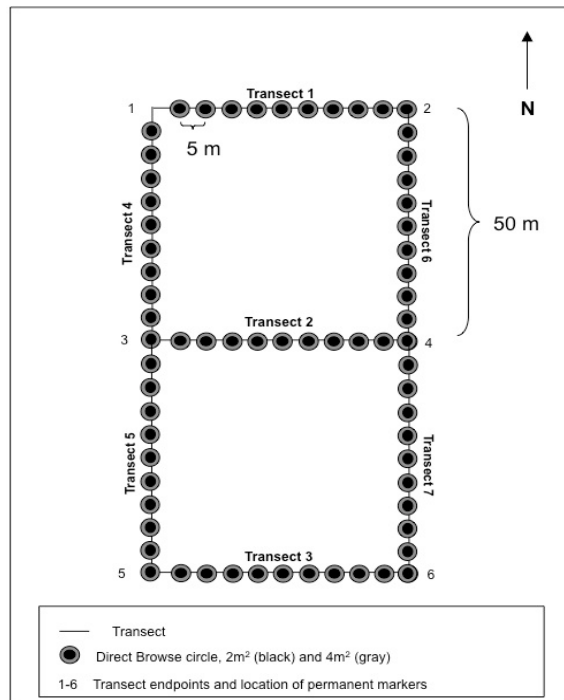


Figure 3. Diagram of woody browse sampling design at GLN permanent monitoring site.

Methods to Assess Impacts of Ungulate Browse

Basic Woody Browse Metrics

We sought to use the data generated from the browse circles described above to characterize patterns of ungulate browsing at several hierarchical levels. We first constructed metrics to describe the proportions of available stems browsed in each species at each site using the data obtained from both the 2- and 4m^2 browse circles. These data were then summed over species to obtain an aggregate measure of browsing at each site. These, in turn, were summed over sites to generate aggregate measures of browsing for each park and the region as a whole. We used these metrics to analyze variation in browsing within and among parks. We also analyzed the data by individual species within and among parks. To do this, we devised metrics to evaluate browse on each species relative to the overall incidence of browsing at each site. We used these relative browse indices to evaluate ungulate preferences and to test whether these preferences varied in a density dependent fashion or in response to overall woody browse abundance. Finally, we used

these metrics of browsing on woody species to test whether the abundance of particular understory plant species co-varied with woody species browsing. To correct for the effects of local community composition on these relationships, we devised path-analysis models to control for forest community composition.

In this report, we seek not only to identify general patterns of browse across parks, but also to demonstrate the different types of information that can be obtained when data are analyzed at the region-, park-, site-, or species-level. Different results can emerge at different scales given the different types of vegetation and the differences in ungulate type and density at each park. We therefore calculated summary browse metrics at each level as defined below and in Figure 4. We summarize the symbols used and their ranges in Table 1.

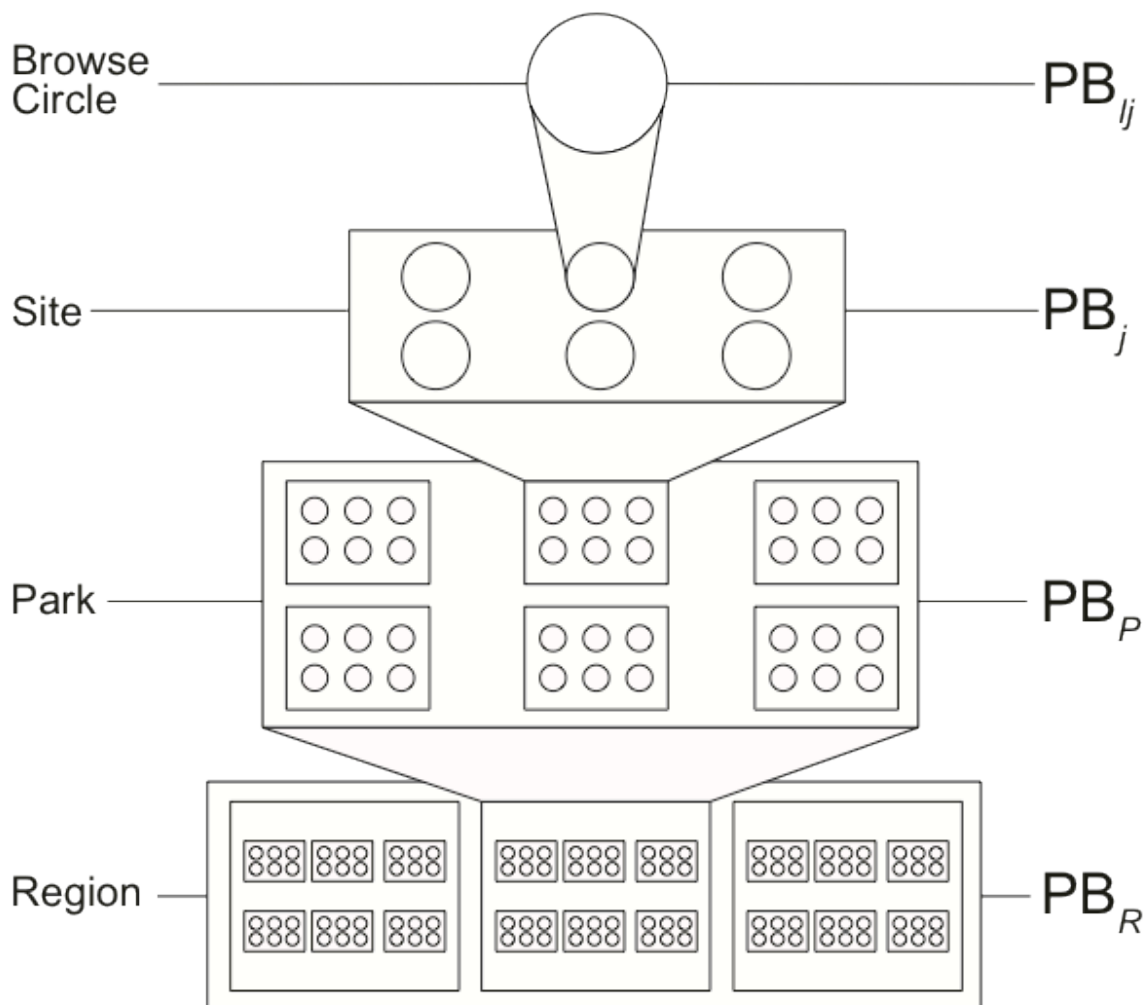


Figure 4. Visual display of nested calculations used in this report.

Table 1. Key to variables used in equations throughout the report.

Variable	Definition	Range of Calculation
i	Species	
l	Browse circle	
j	Site	
P	Park	
R	Region	
PB_{lj}	Proportion of browse in a browse circle	$i=(1, \dots, m)$ where m is the total number of woody taxa occurring at site j
PB_j	Proportion of browse on a site	$l=(1, \dots, q)$ where q is the total number of browse circles occurring at site j
PB_P	Proportion of browse at a park	$l=(1, \dots, w)$ where w is the total number of browse circles in each park
PB_R	Proportion of browse across the region	$l=(1, \dots, v)$ where v is the total number of browse circles in the region
π_{bj}	Morrellet Browsing Index	$l=(1, \dots, p)$ where p is the total number of browse circles with woody species present at site j
RBP_{lj}	Relative Browsing Preference for species i at site j	$i=(1, \dots, q)$ where q is the total number of browse circles occurring at site j

For each site j , we represent the occurrence of species i within browsing circle l as a binary variable (1 if present, 0 if absent) we term S_{ilj} . We then define the binary browse variable, B_{ilj} , to be 1 if any individual of species i within circle l is browsed and 0 if none are browsed. Using these variables, we can then define the proportion of browsing across all species within circle l as:

$$PB_{lj} = \frac{\sum_{i=1}^m B_{ilj}}{\sum_{i=1}^m S_{ilj}} \quad (1)$$

Here, m is the total number of woody taxa occurring at that site (Table 1). Note that if the circle is small, the probability of having several individuals of a given species in the circle is small so, browsing is being scored on individual stems. However, as circles become large enough to contain several individuals of a species, browsing on any of the individuals will cause that circle to be scored 1 for browse, tending to inflate the browsing metric relative to smaller circles. By repeating these calculations for both the 2- and the 4 m² browse circles, we could test for this effect (cf. Figure 16).

We can calculate the overall proportion of woody plants browsed at site j by taking the sum of all browse across each species i and dividing by the sum of occurrences of all species across all q browse circles on the site:

$$PB_j = \frac{\sum_{l=1}^q \sum_{i=1}^m B_{ilj}}{\sum_{l=1}^q \sum_{i=1}^m S_{ilj}} \quad (2)$$

where, q is the total number of browse circles occurring at site j (here 68).

To extend this to the park-level, we modify the above equation (Eq. 2) and calculate the overall proportion of woody plants browsed in a park P by taking the sum of all browse across each species i and dividing by the sum of occurrences of all species across all w browse circles in the park:

$$PB_P = \frac{\sum_{l=1}^w \sum_{i=1}^m B_{ilP}}{\sum_{l=1}^w \sum_{i=1}^m S_{ilP}} \quad (3)$$

where w now represents the total number of browse circles in each park. PB_P was then calculated for each individual park (SLBE $w = 3,400$ browse circles, PIRO $w = 4,012$ browse circles, ISRO $w = 3,536$ browse circles).

To identify overall browsing trends at the regional level, we further modify Equation 2 and calculate the overall proportion of woody plants browsed in the region R by taking the sum of all browse across each species i and dividing by the sum of occurrences of all species across all v browse circles in the region:

$$PB_R = \frac{\sum_{l=1}^v \sum_{i=1}^m B_{ilR}}{\sum_{l=1}^v \sum_{i=1}^m S_{ilR}} \quad (4)$$

where v represents the total number of browse circles in the region, across all sites and parks ($v = 10,948$ browse circles).

Site-specific Analyses

To track browsing trends across sites, we performed an ANCOVA using the proportion of woody browse on a site (PB_j) as our response variable, the total abundance of woody species detected on a site as our covariate, and park as our treatment. We then performed Tukey's HSD test to assess the differences between parks. Finally, we performed a one-way ANOVA to assess the differences in the mean values of PB_j across the three parks.

We also sought to test the utility of a site-level measure of browse established by Morellet et al. (2001) known as the "browsing index". While this index was developed as a way to assess browsing pressure as a proxy for deer densities, it has the potential to be useful for vegetation monitoring interests like those of the GLN particularly because it is efficiently measured in the field. The efficiency of this measure reflects the fact that individual species are not identified. Instead, the observer looks for any evidence of browse on any woody species. The Morellet Browsing Index (π_{bj}) is calculated as the number of browse circles l on a site with ≥ 1 woody species browsed (n_{bj}) at site j divided by the number of browse circles on a site with ≥ 1 woody species present (n_{aj}). For each circle l , we represent the occurrence of woody stems as a binary variable (1 if present, 0 if absent) we term S_{lj} . We then define the binary browse variable, B_{lj} , to be 1 if any woody individual within circle l is browsed and 0 if none are browsed:

$$n_{bj} = \sum_{l=1}^p B_{lj} \quad (5)$$

$$n_{aj} = \sum_{l=1}^p S_{lj} \quad (6)$$

$$\pi_{bj} = \frac{1 + n_{bj}}{2 + n_{aj}} \quad (7)$$

Here, p is the total number of browse circles with woody species present. The Morellet Browsing Index differs from our calculation of the proportion of browse at a site in two ways: (1) It estimates browsing pressure using a Bayesian approach, assuming a beta distribution. (2) At the site level, the Morellet Browsing Index uses a binary measure of browse and species presence within a sample unit (in our case a browse circle) rather than distinguishing among, and summing across, species within the sample unit. Using this metric, we repeated the analyses described above for PB_j .

Species-specific Analyses

The degree to which ungulates browse on a woody species clearly depends on their inherent preferences, which may vary locally in accord with differences in plant palatability and/or levels of toxic defensive compounds. Local patterns of browsing might also vary depending on the plant's abundance and the amount and types of alternative browse present. Landscape-level factors such as the amount of protective cover or shelter available and predation pressure can also play a role at a given site.

Current methods for evaluating ungulate browse on woody species extend from detailed demographic analyses of particular species (e.g., Rooney et al. 2000, 2002, McGraw and Furedi 2005) to 'blind' surveys that only score the presence of any woody species and whether they have been browsed (Morellet et al. 2001). Other attempts to create a browse index use an ordinal scale to categorize browse impacts (Boulanger et al. 2009) but these can be subject to observer bias.

We introduce here an alternative method to assess preferential browsing behavior on woody species. For each park, we first identified the 20 most abundant species as tallied in the 4 m² browse circles. Next, we calculated PB_{ij} , or the proportion of browse circles where species i is browsed out of the total number it is present on site j . We used a slight modification of Equation 2 where rather than summing across all species at a site, we calculated a unique PB_{ij} value for each species, i , at site j . For each species, we divided the total incidences of browse observed on that species by the total number of times the species was present in browse circles on the site:

$$PB_{ij} = \frac{\sum_{l=1}^q B_{il}}{\sum_{l=1}^q S_{il}} \quad (8)$$

In this equation, q represents the total number of browse circles at site j . PB_{ij} values range from 0 to 1.

We then calculated PB_j (Eq. 2) to estimate the browsing pressure across all species at that site. These values also range from 0 to 1.

Finally, we used these estimates to calculate the Relative Browsing Preference (RBP) for each species at a site in order to identify which species were taken at a rate greater or less than the site's average rate of browsing on woody species overall. This quantity represents the degree to which a particular species is browsed relative to the average browsing pressure experienced by all woody species present at a site (see Figure 5 for an example calculation):

$$RBP_{ij} = \frac{PB_{ij}}{PB_j} \quad (9)$$

After calculating this score at each site for the more abundant woody species in our sample, we performed t-tests on the log-transformed means of RBP_{ij} to test whether species were browsed preferentially ($RBP > 1$, or $\log RBP > 0$) or were avoided relative to other species ($RBP < 1$, or $\log RBP < 0$). Figure 5 gives an example of how to calculate RBP at one site. These analyses only tested samples with $n > 10$. We removed clear outliers as determined by the Grubbs outlier test. These consisted of 12 data points (5 at PIRO and 7 at ISRO) out of 3,220 total. To test whether the absolute and relative abundances of each of these species present at a site was related to PB_{ij} , we performed an ANCOVA using PB_{ij} as our response variable, the different abundance measures as our covariate, and park as our treatment.

Species (j) Browsed						
Browse Circle (i)	Species A	Species B	Species C	...	Species m	Browse Circle Total
1	--	1	--	--	1	2
2	0	0	--	--	--	0
3	1	--	0	1	1	3
...	...	...	...	...	...	...
q	0	--	--	--	--	0
Total	1	1	0	1	2	5

Species (i) Present						
Browse Circle (j)	Species A	Species B	Species C	...	Species m	Browse Circle Total
1	0	1	0	0	1	2
2	1	1	0	0	0	2
3	1	0	1	1	1	4
...	...	...	...	...	...	...
q	1	0	0	0	0	1
Total	3	2	1	1	2	9

In the above table, data are presented for a single site (j). Relative Browsing Preference (RBP) can be calculated for Species A as follows:

1. First, we calculate the proportion of browse on Species A at the site: $1/3 = 0.333$
2. Next, we calculate the proportion of browse on the entire site:
 $(1+1+0+1+2)/(3+2+1+1+2) = 5/9 = 0.556$
3. The Relative Browsing Preference for Species A can then be calculated as: $0.333/0.556 = 0.60$

Figure 5. Example calculation of RBP for one site.

Correlating Woody Browse to Understory Composition

One of our goals was to relate local patterns of browsing on woody plants to the abundance and characteristics of the herbaceous community present at a site. The monitoring conducted by the National Park Service fortunately provided considerable information on the abundance of forbs, shrubs, and tree seedlings at each site to compare with measured levels of woody browsing. However, we also know that environmental conditions and community composition vary widely across parks in ways that might affect this relationship. We therefore considered it important to control for the effects of potentially confounding factors likely to affect herbaceous communities in testing relationships between woody browse and potential understory indicators. For example, we know that ungulate species and densities vary across the region and among the three parks studied here. Within a region, ungulates may be more likely to favor certain forest canopy or understory community types. Their impacts may also vary in response to local variation in available browse and community composition. Koda and Fujita (2011) found a nonlinear relationship between deer density and deer herbivory on forest vegetation, particularly with regard to saplings. Krueger et al. (2009) stressed the importance of including herbivory as an environmental factor when seeking to predict forest succession. Ungulates can also have cascading effects on forest nitrogen cycles by affecting the quantity and quality of leaf litter and by increasing nitrogen through scat pellets (Pastor et al. 1993, Jensen et al. 2011, Bressette et al. 2012). As all these factors could affect the relationship between local woody plant browse and understory plant composition, it was important to consider various site factors.

To quantify browsing impacts on the understory, we sought to identify particular understory species whose presence, absence, or abundance could be used to indicate the local importance of browsing. We therefore explored our data for correlations between overall herb abundance or the abundance of particular understory species at sites and observed rates of browsing on woody plants at those sites. Because local environmental conditions and species dominance vary widely across parks, we sought to create a model accounting for the confounding variables of forest and habitat type that could influence either the abundance of deer and moose (and hence the level of browse) at a site or the abundance of understory species there.

To analyze both the direct and indirect effects of rates of woody browse on understory species, we constructed separate path analysis models for each park that incorporated possible effects of the overstory plant community on the overall (or particular) abundance of understory species. In these models (Figure 6), path (c) represents the relationship of interest, namely the direct effect of woody browse (our overall proportional browse index here) on the abundance of understory species. Path (b) represents the (direct) effect of the overstory community on herb layer abundance. The total effect of the overstory on herb communities reflects both this direct effect and an indirect effect mediated by how the overstory affects rates of woody browse ($a * c$). If paths (a) and (b) are important, using a simple regression to evaluate the strength of path (c) could be inaccurate and misleading. We estimate the importance of these paths in path analysis by applying a multiple regression to the dependent variable (overall or individual understory species abundance). We then use the standardized partial regression coefficients to estimate (b) and (c) and the simple correlation coefficient between the predictors to estimate (a).

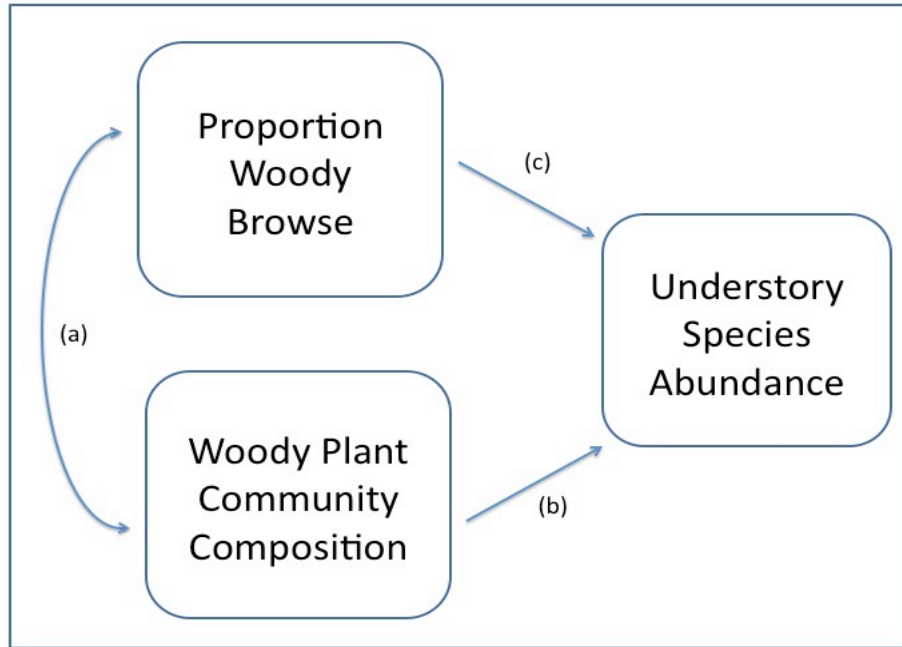


Figure 6. Path analysis diagram demonstrating direct and indirect effects of woody plant community and proportion of browse on understory species composition.

Constructing this model involved additional steps. First, to characterize how sites within parks differed in overstory species composition, we examined the similarity in woody species abundances in each park using Non-metric Multidimensional Scaling (NMDS). Our distance matrix was computed from Bray-Curtis measures of dissimilarity (PC-ORD Version 6.0, McCune and Grace 2002) using woody species frequencies. We extracted the resulting axis scores from the ordination. We determined the appropriate number of axes using a stress test in PC-ORD. We then used these axis scores (“woody plant community composition values”) to obtain the correlation coefficient (a) between overstory composition and the proportions of browse (PB_{ij}) across sites within each park. To ensure proper fits, we also plotted these relationships and how understory species abundance covaried with the proportion of browse at a site to ensure that they met our assumption of linearity.

Finally, we performed a multiple regression of the abundance of understory species i at a site against the woody plant community composition axis scores and the proportion of woody browse (PB_{ij}) to extract the path (partial regression - β) coefficients (b) and (c).

We analyzed predictors of total understory plant abundance using a similar technique. Here, in addition to using the average proportion woody browse at a site as a predictor, we also used park and the abundance of a few particular woody browse species. We used the Model routine in JMP (Vers. 9.0) for all these analyses, checking for linearity of effects and possible interactive effects among the predictor variables. In two cases, single outlier points were omitted from the analysis to improve the reliability of estimates for the path coefficients.

Methods to Assess Sampling Efficiency

We investigated sampling aspects of the woody browse dataset in order to determine whether an equally informative dataset could be gathered using fewer sampling locations and one of the two browse circle sizes. Our goal here was to identify and eliminate redundancies in sampling. Currently, the GLN's sampling protocol assesses woody browse in browse circles of two sizes at each of 68 locations within the Hybrid plot (see Figure 3). While the browse circles in Transects 1-3 are sampled in concert with other metrics of the vegetation monitoring program, those along Transects 4-7 are areas where only woody browse is assessed. This high number of replicates (68) was selected at the outset of the program to ensure adequate sampling coverage. At each sampling location, a 0.80 m radius browse circle allows browse monitoring in a 2 m² area; extending this radius to 1.13 m then includes an additional 2 m² area for a total of 4 m². This tiered plot size was initially employed because ecologists were unsure of the level of browse that would be encountered. Sampling too small of an area risks detecting only a fraction of actual browse, such that it is potentially only observed in a few circles. While sampling a larger area is often more informative, it is also more time consuming in the field, especially on sites with dense understories. In addition, a swamping effect can occur whereby some browse is observed within most, or nearly all, large browse circles. Because GLN staff wish to make long-term comparisons of browse change, it is essential to use browse circles that capture a level of browse around which long-term changes in means and variances can be expressed.

To determine the relationship between sampling effort (i.e., number of browse circles) and information gained, we created a program using R 2.11.0 software (R Development Core Team 2010). We were particularly interested in seeing how the estimated error changes when 15, 30, or 68 browse circles are sampled on a site. Sampling 68 circles (the current amount of effort) will likely be the most informative and have the smallest sampling error, but it is very time consuming in the field. Sampling 30 browse circles would reduce the effort by more than half and could coincide with the 30 understory quadrats on a site. Sampling 15 circles would reduce the effort even further, although we expect the largest sampling error at this level.

For each site ($n = 161$), we calculated the proportion of browse (PB_j) using 15, 30, and 68 randomly selected 2 m² browse circles. We repeated this process 100 times to create a sampling distribution from which we calculated the standard error associated with the proportion of browse calculated at every site for each level of browse circle inclusion. We used the same process to evaluate the 4 m² browse circles.

To test whether 2- and 4 m² browse circles differed in their ability to detect the abundance of browse and woody species per unit area, we calculated PB_j at each site (Eq. 2, where $q = 68$) and divided by their respective sample areas on a site (272 m² total sampling area for the 4 m² browse circles and 136 m² total sampling area for the 2 m² browse circles). We then performed a paired t-test between 2- and 4 m² abundance and browse and tested the means against zero.

Counting herbaceous indirect-indicator species is another potential redundancy in the sampling methodology. To test whether the individual counts of the herbaceous indirect-indicators and the abundance data measured in the understory quadrats relayed similar information, we plotted quadrat abundance measures against the total density counts for all indirect-indicators across the parks. Since we expect understory species to have a patchy rather than even distribution on a site, we tested our observed quadrat abundance data against the Poisson distribution and performed a

χ^2 analysis to see if they differed. Finally, we performed a test for overdispersion on the quadrat abundance data using the qcc package in R (qcc.overdispersion.test {qcc}, R Development Core Team 2010). Data for indirect herbaceous indicators was consistently collected at seven of the parks sampled (St. Croix National Scenic Riverway, Grand Portage National Monument, Indiana Dunes National Lakeshore, Voyageurs National Park, Sleeping Bear Dunes National Lakeshore, Pictured Rocks National Lakeshore, and Isle Royale National Park), so the full dataset was used for this analysis.

Results and Discussion

Browsing Impacts

Overall Browsing Patterns

Regional Browsing Behavior

Across the region, the proportion of browse is 0.098, indicating a low overall rate of browsing across the region and/or preferential feeding on more palatable species. As these become scarce at sites like many of those in SLBE, the proportion of browse could decline even as browsing pressure on palatable species remains high.

Browsing Trends Across Parks

The mean proportion of browse differed greatly across the three parks. SLBE had the highest ($PB_p=0.27$) followed by PIRO ($PB_p=0.09$) and ISRO ($PB_p=0.04$). Overall, browsing pressure increased across the three parks in accordance with increased ungulate densities. ISRO had both the lowest browsing pressure and the lowest ungulate density at 0.60 moose/km² (1.5 moose/mile²; Vucetich and Peterson 2011). PIRO had intermediate browsing pressure ($PB_p=0.09$) and ungulate densities of 2.6-3.1 deer/km² (5-8 deer/mile²; Sanders and Grochowski 2010). SLBE ranked the highest with a browsing pressure of 0.27 and deer densities estimated at 8.5-11.2 deer/km² (22-29/mile²; Figure 7) (Sanders and Grochowski 2010).

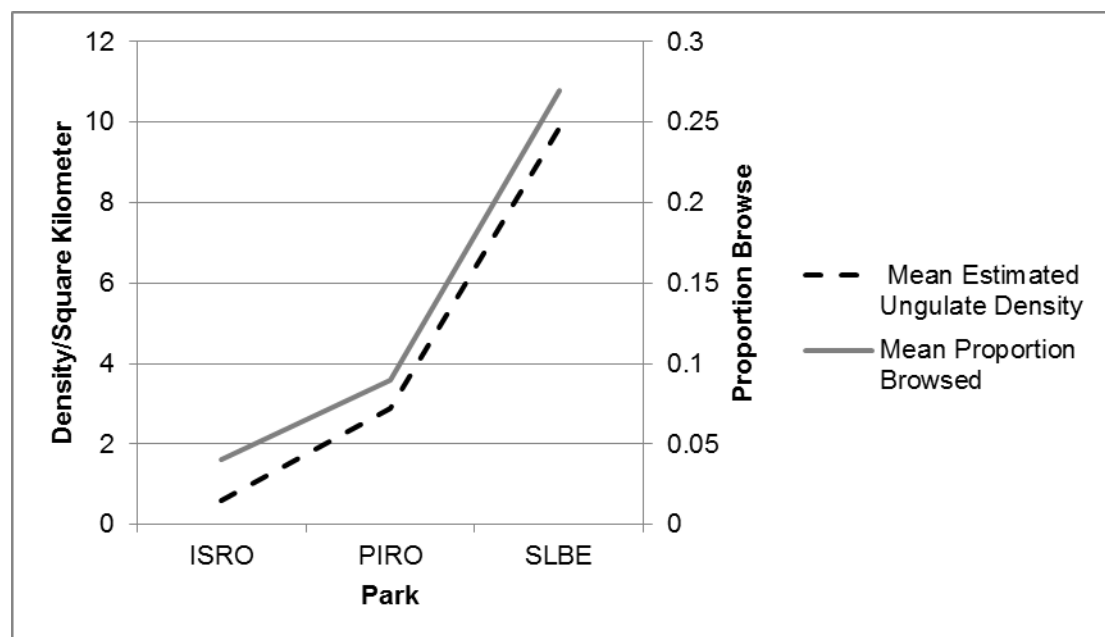


Figure 7. Browsing trends and ungulate densities across the three parks in the study.

Site-level Browsing Trends

The mean proportion of browse at a site differed significantly across the three parks ($F_{(2,158)} = 30.3$, $p < 0.0001$; Figure 8a). SLBE had the highest browsing levels ($PB_j=0.29$) followed by PIRO ($PB_j=0.11$) and ISRO ($PB_j=0.04$). All differences in the proportion of browse at the different parks were significant by Tukey's Honestly Significant Difference test when the square

root or log transform was applied to the proportion browse variable. Transforming proportion browse in this way also better met the equal variance among parks assumption of ANOVA.

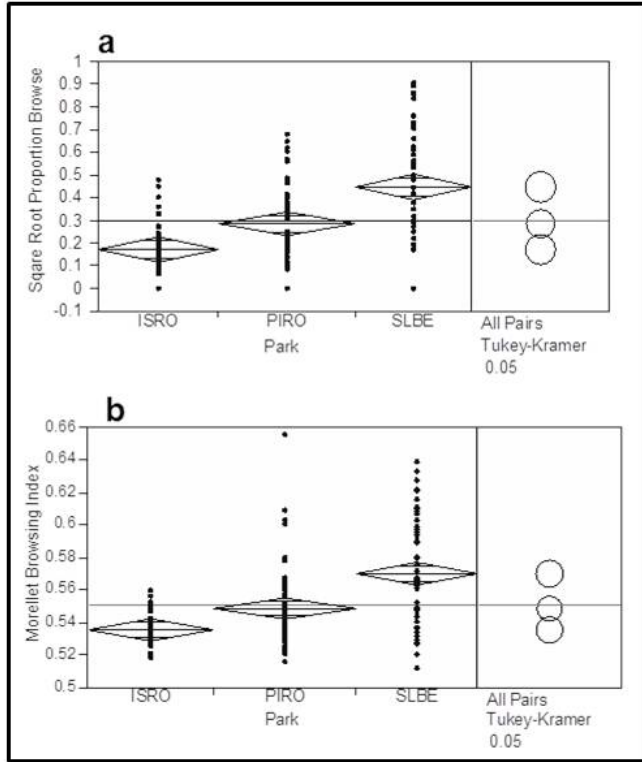


Figure 8. Variation among parks in levels of browsing as inferred from a) the square root of the proportion of woody stems browsed, and b) the Morellet Browsing Index.

The mean Morellet Browsing Index also differed significantly across the three parks ($F_{(2,158)} = 24.910$, $p < 0.0001$; Figure 8b). SLBE had the highest (0.57) followed by PIRO (0.55) and ISRO (0.54). Tukey's HSD test revealed that all pair-wise differences among means were significant, $p < 0.05$. In this case, square root and log transformations did not improve the fit of the data. Over sites, the Morellet Browsing Index appears to allow good discrimination between areas with low levels of browsing.

To test the hypothesis that rates of browsing respond to the amount of woody plants available, we also applied ANCOVA analysis with park as the factor and total abundance of woody material (S_{ij}) as the covariate. This analysis reveals that different relationships between the amount of woody plants present at a site and the proportion of those that were browsed occur among parks (Figure 9a). In particular, this relationship was positive at ISRO ($t=2.33$, $p=0.0213$) and non-significant at PIRO ($t=-1.47$, $p=0.1438$) and SLBE ($t=-0.92$, $p=0.3614$). A positive relationship might be expected if ungulates are attracted to sites with more browse, whereas a negative relationship might occur if the presence of additional woody browse saturates the ungulate's functional response, decreasing the risk that any given stem is browsed. In the ANCOVA, a park had a similar level of importance as levels of available woody plants ($F=5.24$ and $F=4.10$, respectively), while the interaction was less important ($F=2.89$) and significant only at the 10% level ($p=0.059$).

The Morellet Browsing Index also varied strongly across parks ($F=10.14$, $p<0.0001$, adjusted R -squared=0.22; Figure 9b). Unlike the proportion browsed, however, the Morellet index proved to be independent of woody plant abundance (interaction term $p=0.509$). In fact, these two browse indices are not closely correlated (R -squared <0.10) and thus appear to track different aspects of browsing. In particular, the Morellet Browsing Index appears insensitive to local variation in available browse. This might be a virtue in some situations.

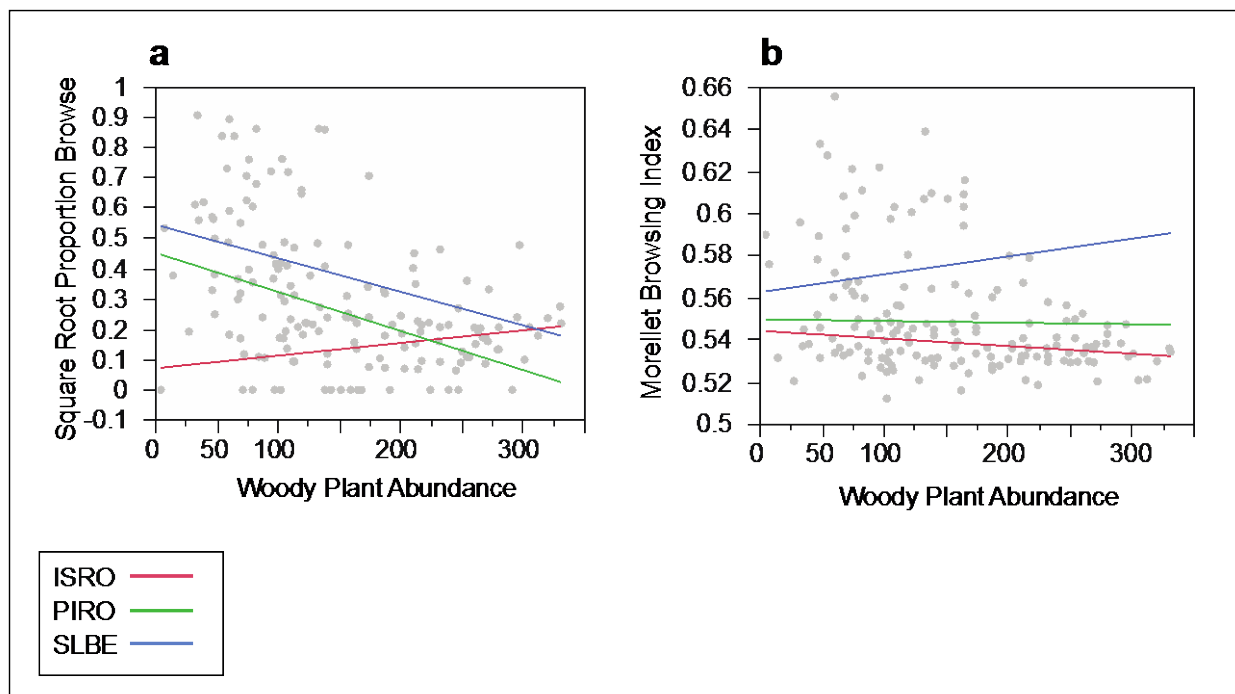


Figure 9. Relationships between the overall abundance of woody plants available at a site and the amount of browsing on those plants as estimated by either the proportion of plants browsed (a; square-root transformed) or the Morellet Browsing Index (b). Note that relationships vary among the parks for proportion browsed.

Species-level Trends

At least one woody species at each park displayed an increased susceptibility to browse as reflected in a log Relative Browse Preference significantly greater than zero (Figure 10). A significant negative Relative Browse Preference score indicates that the species is avoided by ungulates. At SLBE, based on the six species that matched our criteria (abundance of $n > 10$) only bigtooth aspen (*Populus grandidentata* Michx.) had a highly significant and positive mean Relative Browse Preference ($p<0.001$). At PIRO, four of the five species meeting the selection criteria had positive Relative Browse Preference scores: *Acer rubrum* L. (red maple, $p<0.001$), *Acer saccharum*, $p=0.047$), *Lonicera canadensis* Bartram and Bartram ex Marshall (fly honeysuckle, $p=0.023$) and *Sambucus racemosa* var. *racemosa* L. (red elderberry, $p=0.029$). *Fagus grandifolia* Ehrh., (beech) had a negative Relative Browse Preference score suggesting that deer avoid this species ($p=0.07$). At ISRO, all seven species meeting our criteria were favored by moose: $p<0.001$ for *Amelanchier* sp. Medik. (serviceberry), *Betula papyrifera* Marsh (paper birch), *Cornus sericea* L. (redosier dogwood), *Corylus cornuta* Marsh. (beaked hazel),

and *Sorbus decora* (Sarg.) C.K. Schneid (mountain ash); $p=0.012$ for *Acer spicatum* Lam. (mountain maple); and $p=0.004$ for *Populus tremuloides* Michx. (trembling aspen). Note that this pattern of ungulate selectivity (seven favored species at ISRO to four at PIRO and one at SLBE) is inversely related to levels of overall browsing pressure among the three parks (Figure 11). This trend of having fewer species with demonstrable responses at higher browsing levels could reflect a "browsing uncertainty principle." That is, in parks with higher ungulate densities, species that are preferred could have been browsed so intensively that they are no longer abundant enough to be included in such analyses (our minimum sample size was 10).

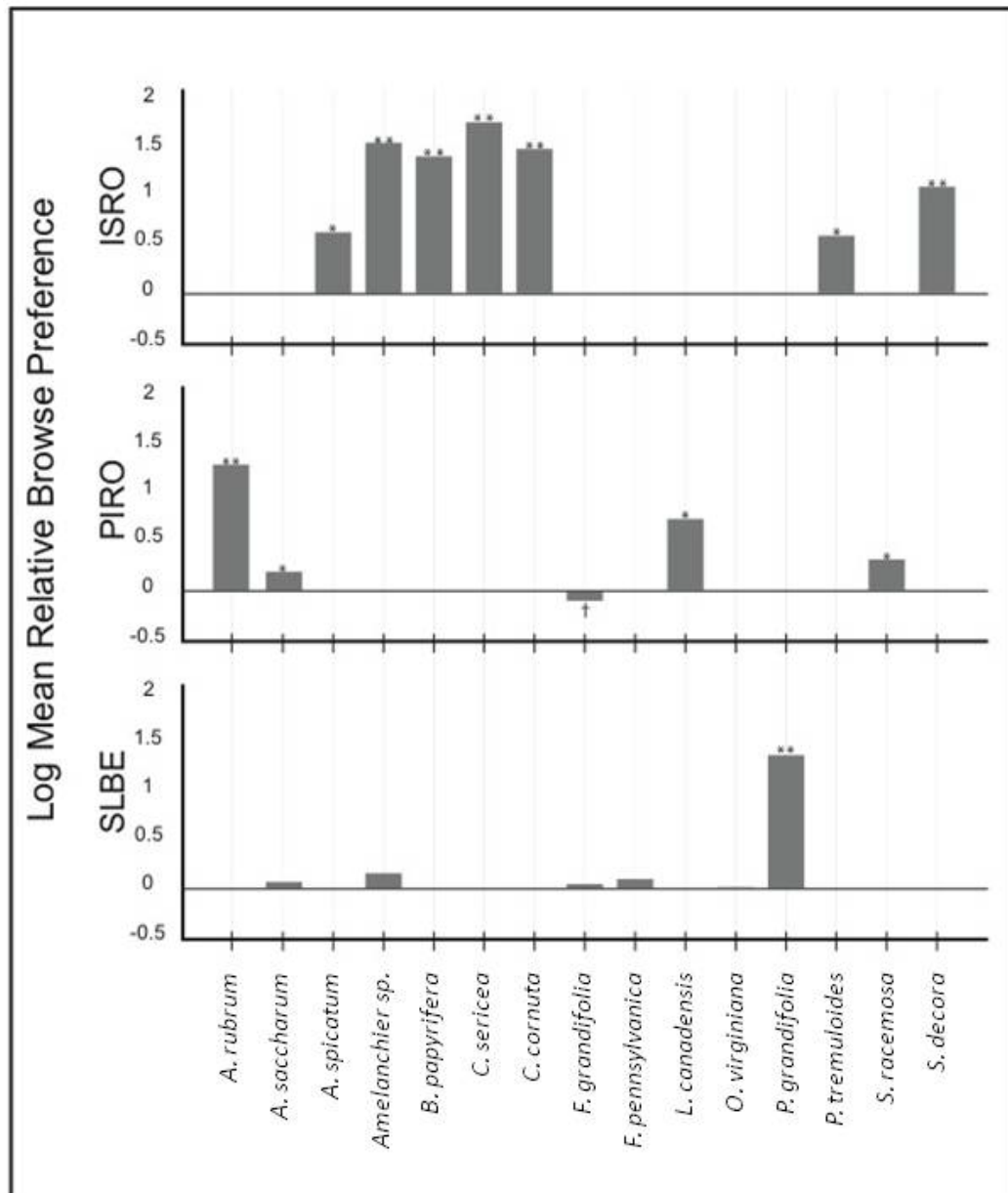


Figure 10. Log Mean Relative Browse Preference of woody species ($n>10$) at SLBE, PIRO and ISRO. Significance levels indicated as follows: † $p<0.10$; * $p<0.05$; ** $p<0.001$.

Interestingly, although similar species occurred across parks, no species responded significantly to ungulates in more than one park. This suggests that browsing preferences tend to be local and context-sensitive at this scale. It also indicates that different species respond to increased levels of browsing pressure (as noted above).

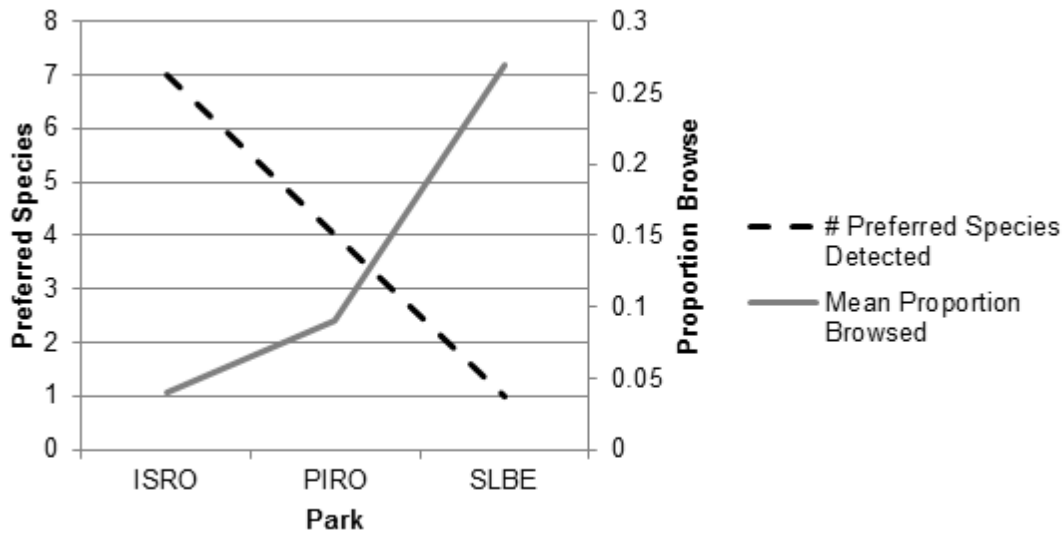


Figure 11. The number of preferred woody browse species we were able to identify as such plotted against the overall proportion of browse across the three parks.

Interestingly, the probability that a woody species was browsed generally did not depend on its **relative** abundance at a site. Only *Ostrya virginiana* (Mill.) K. Koch (hop hornbeam) showed positive density dependence (Figure 12). An ANCOVA reveals that the proportion of browse on *O. virginiana* also varies significantly across parks (adjusted R-squared = 0.332) with both park and density dependence (based on relative abundance) having similar and independent effects ($F=16.64$ and $F = 15.95$, both $p < 0.0001$). Thus, browsing pressure increases with *O. virginiana*'s relative abundance at about the same rate across parks even though browsing pressures vary in intensity among parks.

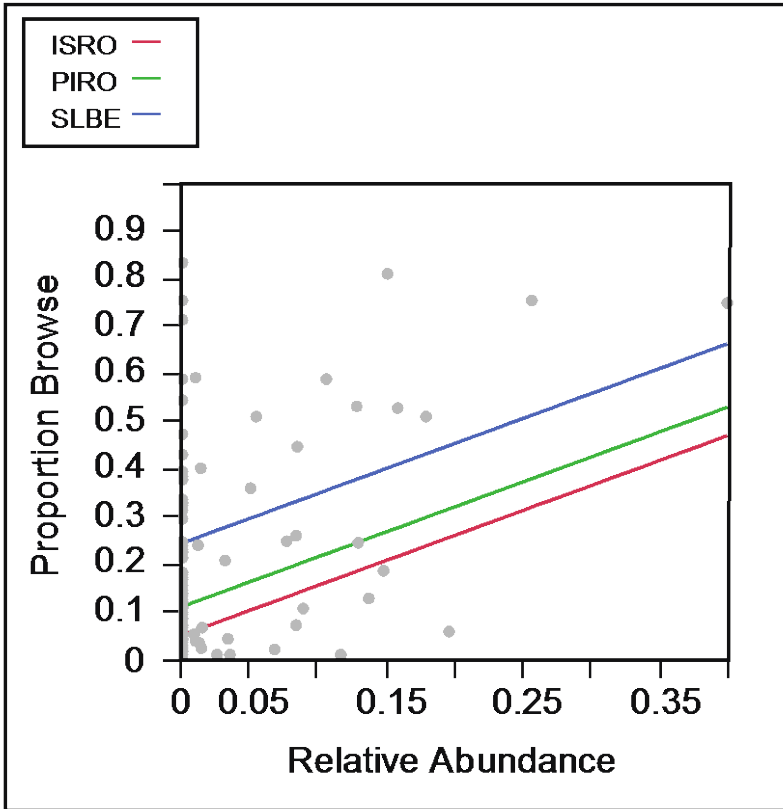


Figure 12. The proportion of browse on *Ostrya virginiana* as a function of its relative abundance at a site.

Species also showed relationships between their **absolute** abundance at a site and their probability of being browsed. The proportion of browse on *O. virginiana* increases with absolute abundance ($t=2.05$, $p=0.0498$, adjusted R-squared=0.35) and varies among parks ($t=-2.99$, $p=0.0057$). The proportion of browse on *F. grandifolia* also appeared to increase with its abundance. The ANCOVA, however, reveals that this reflects differences among parks ($t=-4.21$, $p<0.0001$) rather than a sensitivity to abundance within parks ($t=0.47$, $p=NS$).

In contrast to these cases of positive density dependence, proportions of browse on *A. saccharum* and *T. occidentalis* (L.) decreased in response to absolute abundance ($F_{Acer}=7.61$, $p=0.007$, $F_{Thuja}=2.93$, $p<0.001$). Park significantly affected the proportion of browse in *T. occidentalis* ($F=23.15$, $p<0.0001$) but not in *A. saccharum*.

We conclude that increases in the absolute abundance of both *O. virginiana* and *F. grandifolia* tend to increase browsing on those species across sites. This could reflect the fact that both species may tend to become more prevalent in the molar zone at more heavily browsed sites. In *F. grandifolia*, however, the apparent density dependence reflects the effect of park (i.e., different browsing pressures and species abundances covary across parks). In contrast, increases in the abundance of *A. saccharum* and *T. occidentalis* lead to declines in the proportion of browsing on those species, and the fixed effect of park accounts for only some of this (Figure 13). This pattern implies that ungulates prefer *A. saccharum* and *T. occidentalis*; hence these species are only abundant at sites where browsing pressure is low.

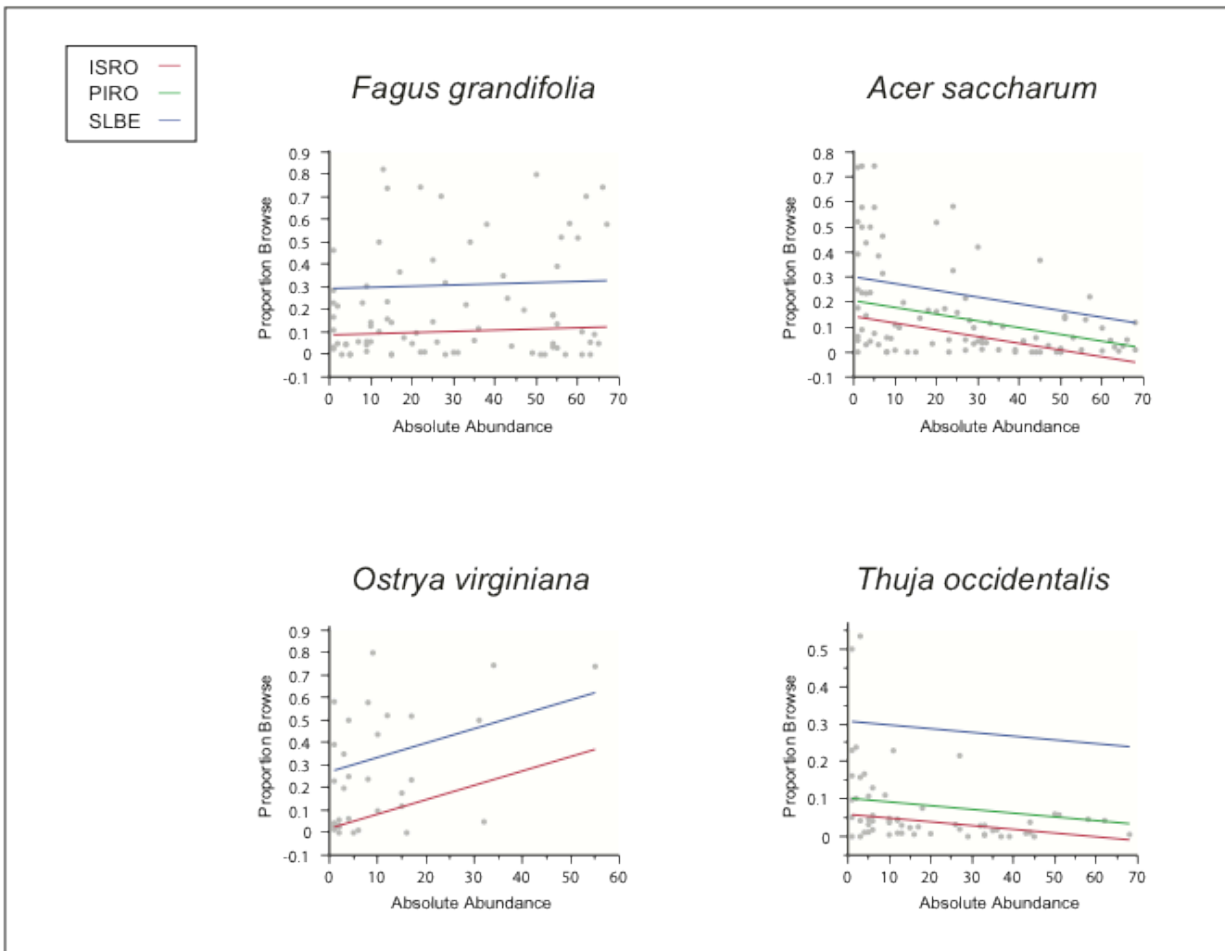


Figure 13. Results of ANCOVA analyses comparing absolute abundance of tree species to the proportion of browse across parks.

Understory plant communities clearly respond to both overstory conditions and ambient levels of past and current browsing. As expected, total understory abundance (frequency summed across species and quadrats) declined at sites subject to greater browsing (as inferred from the proportion of browse; $r = -0.176$, $p = 0.0256$).

Total understory plant abundance on a site responded to the absolute abundances of two of the four woody species analyzed above (Table 2). As the abundances of the shade tolerant species *A. saccharum* and *F. grandifolia* increased at a site, the abundance of understory plants declined (but this was only significant for *Fagus*: $F=7.83$, $p=0.006$). In contrast, understory plant abundance increased with increases in the abundance of two favored browse species: *O. virginiana* (NS) and *T. occidentalis* ($F=4.73$, $p=0.034$). Surprisingly, understory plant abundance consistently increased in apparent response to the proportion of woody plant browsing (see path coefficients in Table 2). This could reflect the fact that ungulate browsing on woody tree saplings and shrubs increases the amount of light and consequent opportunities for understory growth. It might also reflect an effect whereby herbivory on larger and taller understory plants allows a higher density of shorter, perhaps more ungulate-tolerant, plants to thrive. Note, however, that

the sizes of these effects in the path analyses reflect the remainder left over after accounting for variation among parks. This among-park variation was highly significant in the analyzing the effects of *A. saccharum* and *T. occidentalis* abundance.

Table 2. Responses of total understory herb abundance to park, local overall levels of browsing, and the local abundance of particular woody species as available browse. Statistics represent the direct effects of the variables listed as derived from path analysis models that include all three predictor variables. In *Populus tremuloides* (analysis not shown), only park had a significant effect ($p < 0.001$). Significance levels: *** $p < 0.001$, ** $p < 0.01$.

Woody Species (N)	Predictor Variable	F-value	Path Coefficient	Overall Adj r^2
<i>Acer saccharum</i> (92)	Proportion browsed	24.28 ***	+0.46	0.45
	<i>A. saccharum</i> abundance	1.23	-0.12	
	Park	32.36 ***		
<i>Fagus grandifolia</i> (79)	Proportion browsed	10.99 **	+0.38	0.164
	<i>F. grandifolia</i> abundance	7.83 **	-0.30	
	Park	2.83		
<i>Ostrya virginiana</i> (31)	Proportion browsed	14.48 ***	+0.71	0.40
	<i>O. virginiana</i> abundance	0.51	+0.12	
	Park	1.76		
<i>Thuja occidentalis</i> (59)	Proportion browsed	5.98 *	+0.59	0.34
	<i>T. occidentalis</i> abundance	4.73 *	+0.33	
	Park	11.72 ***		

Thus, as *Fagus grandifolia* and *Acer saccharum* increase in abundance, the abundance of understory species tends to decline. Conversely, as *Ostrya virginiana* and *Thuja occidentalis* increase in abundance, understory plant abundance increases.

Using Variation in Woody Browse to Infer Understory Indicators of Herbivory

We first explored the general relationships among the abundance of available woody plant material, levels of browsing on those woody plants, and the overall abundance of plants in the understory. The appropriate path model (Figure 14) employs park/region, the abundance of woody plants at a site, and the square root of the proportion of those plants browsed as predictors of overall understory herb abundance using data from all sites sampled (one outlier was excluded). As noted before, park/region had highly significant effects on downstream variables and the effects of woody plant abundance on the proportion of woody plants browsed depended on park (Figure 9a).

After taking the park effect into account, both the overall abundance of woody plants and the proportion of those woody plants browsed had strong positive direct effects on understory herb abundance (betas = 0.51 and 0.22, respectively, both $p < 0.0001$). The positive effect of woody plant availability could reflect an overall site favorability effect. However, when we tested for an effect of forest community composition (the value on the first NMDS axis), we found no

significant effect. Alternatively, both woody plants and overall understory herb abundance could have responded positively to lower ungulate abundance at some sites. In this case, however, we should expect that herb abundance declines at sites with higher rates of browsing. Instead, the direct effect here is positive (Figure 14). This could reflect a tendency for some browsing at a site to improve conditions for understory growth (e.g., by reducing shading). The positive effect of browsing on herb abundance was most pronounced for moose browsing at ISRO where herbs were generally most abundant, perhaps because of lower shade. Because both woody plant abundance and browsing affect overall herb abundance, analyses of more specific relationships between browsing and the abundance of particular herb-layer species need to take these factors into account.

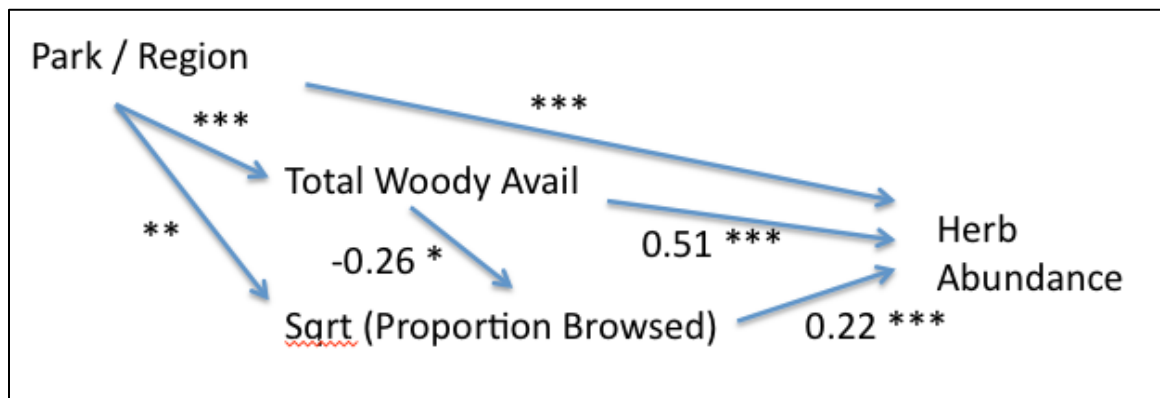


Figure 14. Path analysis of effects of park, the amount of woody plant material available at a site, and the proportion of those woody plants browsed on the overall abundance of herbs at that site. (N=160, $r^2 = 0.64$).

The path analysis models we used to explore associations between woody browse and the abundance of particular understory species (Figure 6) allowed us to identify several useful indicator species that had significant associations (Table 3). In particular, this approach allowed us to examine and test the direct effect of woody browse on understory plant abundances (path c) while controlling for some of the confounding effects of forest composition on these species (path b). If we had followed the easier approach of examining simple correlations between woody browse and the abundance of these understory species, we would have underestimated these relationships in eight of these 14 cases where the indirect effects ($a*b$) were opposite in sign to the direct effects (Table 3). Such effects could have precluded finding significant associations in these cases where our analyses demonstrate significance. In other cases, when the direct and indirect effects are of the same sign, the simpler analysis would have over-estimated the strength of these relationships.

Table 3. Significant understory indicators of browse based on constructed model (Figure 6). Significance levels indicated as follows: * $p < 0.05$; ** $p < 0.0001$; *** $p < 0.0001$.

Park	Species	Direct Effect	Indirect Effect (a*b)	Total Effects
SLBE	<i>Acer saccharum</i>	-0.33138*	0.067787	-0.26359
	<i>Osmorhiza</i> sp.	0.352873*	0.07081	0.423683
PIRO	<i>Allium tricoccum</i>	0.284571*	-0.13309	0.15148
	<i>Dryopteris intermedia</i>	-0.29019*	-0.15878	-0.44897
	<i>Galeopsis tetrahit</i>	0.242846*	-0.21593	0.026913
	<i>Milium effusum</i>	0.315613*	-0.18774	0.127868
	<i>Osmorhiza</i> sp.	0.468363***	-0.18059	0.287774
	<i>Viola</i> sp.	0.237747*	-0.26826	-0.03051
ISRO	<i>Aralia nudicaulis</i>	0.299569*	-0.10789	0.191682
	<i>Dryopteris intermedia</i>	0.30772*	0.043347	0.351067
	<i>Gymnocarpium dryopteris</i>	0.43472*	0.137823	0.572543
	<i>Milium effusum</i>	0.463935**	-0.06984	0.394099
	<i>Oxalis montana</i>	0.382209*	0.062036	0.444245
	<i>Trientalis borealis</i>	0.399014*	0.171576	0.57059

Most (12/14) of the understory species showing significant associations (direct effects) with woody browse increased in abundance at sites with more woody browse (Table 3). We might term these positive indicators of browse, or increasers. Only *A. saccharum* seedlings and *Dryopteris intermedia* (Muhl. ex Willd.) Gray (intermediate wood fern) declined significantly in abundance at sites with more browse. The preponderance of positive over negative indicators of browse may reflect the higher abundance of these species overall or at browsed sites, leading to greater statistical power. All these significant path coefficients were greater than 0.24, indicating that an increase of one standard deviation in the proportion of woody stems browsed at a site is associated with an increase (decrease) in the abundance of these indicators of at least a quarter of a standard deviation. The positive indicators, *Milium effusum* L. (milletgrass) and *Osmorhiza* sp. Raf. (sweet cicely) had the highest associations (0.46 and 0.47, respectively) approaching half a standard deviation increase in their abundance at sites that were one standard deviation above the mean in the proportion of browsed stems.

Three taxa (*Dryopteris intermedia*, *Osmorhiza* sp., and *Milium effusum*) emerged as indicators at two parks. Although *Osmorhiza* and *Milium* responded similarly across parks, *Dryopteris* increased in apparent response to browsing at ISRO but decreased at PIRO at sites with more browsing. This could reflect a difference in either the inherent plant preferences of moose and deer or perhaps differences in how *Dryopteris* responds in the different ecological contexts of these two parks.

Across parks, the number of species directly affected by the proportion of browse varied from two at SLBE (with the highest levels of browsing) to six at PIRO and ISRO. At SLBE, *Acer saccharum* seedlings became scarce at sites showing more woody browse. At ISRO which is subject to browsing by moose rather than deer, no species had significant negative associations with our estimates of browse.

We also tested the performance of a composite indicator of ungulate impacts based on the combined abundance of four positive indicators (species that increased in the presence of more browsing): *Aralia nudicaulis* L. (wild sarsaparilla), *Galeopsis tetrahit* L. (hempnettle), *M. effusum* and *Osmorhiza* sp. A simple analysis of this composite indicator showed no significant correlation to variation in the proportion of browse among sites. However, when we performed an ANCOVA on the proportion of woody browse at a site as our response variable that included both park and this composite indicator, both variables emerged as highly significant (Figure 15; $F_{Park}=47.55$, $p<0.0001$, $F_{Composite}=32.74$, $p<0.001$). Together these variables explain 42% of the variance in the proportion of browse across sites (adj. R-squared=0.417). Increases in total abundance is highly significant ($p<0.0001$) as are the effects of individual parks. The park x composite indicator interaction is also significant, reflecting the different slopes among parks (ISRO: slope=0.073, PIRO: slope=0.164, SLBE: slope=0.388). This suggests that the positive relationship between the composite indicator (the sum of the four increasers) and woody browse increases as overall browse levels increase. Therefore, the more browsing pressure at a given park, the more we can rely on these four increasers as indicators of browse and browse impacts. The converse is also true: species we identify as decreasers are more conspicuous and useful as indicators at parks where browsing pressure is low (ISRO and PIRO).

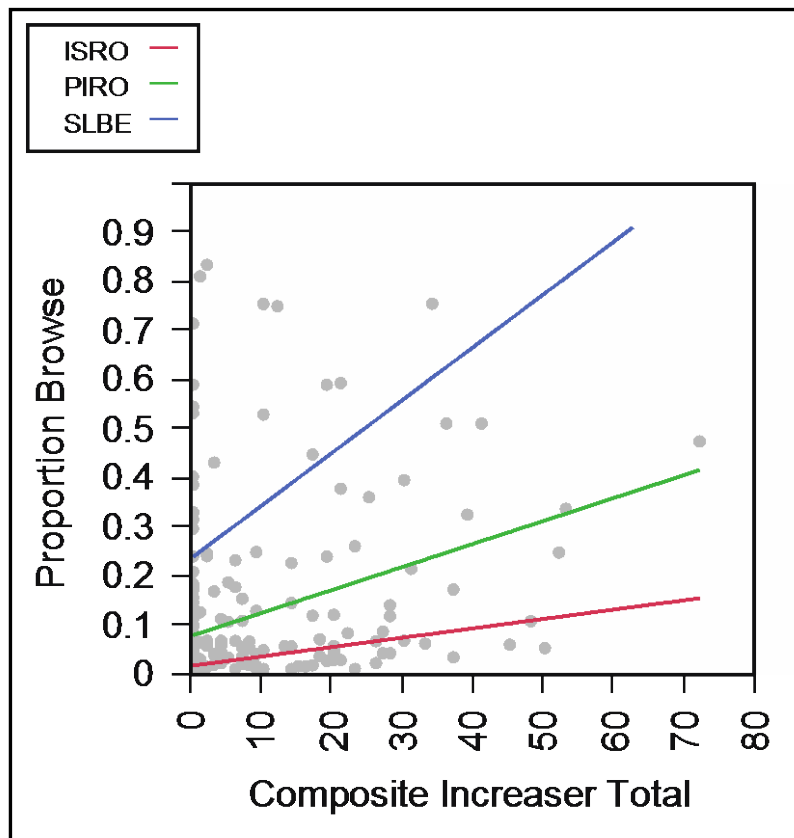


Figure 15. Proportion of browse as a function of increaser abundance by park.

Sampling Efficiency

Our results show that the proportion of browse and standard error are positively correlated. However, the standard error was zero when all 68 browse circles were included in the analysis (Figure 16). The standard error estimate associated with the proportion browse decreased as more browse circles on a site were sampled. While the same general pattern was observed in both the 2 and 4 m² data, the standard error was inflated with the 2 m² data in comparison with the 4 m² data (15 browse circles: respective intercepts = 0.0026 and 0.0025, respective slopes = 0.019 and 0.016; 30 browse circles: respective intercepts = 0.0017 and 0.0016, respective slopes = 0.011 and 0.009).

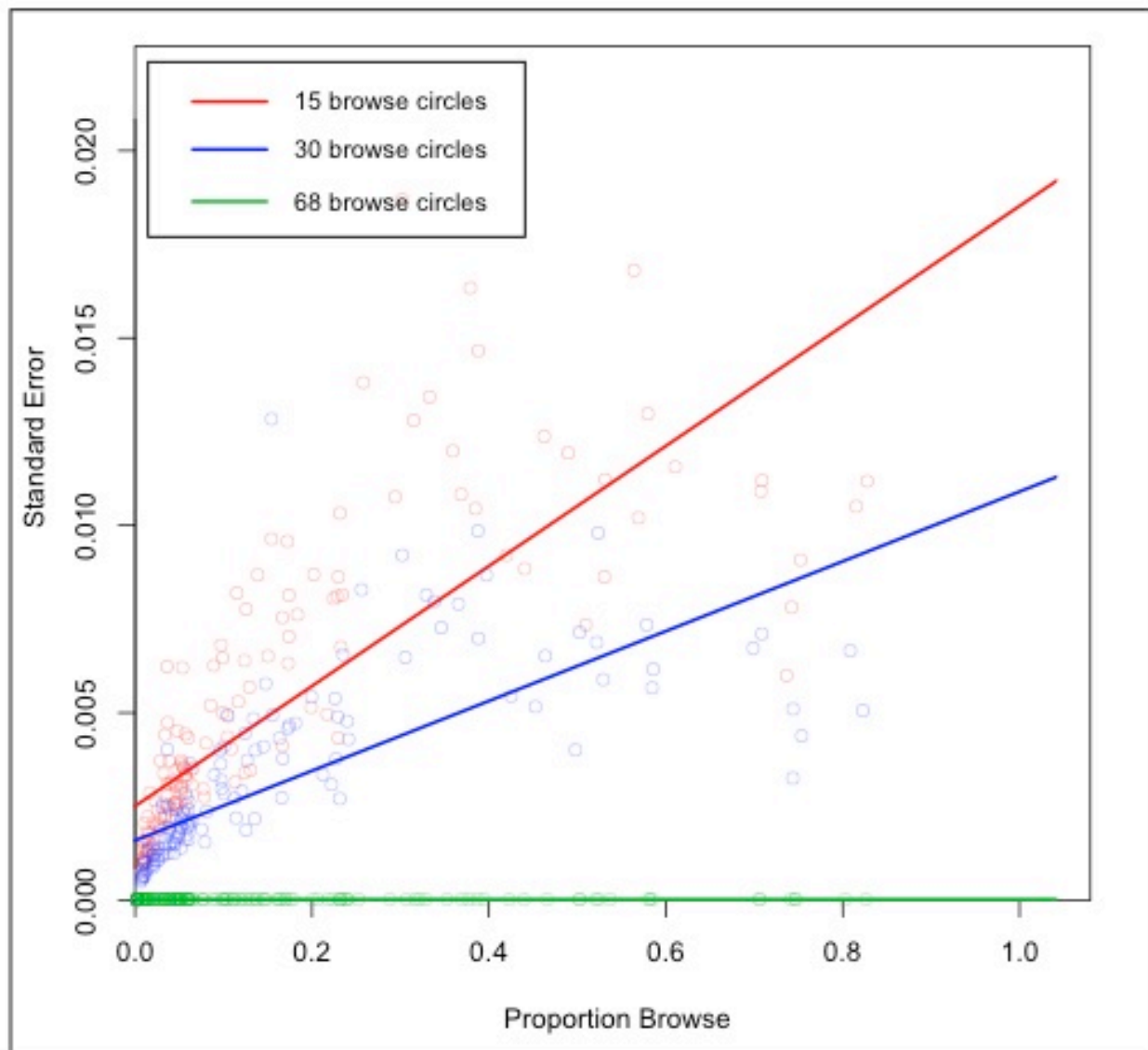


Figure 16. The standard error estimate associated with the proportion of browse calculated using 15, 30 and 68 4 m² browse circles.

As expected under simple species-area relations, the dispersed set of 2 m² sample areas detected more species (0.936) and instances of browse (0.079) per unit area than an equivalent area within the 4 m² circles (0.555 and 0.055 respectively). If the effort expended in the field to sample browse circles of both sizes is the same, the 2 m² sampling area yields more information per m².

Counts of the incidence of herbaceous indicator species increased with the number of quadrats sampled (Adjusted R-Square=0.80, $p < 0.0001$) (Figure 17). Here, we used log transformed data to meet the assumptions of equal variance. As the number of individuals of a given indicator species on a site increased, its presence in the quadrats also increased. Only 30 quadrats were sampled on each site and our results show that species with very high density counts were detected in all the quadrats on the site. Species abundances did not follow a Poisson distribution ($\chi^2 = 7.077e^{-284}$, $p < 0.0001$), however, indicating that species are clumped across the landscape rather than randomly dispersed. A test for overdispersion ($\chi^2 = 9614.282$, $p < 0.0001$) confirms that herbaceous indicator species are overdispersed across the landscape.

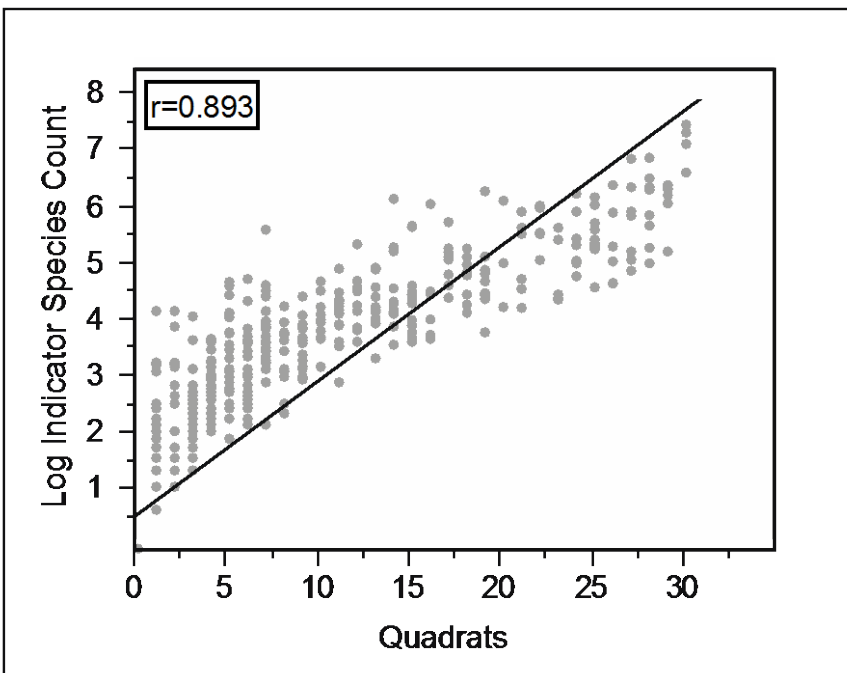


Figure 17. The number of herbaceous indicator species found at a site as a function of the number of quadrats in which they were present.

Interpretation of the Data and Its Usefulness

Long-term vegetation monitoring programs such as the one employed by the GLN allow us to track changes in the distribution and abundance of plant species over time. They also give us the opportunity to refine our methodology in order to establish the most efficient and informative means of gathering information in the field. The utility of this report is two-fold: 1) we analyze the browse information in the dataset to assess the baseline trends and conditions in the GLN's parks, and 2) we revise and reform the methods used to gather this information. One could refer to the latter as adaptive monitoring by analogy to adaptive management (Lindenmayer and Lacy 2009).

Browsing Impacts

As we move from coarse to fine scales of information, the browse data reveal different trends. At the regional level, overall browsing pressure appears fairly low (0.098 on a scale of 0 to 1), though not all species were browsed at this same, low level across the region. Certain species and certain areas were browsed at far greater rates than others, varying in response to differences in ungulate density and type and differences in vegetation. This means that species differ in their usefulness as monitoring tools depending on their abundance, attractiveness to ungulates, and susceptibility to browse. Their suitability as indicators thus also varies across the region.

Among parks, browsing pressure was closely linked to ungulate density. The Relative Browsing Preference measure identified 12 “preferred” and one “avoided” woody species across parks. While the majority of these are consistent with results from previous studies (Snyder and Janke 1976, Risenhoover and Maas 1987, Tilghman et al. 1989, McInnes et al. 1992, Balgooyen and Waller 1995, Horsley et al. 2003, Kraft et al. 2004, Boulanger et al. 2009, De Jager and Pastor 2009, Kribel et al. 2011, Randall and Walters 2011), an uncertainty principle also emerged. As browsing pressure and ungulate densities increased, our ability to identify and use particular species sensitive to herbivory as indicators declined. The number of preferred species we were able to characterize as such decreased from seven to four to one across parks as ungulate densities increased (Figure 11). This implies that as browsing gets more intense, it is harder to find palatable species that can be used as indicators. In such cases, it is more practical to use “positive” indicators - species that increase in abundance in the presence of increased ungulate impacts. The abundance of these species tends to increase their statistical power under conditions where negative indicators (species that decline with increased impacts) lose power. Thus, using both negative and positive indicators in combination allows data from these two categories of species to complement each other across the varying conditions in each park.

At the site level, the proportion of browse and the Morellet Browsing Index are both useful in different ways. Although these measures are distinct and surprisingly uncorrelated, both worked well to capture the differences in browsing levels among parks. However, the proportion of browse measure showed greater sensitivity to the type and amount of woody browse material present at each site. We noted that the proportion of browse tended to decline as available woody material increased across sites within all three parks. This could reflect a simple satiation effect wherein ungulates take a lower proportion of the browse when this is plentiful. Alternatively, ungulate browsing itself could favor less-palatable or more resistant woody plants that subsequently tend to dominate the site and increase in cover. Although we initially expected browsing pressure to diminish the amount of plant material available for ungulates to eat (and for

researchers to use as indicators), we also observed that the cover of understory herbs increased at sites subject to higher rates of browsing (as inferred from the proportion browsed – see direct effects in Table 2).

The Morellet Browsing Index, on the other hand, proved to be independent of the amount of woody plant material present on a site. This may make it a superior metric for quickly comparing areas that differ considerably in available woody browse in the molar zone without having to construct the more elaborate models that we used to analyze the proportions of browse metrics. Calculating the Morellet index also requires less field expertise in taxonomy in that browsing is scored without regard to species. Thus, the Morellet Browsing Index could provide an efficient descriptor of general browse impacts among sites and parks, particularly when browsing pressure is low. However, the proportions of browse provide more sensitive and informative measures for calculating and comparing both overall levels of browsing and how browse preferences vary across sites and species. *Given that the Morellet index can always be calculated from the species-specific data gathered for comparing how proportions of browse vary across sites and species, but not vice versa, we urge the GLN to continue to gather browsing data by species.* The proportion browse metrics also better fit their goal of monitoring the particular plant species in each of the parks and across the region (Figure 18).

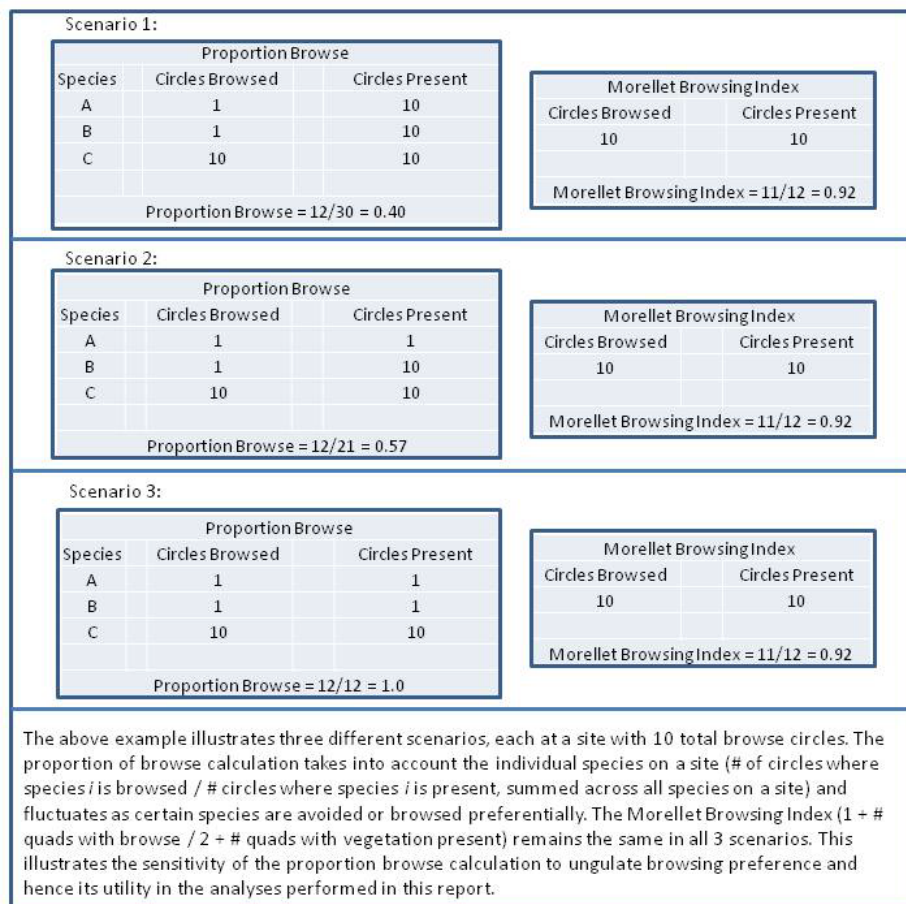


Figure 18. Three scenarios illustrating the sensitivity of the proportion of browse calculation compared to the Morellet Browsing Index.

Overall, our coarse- to fine-scale analyses show that browsing effects depend on local conditions. As ungulate impacts become more severe, it behooves managers to consider using plants that are avoided or resistant to browse as indicators.

For most of the woody species we tested, the levels of browse they experienced did not depend on their relative or absolute abundance at a site. This lack of density-dependence in the relative browse ratios implies that ungulates are consistent in their preferences even as the rates at which they encounter each species vary. That is, they continue to browse with a consistent pattern of preferences and discrimination even as their preferred browse species become scarcer. Likewise, they do not prefer to browse species that become more abundant. The exception to this rule was *Ostrya virginiana* where proportional browsing increased with this species' abundance (Figure 12). Published sources commonly refer to *O. virginiana* as being unpalatable to deer although there is no direct evidence that supports this claim beyond field observations (Matonis et al. 2011). Our results from the relative abundance analyses support the theory that it is avoided and eaten mainly when other more palatable options become unavailable. Thus, *O. virginiana*'s positive density-dependence could reflect the fact that ungulates are mainly eating this species when other browse species have become scarce.

The associations we observed within species between their absolute abundance and their proportions of browse most likely result from differences in what species were present as well as gross differences in browsing pressures across parks. Again we see the importance of considering local conditions when attempting to monitor browse. For instance, *O. virginiana* increased in absolute abundance with increased browsing pressure, but was only present at SLBE and PIRO, the two parks with higher ungulate densities and browsing pressure. The local plant community and browsing pressures influence these results with a *relative* abundance measure of woody species proving to be more informative and useful. In general, species that increased in absolute abundance with increased browsing pressure tend to be avoided by ungulates, and those that decreased tend to be preferred, suggesting that browse may help to explain these trends. We also found that total understory species abundance decreased as *Fagus grandifolia* and *Acer saccharum* increased in absolute abundance, perhaps reflecting shady late-successional conditions. In contrast, understory abundance increased as *Ostrya virginiana* increased in absolute abundance. This could reflect resurgent understory growth under more open conditions if ungulate browsing and/or other disturbances opened up the shrub or sapling layer, allowing more light to penetrate. Note that the differences between parks strongly influenced these results. As a result, the particular positive and negative understory indicators that we identified differed among parks and in one case reversed sign. Further analyses might be conducted to examine just which species or guilds of understory species increased across sites in the presence of more browsing. Certain understory species increased in abundance with increased browse due to their ability to withstand and/or deter browse. This may reflect “apparent competition” as mediated by deer.

Different woody species emerged as preferred or avoided across parks. The stark differences in ungulate density and species likely explain this discrepancy. SLBE has no moose and the highest estimated deer density of the three parks evaluated (22-29 deer/ mi²; Sanders and Grochowski 2010). Deer densities at SLBE are reportedly well above established management goals (Sanders and Grochowski 2010). As a result, browsing levels at SLBE are so extreme that the molar zone

is left vacant, leaving little for deer to browse. Indeed, at most of the sites sampled one could easily see 50+ m across the forest due to the lack of shrubs and saplings (K. Frerker, personal observation). Currently, SLBE's forests have been so heavily impacted by deer that it is difficult to extract sensitive species from the data collected because the understory and woody plant layers have been browsed to unhealthy and unsustainable levels. Deer at SLBE may be eating whatever is available to them, showing little preference due to a limited food supply. In fact, Koda and Fujita (2011) found that browsing frequency on woody vegetation tended towards a saturation point, after which deer shift from eating palatable saplings to unpalatable saplings and leaf litter. This implies that at high densities, deer will shift their feeding habits to unpredictable and often undetectable food sources.

Bigtooth aspen was detected as an indicator at SLBE because it has the ability to resprout vigorously after breakage or browse and therefore may persist in the molar zone as vegetative sprouts while other species either grow beyond the molar zone or die from the damage. Sugar maple is generally considered a preferred browse species, yet it does not stand out as an indicator at SLBE whose forests are dominated by this tree. This, again, emphasizes our inability to detect preferred species at SLBE due to its high deer densities. Nevertheless, sugar maple does stand out as an indicator at PIRO, a park with lower deer densities, along with beech. This preference for sugar maple and avoidance of beech is relevant at both SLBE and PIRO where beech bark disease (BBD), primarily caused by the fungus *Nectria coccinea* var. *faginata*, was recently discovered. Beech is a major canopy species in both parks and the threat of decline and mortality due to BBD is of primary concern. Deer are avoiding beech at PIRO but are at high enough numbers at SLBE that they have begun to browse beech at some frequency. Sugar maple and beech dominate the canopies at SLBE and PIRO and as BBD continues to progress, the combined effects of browse and BBD could dramatically alter the succession of the forests. If deer browse the few trees that manage to survive the wave of BBD due to some natural resistance, beech could completely disappear from the forests. *Action should be taken now to reduce deer densities, particularly at SLBE, in order to preserve the valuable sugar maple and beech forests that make this park such an attraction and foster their well-known spring ephemeral displays.*

At PIRO, fly honeysuckle emerged as a previously undocumented preferred species. In fact, Belovsky (1981) cited this species as being avoided by moose due to its low nutrient content. Heavy snowfalls along Lake Superior's south shore limit deer numbers to approximately 5.8 deer/mi² in Alger County, MI (Sanders and Grochowski 2010), very close to historic healthy levels. Indeed, browsing pressure in PIRO was half that of SLBE while the deer densities are estimated to be four times lower. It is possible that densities within PIRO's boundaries exceed these county-wide estimates. When ungulates occur at high densities in the absence of predation, they can adjust their feeding habits and behaviors, choosing habitats based on forage abundance rather than seeking a balance of forage and cover (Ripple and Beschta 2004, Massé and Côté 2009). PIRO and SLBE both allow hunting, but it appears that these measures have not curbed the detrimental effects of deer browsing. If PIRO is acting as a refuge, fly honeysuckle may be favored despite its lower nutrient content because deer browse less discriminately at this park, as they have fewer options in the mid-canopy layer.

ISRO, with its resident wolf population, had the lowest browsing pressure and highest groundlayer densities of all three parks. (However, wolf populations on Isle Royale are currently

declining and below the long-term average; see Vucetich and Peterson 2011.) Moose and deer have different browsing preferences, e.g., moose favor balsam fir (*Abies balsamea* (L.) Mill) while deer tend to avoid it. Although balsam fir is a canopy dominant at ISRO, it did not occur commonly enough in the browse circles to even be included in the browse analysis. This could reflect either the fact that moose have browsed it out of the molar zone or that self-shading has eliminated foliage from its lower branches. We did find that moose prefer to browse nutrient-rich deciduous shrubs and mid-canopy trees such as trembling aspen, paper birch (*Betula papyrifera*), redosier dogwood (*Cornus sericea*), beaked hazel (*Corylus cornuta*), serviceberry (*Amelanchier* sp.), mountain maple (*Acer spicatum*), and mountain ash (*Sorbus decora*). Many of these species can resprout after experiencing mechanical damage and thus are able to persist in the molar zone as vegetative shoots. Other studies at ISRO also reveal declines in the dominance of deciduous trees as these forests shift toward spruce dominance in response to moose browsing (e.g., Pastor et al. 1993).

We devised a new method to detect indirect indicators of browsing among understory species based on covariation between their abundances and local rates of browsing on woody species, controlling for local differences in forest community composition (Figure 6). Most of the indicator species we identified increased in abundance at sites with higher browsing pressure. Indicator species that decline in the presence of browsing occurred too rarely in the understory of sites with a history of browsing to provide large enough sample sizes for their response to deer browsing to be detected. The exception was sugar maple which combines prolific seed production with some tolerance for browsing. We conclude that 'positive' understory indicator species that increase in abundance under browsing pressure may be of more practical use than indicators that decline and become scarce. We consider some of these increasers to be undesirable from an ecological point of view, supporting previous reports that unpalatable herbs tend to increase while the overall abundance of herbs declines under high browsing pressure (Horsley 2003, Wiegmann and Waller 2006). Thus, we were most able to identify species that are resilient to browse or that benefit from increased light availability, aided animal dispersal, or the ability to survive and recover from browse via rhizomatous growth.

Like woody indicators, the understory indicators we identified varied among parks, probably reflecting differences in habitat conditions, ungulate species, and ungulate densities. SLBE had the fewest understory indicators of browse, presumably reflecting the fact that these forests have been browsed so heavily that the understories are now depauperate. We may thus be witnessing "the ghost of herbivory past" where the relationship between browse and herbs decays because sustained high browsing levels have eliminated favored and more nutritious plants (Knight 2009). At SLBE, sugar maple seedlings (DBH <2.5 cm and exhibiting second season growth) became scarce at sites with heavier deer browse, yet saplings and trees did not emerge as a preferred woody species in the analyses using data from the browse circles (using variables that consider other size/age classes). Because woody vegetation is scarce in the molar zone at SLBE, rates of encountering sugar maple in the browse circles are low relative to rates of encountering smaller seedlings in the understory quadrats. This implies that deer have nearly eliminated the recruitment of larger sugar maple seedlings to saplings. Further shifts in soil quality and nutrient cycling in response to deer herbivory could also hinder plant growth, preventing herb and tree seedlings from reaching maturity (Stewart et al. 2008, Heckel 2010). Although the GLN has previously focused on herbaceous species as understory indicators of browse, our study suggests

that sugar maple seedlings could also be a useful indicator, particularly at SLBE where other understory species are uncommon.

Several positive indicator species that increase in the presence of browsing could also prove useful to the GLN. Sweet cicely increased in abundance in apparent response to higher levels of herbivory at both SLBE and PIRO. Webster and Parker (2000) found it to decrease in height with increased browsing pressure. Although we did not evaluate the height of sweet cicely here, its abundance did increase with increases in browsing pressure. Wild sarsaparilla also increased in abundance with browsing at ISRO. Again, previous studies have shown that it decreases in height with increased browsing pressure (Edwards 1985). Nevertheless, our study suggests that survivorship remains high. The persistence of these two species is likely due to their dispersal and reproductive strategies. Wild sarsaparilla can reproduce by underground rhizomes and has the ability to produce clonal clusters of plants. Sweet cicely's success is perhaps due to animals dispersing its seeds and its ability to form persistent seed banks (Hawkins et al. 2007). Another positive indicator at ISRO and perhaps PIRO was *Milium effusum*, a native grass. Like many graminoids, it may be resilient to browse because of basal meristems and a rhizomatous growth pattern. Its increase at more browsed sites is consistent with reports from the region that increases in graminoid dominance are occurring often in apparent response to ungulate browsing (Rooney et al. 2004, Rooney 2009). Another positive indicator at PIRO was *Galeopsis tetrahit*, an exotic species that is also increasing in the region (Wiegmann and Waller 2006). It prefers disturbed habitats and may be responding to soil disturbance and/or increases in light from browsing.

The composite abundance of these four increasers was positively related to the proportion of browse at a site within parks. Using the abundance of these four species in combination to infer likely browsing impacts could emerge as an efficient metric in that it averages over several species whose individual abundances may fluctuate locally. However, local forest composition within each park affected these relationships. For instance, *Galeopsis tetrahit* was found exclusively at PIRO but not at the other two parks. While the utility of increasing species as positive indicators holds potential, a possibly confounding factor concerns the effects of light availability at a site. While the growth habit of these species likely makes them resilient to browse, they may also be responding to increases in light in the understory and/or a general release from competition. High composite abundances of these species at a site need not necessarily imply high browsing pressure if they are responding to some other type of disturbance that increases light levels. Nevertheless, the composite abundance of these four species could potentially save time and allow the GLN to streamline techniques of measuring impacts when used together with a simple and direct measure of woody browse.

Other increasing species may be less suitable to serve as understory indicators of browse. Wild leek (*Allium tricoccum*) is generally avoided by deer because of its organosulfur compounds (Anderson 1994). The ephemeral nature of the leaves also makes it unreliable as an indicator. As already mentioned, interactions with light levels may also be influencing the abundance of potential positive indicators in our models. Several small, herbaceous species are too diminutive to respond directly to browse. For example, at ISRO moose appear to have the opposite effect on understories than deer with increases in browse associated with increases in herb and shrub abundance but declines in tree (particularly balsam fir) abundance (Snyder 1976, McInnes 1992). Because balsam fir casts dense shade year-round, it inhibits the growth of understory herbs.

Several positive indicators of browse are small forbs that are no more than a few centimeters tall. They may be increasing in abundance with increased browse because browsing reduces their shade and releases them from competition (an example of 'apparent competition' mediated by an herbivore). These species include starflower (*Trientalis borealis*), oakfern (*Gymnocarpium dryopteris*), and woodsorrel (*Oxalis montana*) at ISRO and violet (*Viola* sp.) at PIRO (Table 2). Such browsing impacts could be particularly important for short plants that are too low to be heavily consumed by ungulates but who benefit from the increased light levels herbivory on tall neighbors provides. Although both light and browsing are involved here, we need not concern ourselves with detailed mechanisms provided that their abundance provides a reliable signal of higher ungulate herbivory at a site. It appears to be particularly useful to combine data on the abundance and identity of understory plants and the local incidence of browsing on woody plants, as in this study, when monitoring vegetation.

We also face the issue about how to explain, and whether to use as indicators, species that appeared to increase in apparent response to ungulate browse in one park but decreased in another. Both *Osmorhiza* and *Milium* behaved consistently, increasing in abundance at sites with more woody browsing (Table 3). In contrast, intermediate woodfern (*Dryopteris intermedia*) increased in abundance with browsing pressure at ISRO but decreased in abundance with browsing pressure at PIRO. This difference in response could reflect at least two different mechanisms at work. First, moose at ISRO may have ignored this species or avoided it actively, whereas deer may have eaten or trampled it at PIRO. Previous research in the region noted that several fern species have increased in abundance over the past half-century along with the abundance of white-tailed deer, suggesting that deer may avoid ferns because they provide little sustenance or sustain high quantities of secondary compounds (Wiegmann and Waller 2006). Alternatively, this fern may be responding more to changes in light availability. At both parks browse is probably causing light levels to increase. Intermediate woodfern is found most often under intermediate light conditions, not dense shade nor bright gaps (E. Sessa, pers. comm.). At ISRO, browsing activity could be opening up dense patches of mountain maple and beaked hazel so as to increase light, favoring the growth of this species. At PIRO, however, the mix of hemlock and sugar maple may tend to favor intermediate woodfern at many locations, but heavy browsing by deer may create light environments too bright for this species. Deer browsing does appear to be associated with changing light and disturbance regimes (Amatangelo et al. 2011). Active logging at PIRO in an inland portion of the park (the Inland Buffer Zone) could also both increase light levels and boost the local density of deer (attracted to logging 'tops'). If these light levels exceed those favorable to the woodfern, its abundance could decline at sites showing higher browse levels.

This case suggests that we should be cautious in attributing the statistical associations we find to the direct impact of deer herbivory. Intermediate woodfern's sensitive response to light and these potentially confounding effects of habitat heterogeneity may limit this species' utility as an indicator of browse. Obtaining light measurements could allow us to test these alternative hypotheses and perhaps control for light effects when using the abundance of certain indicator species to infer browse. Future studies, and perhaps the GLN protocol, should include some simple measure of light levels at each site to quantify how these are influencing understory species perhaps in combination with ungulate browse. Given the notorious amounts of variation in instantaneous measure of absolute light intensity, we recommend that such measurements rely instead on either line-intersect estimates of tree coverage along the transects (see Warren and

Olsen 1964) or vertical hemispherical photos of the canopy that can be analyzed to estimate incident light.

Refining the Browse Circle Method

Based on our results, the GLN can increase the efficiency of monitoring parks in the region by reducing the sampling intensity and adjusting the size of the browsing circle while still retaining the ability to detect trends in the data. First, the GLN should reduce the number of browse circles sampled from 68 to 30. Reducing the sampling size to 30 gives a low standard error ranging from 0.001 to 0.01 as the proportion of browse increases (see Figure 16). Including only 30 browse circles would greatly reduce sampling time at each site. For convenience, and perhaps to allow micro-spatial comparisons, these 30 browsing circles could be placed so as to coincide with the 30 understory sampling points along the three transects at each site. Further reducing the sample size to 15 browse circles increases the standard error to a level that may be unacceptable to the GLN in order to achieve its monitoring goals.

Second, the GLN should use a 1 m radius (3.14 m²) browse circle sampling area and discontinue using the 2 and 4 m² areas. In sum, the 2 m² area is a bit more efficient in terms of data yield per unit area, and the 4 m² circles tend to yield a lower standard error. To achieve a balance of efficiency and reduced error, we recommend using a 1 m-radius browse circle. This would be convenient in the field as workers are already carrying 1 m understory quadrat measuring sticks that they could use to establish the browse circle. In addition, the resulting 3.14 m² area is close to the 4 m² area in terms of the lower standard error relative to the 2 m² circles (but might take slightly less time to sample).

Whether the GLN should continue to count the numbers of individuals for the indirect-indicator plant species depends on the monitoring goals. The positive relationship between abundance and individual counts (see Figure 17) shows that if there are many individuals on a site the species will appear in every quadrat. If the monitoring goal is to gauge the abundance of species on a site, the presence/absence data collected in the understory quadrats fulfills this need and is much more efficient than individual counts. For instance, consider the case of *Maianthemum canadense* (the most abundant understory herb in the region; Rooney et al. 2004). In one case, 2,000 individuals were counted on a single site (ca. 67 per quadrat). This herb is small in stature and can often form a carpet which makes counting each individual a very time consuming process. In this case, a simple presence/absence measure would be enough to gauge its abundance. If, however, the GLN is interested in thoroughly monitoring populations of rare species of special concern in order to perform more detailed analyses, the extra time needed for individually counting these species may well be justified (and would be far less work). Given that it was considerably less time consuming to measure the maximum individual heights and numbers of reproductive individuals of the ungulate indicators, retaining these measures may be worth it assuming that assembling and analyzing such data would address identified monitoring goals.

Conclusions and Recommendations

Ungulates have impacts on the plant communities of the upper Midwest that vary in a complex way across time and space. Ungulate populations in some areas have grown in recent decades to exert major impacts on tree regeneration and plant diversity with cascading effects on many ecosystem processes. Thus, ungulate browsing is of considerable significance to those charged

with monitoring ecological conditions and with making informed decisions on how best to manage land resources. For these reasons, the GLN identified monitoring ungulate impacts as a priority within its recently established monitoring program. Remarkably, no effort has yet been made by any organization in North America to develop a systematic, widespread, and sustained program for monitoring ungulate impacts at the regional (or even the local) scale in order to track how these may vary over plant communities, regions, and time. This lacuna has placed the GLN in a special position whereby they have been obliged themselves to pioneer protocols for assessing and analyzing browse levels and impacts.

The purpose of this report is to refine the initial field protocols developed some years ago to monitor ungulate browse and to devise suitable methods for analyzing those data in order to produce informative, reliable, and timely results to share with other regions and park managers. To accomplish these goals, we first sought to evaluate and analyze the existing data in a variety of ways in order to explore the power and limitations of these data for drawing accurate inferences regarding ungulate impacts. To be of maximal use, our field methods need to be efficient and capable of providing reliable and interpretable results. We also sought to compare alternative measures and methods of analysis in order to assess the different kinds of information they provide and how measures of ungulate impacts based on measurements of woody browse compared to metrics based on understory cover, diversity, and composition. Because the GLN is obliged not only to compile and analyze monitoring data but also to assist park managers in making resource management decisions, they seek a pipeline to transform field monitoring data in a timely way into useful guidance for managers. Finally, it is our hope that the field protocols and methods of analysis we have begun to develop here can develop and spread to other regions and agencies so as to enhance the overall quality and quantity of comparable monitoring results available to all.

General Recommendations

We suggest that the GLN use the results presented here to simplify their field methodology for estimating woody browse. We feel that this method can be made more efficient in several ways. First, we suggest reducing the number of browse circles from 68 to 30. Although there is always a trade-off between sample size and the precision of the parameter estimates we obtain from those samples, our analyses indicate that this number of samples per site will still provide a reasonably low standard error of the estimate. Combining these results across many sites within each park also guarantees that combined park and regional estimates will be correspondingly more reliable. Second, we suggest positioning these browse circles along the three main vegetation monitoring transects in order to minimize the time spent marking transects and moving between sampling points. Finally, we suggest using browse sampling circles of radius 1 m. This would simplify the field equipment needed by each field team yet still provide a sampled area of 3.142 m^2 per point, which our analyses suggest is sufficient to include reasonable probabilities of encountering browsed stems while minimizing the 'saturation' effect that occurs when many stems of a given species occur within larger circles.

We also found different trends for woody browse estimates based on the browse circle data depending on the metric used. Although the Morellet Browsing Index was the simplest in lumping all woody browse into a single metric, it captured a different aspect of browse than our measure based on the overall proportion of woody plants browsed. In addition, results from this study and elsewhere provide ample evidence that browsing rates vary considerably by species.

This implies that lumping all browse together as in the Morellet index could tend to over-estimate browse intensity when favored / palatable plants are common at a site while underestimating it after sustained browsing has eliminated these species from the browsing zone.

In addition, we suggest that it will often be of use to aggregate these browsing data across areas of increasing spatial scale particularly when regional species pools remain the same and/or data can be drawn from similar communities. At larger scales, of course, species pools change and different community types are involved. We recommend that the GLN explore further how data might then be combined to obtain a consistent signal. Of course, the most appropriate scale for making assessments and recommending management activities will depend on the questions of most interest and the resources available.

While it was straightforward to recommend adjusting the size and reducing the number of browse circles, we face more uncertainty and complications in recommending whether and how to use understory plant species as indirect indicators of ungulate browsing. This reflects the different species that proved to be informative among the parks and the general decline in browse-sensitive species in areas where heavy ungulate browsing has already occurred for several years. These differences suggest not only that we will need to use different species but also that we need to use a different mix of species depending on community composition and local ungulate abundance (e.g., a greater fraction of species that respond positively to browse impacts in more heavily browsed areas). Thus, just which species the GLN decides to use and the particular mix of positive and negative indicators that are most appropriate will depend on the goals of future GLN analyses. We encourage others interested in browse impacts to use similar sampling protocols to facilitate cross-study comparisons and testing of alternative indicators.

Specific Suggestions

National Park Service managers should note the woody species we identified as responding positively (*Fagus grandifolia*) or negatively (*Acer* sp., *Amelanchier* sp., *Betula papyrifera*, *Cornus sericea*, *Corylus cornuta*, *Lonicera canadensis*, *Populus* sp., *Sambucus racemosa*, and *Sorbus decora*) to browse. Preferred species have already been extirpated from many areas in the southern parks and are likely to decline further elsewhere where ungulate populations remain high. At such locations, the future of the forests will be significantly altered, suggesting that management efforts to limit ungulate densities are in order.

To obtain accurate and reliable statistical results, our study focused on the more abundant species at each site. Some species not mentioned here have been browsed heavily to low abundance throughout much of the region. For example, hemlock (*Tsuga canadensis*), yew (*Taxus canadensis*), and northern white cedar (*Thuja occidentalis*) are preferentially browsed by deer but occurred so infrequently in our browse circle data that they could not be included in the park by park analyses. Only when we combined data across parks did *Thuja* emerge as a sensitive species (and *Tsuga* still failed to emerge). This indicates that browsing is inhibiting the regeneration of these palatable and slow-growing species in the parks. Efforts to place species along a spectrum of deer or moose preference may often be limited by our ability to detect associations at sites where continued browsing has already eliminated sensitive species. We termed the dilemma of documenting impacts on species that have already been greatly reduced the "uncertainty principle" and noted that it reduces the number of sensitive indicators available as browsing pressure increases. These observations also reinforce the importance of sustaining

monitoring programs over the long-term. Legacy effects decline over time to the point that it becomes difficult or impossible to monitor ungulate impacts in sparse and depauperate understories. However, it is still important to monitor at such locations if we are to document how over-browsed communities recover once ungulate densities are reduced. There is much concern that these recovery dynamics may be slow, especially for highly favored species and ones whose regional abundance have been greatly reduced, limiting the potential for recolonization (Tanentzap et al. 2012).

We found here that *Acer saccharum* seedlings, *Osmorhiza* sp. and *Milium effusum* are good understory indicators of browse with the latter two species increasing in abundance in response to increased browsing pressure. Since the GLN has now completed the baseline data collection at all nine parks in the region, we recommend they use our path analysis approach to identify species sensitive to browse (both increasers and decreasers) for future use as indirect-indicator species. We further suggest that they investigate whether using composite measures that combine abundance data across species (like the four increasers we identified: *Aralia nudicaulis*, *Galeopsis tetrahit*, *Milium effusum*, and *Osmorhiza* sp.) provide greater sensitivity or reliability than metrics based on individual species. It will also be of interest to know how our four species metric performs across the remaining six parks. Ideally, this or similar composite metrics might also serve to track trends in ungulate impacts across parks or the region as a whole, avoiding the problem of having to rely on different particular species as indicators in different parks. This would enhance their utility for both the NPS and other land managers in the region.

We found that controlling for differences among sites in woody community composition enhanced our ability to assess associations between the woody browse metrics and the abundance of particular understory species. However, we did not control for other potentially confounding variables such as understory community composition, light, reproduction, or growth form. Future studies could pursue these multivariate approaches in more depth both to assess the effects of these other variables and to determine how they might extend our ability to apply particular metrics across heterogeneous landscapes. We also urge the GLN to consider reproductive and dispersal traits in choosing browse-sensitive understory indicators.

We recommend that future studies, and the GLN protocol itself, include a measure of light at each site to quantify how this factor influences understory species abundance and flowering / fruiting condition. This would improve our ability to assess how light and browse interact to affect understory structure and composition. Such measurements need not be complex and might be based on either a simple line-intersect estimates of canopy coverage above each sampling point along the transects or hemispherical overstory photos at enough positions to estimate incident light (e.g., as % open sky).

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