An Assessment of Long-term Biodiversity Recovery From Intense and Sustained Deer Browse on North Manitou Island, Sleeping Bear Dunes National Lakeshore

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Abstract: *Forty years of overbrowse by white-tailed deer (Odocoileus virginianus) and the impacts of irruptive population growth in the late 1970's and early 1980's left an enduring ecological legacy on Sleeping Bear Dunes National Lakeshore's North Manitou Island (NMI). Results of an ongoing study reveal that, relative to ecologically similar but unbrowsed forests on South Manitou Island (SMI), historically catastrophic levels of deer browse altered understory species composition and forest community trajectory from the probable composition and trajectory in the absence of browse. The forest herb and shrub communities on NMI show little evidence of recovery, a possible consequence both dispersal limitation and intense competition with tree seedlings and saplings that now occupy much of the understory and herbaceous layer growing space. The sapling layer is dominated by relatively unpalatable American beech (Fagus grandifolia). Sugar maple is absent in the small sapling size classes, likely a consequence of inability to recruit into the sapling layer during a period of especially strong browse pressure. Deer browse shows less of an effect on large saplings and overstory trees. The sapling recruitment patterns on NMI are in stark contrast to patterns documented for SMI, suggesting that past browse will have a lasting effect on future forest development, including an alteration of forest gap dynamics and overstory recruitment patterns. Recovery of herb communities has been particularly slow and warrants further study to determine if current ecological trajectory will result in desired future condition.*

Introduction

Historical land use practices often leave enduring legacies on population, community, and ecosystem dynamics, even where natural processes have largely been restored. Ecologists and natural resource managers have increasingly recognized the influence of land use legacies on current and projected future ecological processes and conditions (Foster et al. 2003). Land use legacies are ubiquitous, even in areas that did not directly suffer direct land conversion. Patches of old-growth forest in the Upper Great Lakes region of the United States, for example, have never been cut or otherwise subjected to logging practices, yet ecological processes within these patches are often heavily influenced by the surrounding "humanized" landscape, even where that landscape remains in a largely forested condition. Aldo Leopold made reference to this phenomenon over 60 years ago in his work for large private land club in Michigan's Upper Peninsula:

"*The size-scale of a wilderness area for scientific study greatly affects its value. A small area may be "natural" in respect of its plants, but wholly unnatural in respect of its mobile animals or water. However, mobile animals greatly affect plant life, so that a small virgin forest may appear to be natural when actually it has been profoundly affected by forces applied to animals,* *waters, or climate at points far distant. (Thus the deer populations determined by laws passed in Lansing, by hunters camping at Big Bay, and by lumbering operations on the Little Huron, have apparently exterminated the ground hemlock [Canada yew, Taxus canadensis] from the "virgin" forest of Mountain Lake*)" (Leopold 1938).

Additionally, the surrounding human dominated 'metacommunity' serves as constant source of propagule pressure for both native and non-native species, with the potential to alter colonization/extinction dynamics and ecological drift within the old growth or otherwise protected patch (sensu Hubbell 2001).

Herbivory by white-tailed deer is a common problem confronting managers of old growth and other natural areas in the eastern United States (Rooney 2001). Current land use practices, coupled with the extermination of natural predators, have resulted in regional deer populations that are much higher than during pre-Euro-American times (Côté et al. 2004, McCabe and McCabe 1997, Russell et al. 2001, Rooney and Gross 2003). In some cases, land managers are confronted with current rates of browse pressure that will inevitably alter community structure and dynamics, with the extinction of browse-sensitive species a likely outcome. In other cases, natural area managers must contend with a legacy of overbrowse that may persist for decades or even centuries.

Numerous studies have documented the effects of deer overabundance on forest ecosystems (Côté et al. 2004, Frankland and Nelson 2003, Ruhren and Handel 2003, Russell et al. 2001, Webster and Parker 1997). This work has led researchers to conclude that deer are a keystone herbivore in eastern deciduous forests of North America (Côté et al. 2004, Rooney 2001, Waller and Alverson 1997). The literature on deer impacts is dominated by studies of the effects of past and current browse levels on forests that currently support large deer populations (Russell et al. 2001, Frankland and Nelson 2003); fewer studies have examined the recovery of forests after deer densities have been reduced to levels that are not likely to have large continuing impacts on forest community structure and composition (e.g., Balgooyen and Waller 1995, Webster et al. 2005).

In this paper, we investigate a legacy of overbrowse on North Manitou Island (NMI), Sleeping Bear Dunes National Lakeshore, Michigan. We use data on current forest conditions to assess recovery of forest understories on NMI from almost four decades of intense, chronic browse. Deer were introduced to NMI in 1926 and populations were artificially maintained at high levels for several decades before a population reduction program was instituted in the mid-1980s. McCullough and Case (1987) studied NMI deer population dynamics and the impacts of the deer herd on plant communities in the late 1970's and early 1980's. They documented dramatic effects of deer on the understory tree and herbaceous plant communities at a time when herbivory pressure was likely at its peak. They also suggested that if deer densities were reduced, the forest community would eventually recover. However, they noted that the time averaged impacts of 40 years of deer overabundance would not likely be evident for many years.

To assess recovery, we use forest conditions on South Manitou Island (SMI) as a deer-free reference system. Deer were never introduced to SMI, and there is currently no evidence that deer ever colonized either island on their own. Thus SMI's Holocene plant communities have evolved in the absence of ungulate browse pressure, and provide a good reference for investigating the recovery of NMI plant communities to pre-deer conditions. Provided SMI remains deer-free, long-term data on the differences in forest structure and community composition between the two islands and between SMI and the mainland will provide a unique and invaluable reference for restoration and management. The greatest scientific value of SMI is its role as a base datum of what a large deer-free system looks like.

Therefore, the specific objectives of this study are to (1) provide baseline forest structure data of a large, deer free system (SMI) for inter-regional comparison with other areas heavily impacted by current or past overbrowse , (2) assess forest recovery on NMI, with emphasis on the herbaceous layer and forest understory, and (3) set up a system of permanent monitoring plots for continued, long-term study of forest development on the two islands.

The Study System

North and South Manitou Islands were included as part of SLBE in 1970, and are, by Great Lakes standards, fairly large at 6,070 ha and 2,020 ha respectively. The lakeshore covers approximately 23,470 ha of land and 4,860 ha of water. There are 103 km of Lake Michigan shoreline included in the Lakeshore. Both islands were predominantly forested before Euro-American settlement, with relatively greater sand dune cover on SMI. Northern hardwood/beech-maple forest is the dominant forest type on both islands, covering over 4,819 ha on NMI and 1,014 ha on SMI. Mixed hardwood/conifer forest covers 136 ha on NMI and 254 ha on SMI. Non-forested cover types on the islands include inland lake, wetland, dunes and shore, and abandoned agricultural fields. The islands experienced extensive logging in the 19th century as forests were cut for firewood, and then converted to agricultural uses. As human populations on the islands declined, forests recovered and currently, the majority of the northern hardwood forest on both islands is mature, uneven-aged second growth, with current conditions reflecting spatially variable but similar 19th century and early 20th century logging. Some areas were logged more recently on both islands (Hazlett 1988), but these areas were excluded from the present study.

Prior to its current ownership and management by the NPS, NMI was privately owned and largely managed as a game preserve for the human-introduced white-tailed deer. The deer were introduced to the island in 1926, and a supplemental feeding program for the deer was instituted in 1937. Supplemental feeding continued until 1977, when NPS acquisition and litigation over the purchase price of the island began. During the time that the feeding program was active, island owners maintained artificially high deer population densities (> 30 deer/km^2). Upon cessation of the feeding program, the deer population went through a period of rapidly fluctuating population levels, with a population crash followed by a boom and then another crash in a period of only five years (McCullough 1997). Case and McCullough (1987) reported detrimental impacts of the irruptive deer population on the woody and herbaceous vegetation in the forest understory, resulting in an obvious browse line and an understory devoid of all but a few unpalatable species such as American beech (*Fagus grandifolia*). Since implementation of population control measures in 1985 (i.e., annual hunts), the deer population has stabilized at a much lower density (~ 3 deer/km^2, S. Yancho, pers. comm.), and the forest understory has visibly recovered (NPS sources, pers. obs.).

Pre-Euro-American settlement data is generally not available on forest understory conditions. Nor is there much useful information on the understory flora for NMI or SMI for the period prior to deer introduction on NMI. There is little reason to believe, however, that the understory flora in the northern hardwood forest type on the two islands differed markedly prior to the introduction of deer to NMI. Any differences stemming from different colonization histories following the last glaciation were likely to be small since both islands are similarly isolated from the mainland and contain similar mixtures of soils, slope, aspect, etc. We would expect that any differences resulting from Euro-American colonists deliberately or accidentally bringing new native plant species to the islands would also be minor since colonists would have had little incentive to pursue such introductions; even if they had, we know of no reason to expect that one island would have experienced dramatically different patterns of introduction. It is likely that we will never know precisely how similar the islands' understory flora was in 1850 or 1900. However, it seems far more likely that they were quite similar than the alternative - two islands, just three miles apart had ground floras that differed substantially in the relative abundance of many species. We therefore, make the assumption that prior to the introduction of deer to NMI, the understory and ground flora of both islands were very similar. We believe that SMI offers the best available model for the restoration of NMI to conditions resembling pre-Euro-American settlement. Moreover, we believe that the differing deer histories of NMI and SMI provide an outstanding opportunity to understand the long-term effects of sustained high densities of deer on forest ecosystems.

Methods

We sampled overall forest community structure, with an emphasis on woody plants in 2003, whereas in 2004 our sampling focused on herbaceous layer in mature northern hardwood forests. For both years, sampling was conducted in mature northern hardwood forest on level to moderately sloping ground. Additionally, soils were either sandy loams or loamy sands, and the sample space, as defined by a GIS analysis, was therefore relatively homogenous. Our intent was not to provide a representative sample of forest communities on the islands, but rather to investigate whether differences existed between the two islands that reflect primarily differences in cultural legacies (e.g., deer browse on NMI) rather than variation in underlying environmental heterogeneity.

Therefore, we selected sites within areas of mature northern hardwoods forest with the constraints that sites had to be located on loamy sands or sandy loams, and slopes had to be less than 10 degrees. We used a GIS (ESRI ArcView, version 3.3) analysis to select suitable areas – correct forest type, soils and slopes. We obtained spatial data, including digital elevation models (USGS 7.5' DEMs), detailed soils data (USDA Natural Resources Conservation Service SSURGO data), and landcover data, from the NPS website http://www.nps.gov/gis/data_info. We first created a polygon theme of suitable areas and randomly selected points within the resultant polygons such that they were at least 240 m apart and 70 m from the edges of the polygons. This ensured that the plots would be distant enough from ecotones or edges where vegetation, soil, slope, might be considerably different. Thus an "edge" effect is not likely in our samples. By selecting relatively homogenous areas for sampling, we effectively reduced the confounding potential of unaccounted variables.

In 2003, we randomly selected 32 sites on SMI and 35 sites on NMI. At each site we used modified Forest Inventory and Analysis (FIA) protocols to set up an array of four 8-m radius circular plots, with the center of plot located at the site center and the center of plots 2, 3, and 4 located 39 m and 0°, 120°, and 240° respectively from the center of plot 1 (see Figure 1a). We recorded species and dbh (diameter at breast height, 1.4 m) of each woody stem with dbh ≥ 10 cm in each plot. We also measured height and age of a single representative canopy tree in each plot. In smaller, 4-m radius subplots centered at plot centers, we recorded species and diameter of saplings, defined here as woody stems with dbh < 10 cm and height > 1.8 m. Finally, we recorded counts (within 4 height classes) and percent cover of woody stems < 1.8 tall in 1 m^2 quadrats. We established 3 quadrats within each plot located 5 m and 30°, 150° and 270° from the plot center (Figure 1b). We also recorded, in each quadrat, coverage by herbaceous plants, litter, bare mineral soil, mosses, and coarse woody debris.

In 2004, we designed our sampling to look specifically at the herbaceous layer. We randomly selected 10 sites on each island, and set up 100 m long transects, with their origin at site center and a direction randomly selected between 0° and 360°. Along each transect, we located a systematic array of 40, 1-m^2 quadrats, as depicted in Figure 1c. Within each quadrat, we recorded species and percent cover of all woody and herbaceous plants. We limited our sampling of woody species to individuals with heights ≤ 1 m. Additionally, we noted flowering status of herb species, and recorded more detailed demographic data for two focal species, Large-flower trillium (*Trillium grandiflorum*) and Jack-in-the-pulpit (*Arisaema triphyllum*). (See appendices for common and latin names of plants). We have not yet analyzed demographic data from these two species, and the methodology and analytical results will be described in a future manuscript.

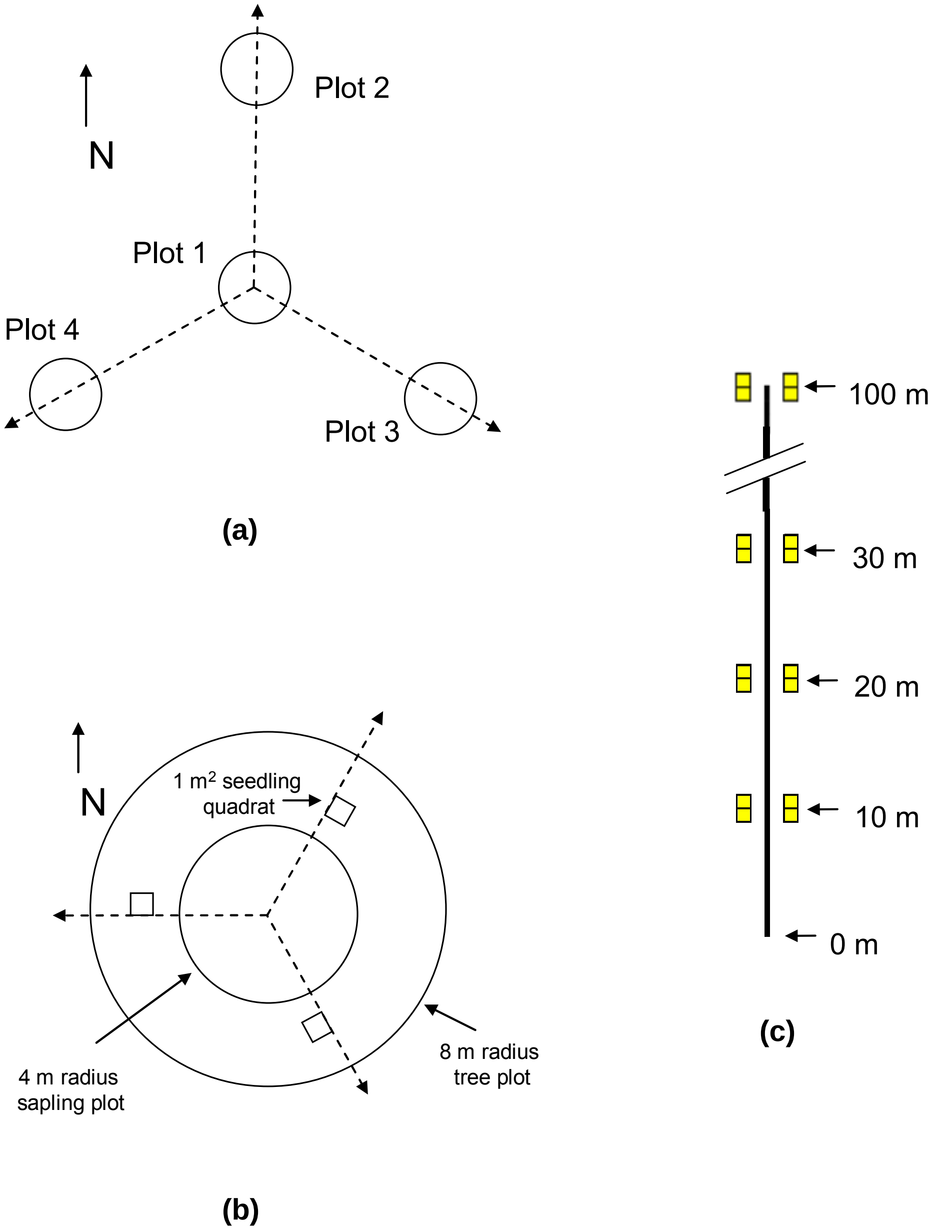

Figure 1. *Plot and transect layout for 2003 and 2004 sampling.*

Results

Our study of the current condition of forest vegetation in the northern hardwood forest type (the dominant vegetative cover type on the islands) reveals that, relative to the ecologically similar but unbrowsed forests of SMI, historically high levels of deer browse have altered understory species composition and forest community trajectory on NMI. Following the peak of deer densities in the late 1980s, anecdotal reports describe much of NMI's forests as having a park-like appearance with little or no green vegetation below 2 m. Today, the understory no longer lacks green vegetation, but its current composition and likely future trajectories are considerably altered from the probable composition and trajectory in the absence of excessive deer browse.

Tree Seedlings

On the two islands, we found dramatic differences in the total abundance and relative abundance of woody seedlings (defined as woody plants less than 1.8 m in height). NMI has more stems of both dominant tree species in all seedling height classes (by approximately 4:1) but is dominated by the relatively unpalatable American beech, especially in the smaller height classes (Figure 2c and 2b). SMI has fewer woody seedlings overall and the difference among the islands in this respect is most pronounced for American beech. In fact, American beech seedlings are more than twenty times more abundant on NMI than on SMI (Figure 2b). Sugar maple seedlings in these height classes are also more abundant on NMI than SMI and the difference is most pronounced in the smallest seedlings. The smallest sugar maple seedlings (height < 0.5 m) are four times more abundant on NMI than on SMI (Figure 2a).

Small diameter saplings

We also found differences among the islands' understory tree species in small diameter saplings (> 1.8 m tall, ≤ 5cm dbh; Figure 3). As with the smaller seedlings, NMI has more small diameter saplings in the two smallest size classes (Figure 3c) and sugar maple is virtually absent in all size classes (Figure 3a), likely as a result of poor recruitment into the sapling layer during a period when browse pressure was especially heavy. On NMI, American beech saplings are abundant in the smaller size classes, a pattern that is also consistent with this unpalatable species being favored by selective browse on its competitors 20-40 years ago (Figure 3b). On SMI, sugar maple saplings are abundant in all size classes and American beech saplings are scarce (Figure 3a). This too is consistent with patterns one would expect from deer preferentially browsing sugar maple (relative to American Beech) on NMI and the absence of deer on SMI. The sapling recruitment patterns on NMI contrast greatly with the patterns documented for SMI, and this difference likely will result in a lasting effect on patterns of future forest development, including an alteration in future patterns of gap dynamics and eventual overstory composition.

Large diameter saplings

Saplings in larger size classes (6-10 cm dbh) and small diameter understory trees on the two islands differed less than seedlings and small diameter saplings. In general, among these larger saplings, SMI had more although differences between the islands were minor for most size classes (Figure 2.6c, 2.7c). Large diameter sugar maple saplings were more abundant on SMI than on NMI but again, differences were not dramatic (Figure 4a). American beech abundance in these size classes was also similar (Figure 4b). This pattern is generally consistent with what one would expect if browsing pressure had its greatest impact on the cohort of tree seedlings and saplings that were within the deer browse zone immediately following the removal of the supplementary feeding program in 1977.

Understory and Overstory Trees

Deer impacts are least evident on the composition of larger diameter stems that comprise the understory and overstory of northern hardwood forest on the islands. There are differences between the two islands (Figure 5 and Appendix 1), but the differences can likely be attributed to a number of historical factors. There is no obvious signal in the data suggesting that a legacy of overbrowse by deer on NMI accounts for the observed differences in overstory trees. Rather, logging and other human activity since settlement may have had differential impacts on forest communities on the two islands. Additionally, GLO survey data suggest that forest structure and composition differed somewhat even prior to Euro-American settlement (unpublished data) and these differences in conjunction with differing human legacies likely account for many of the observed differences.

Notable differences between the two islands include the rarity of white ash (*Fraxinus americana*) on NMI relative to SMI, and the much higher importance of black cherry (*Prunus serotina*) on NMI. Additionally, American beech importance is greater on NMI relative to SMI, whereas sugar maple achieves greater importance on SMI. The role that deer may have played in the historic establishment and recruitment dynamics that determined the current composition of the overstory is not known. We have not yet fully analyzed the age structure of the overstory trees, but preliminary work suggests that establishment of the current overstory in the sampled mature northern hardwood forest occurred prior to the introduction of deer to the island in 1926, and certainly occurred before intensive management and supplemental feeding of deer began in the 1940s.

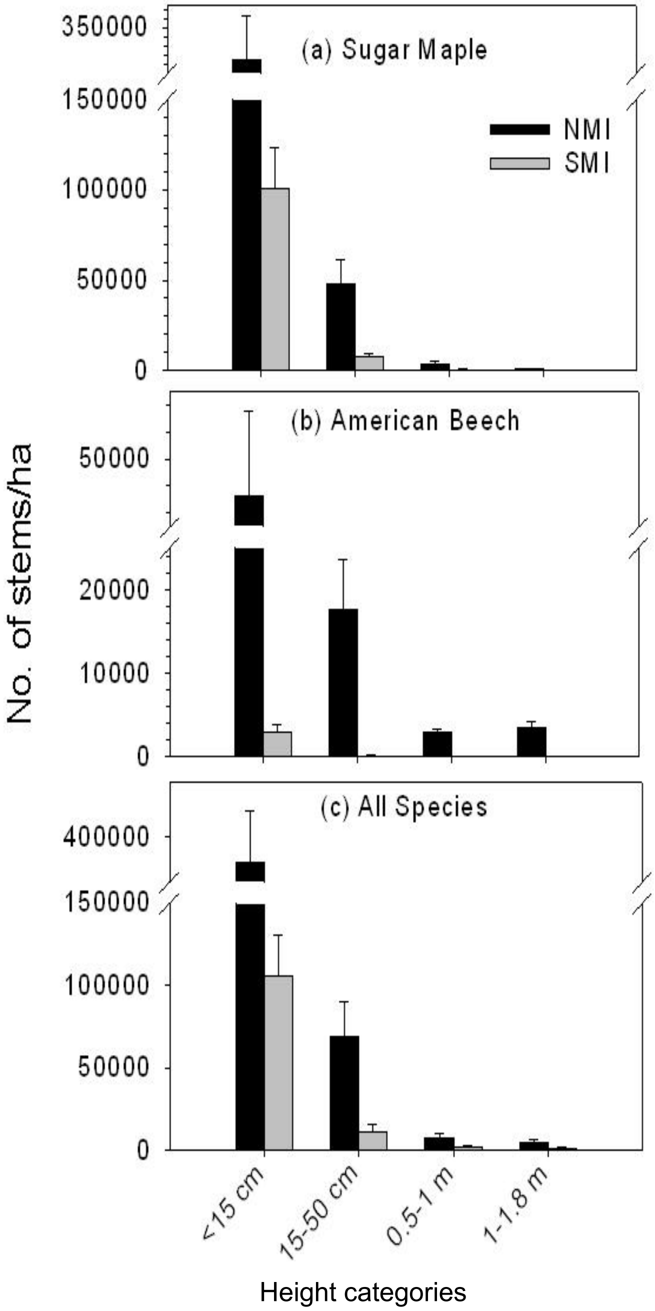

Figure 2. *Mean ± SE for tree seedlings in four height categories across plots on North and South Manitou Islands.*

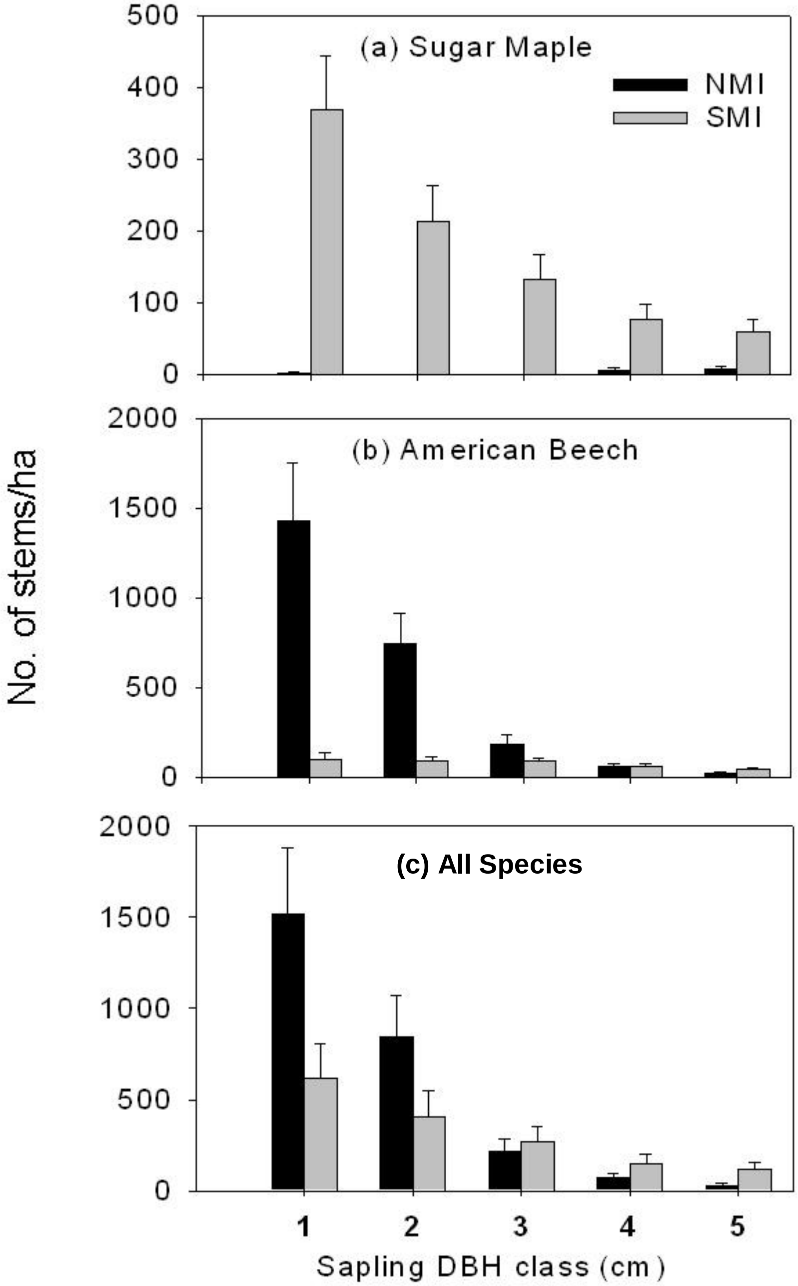

Figure 3. *Mean ± SE for small diameter tree saplings across plots on North and South Manitou Islands.*

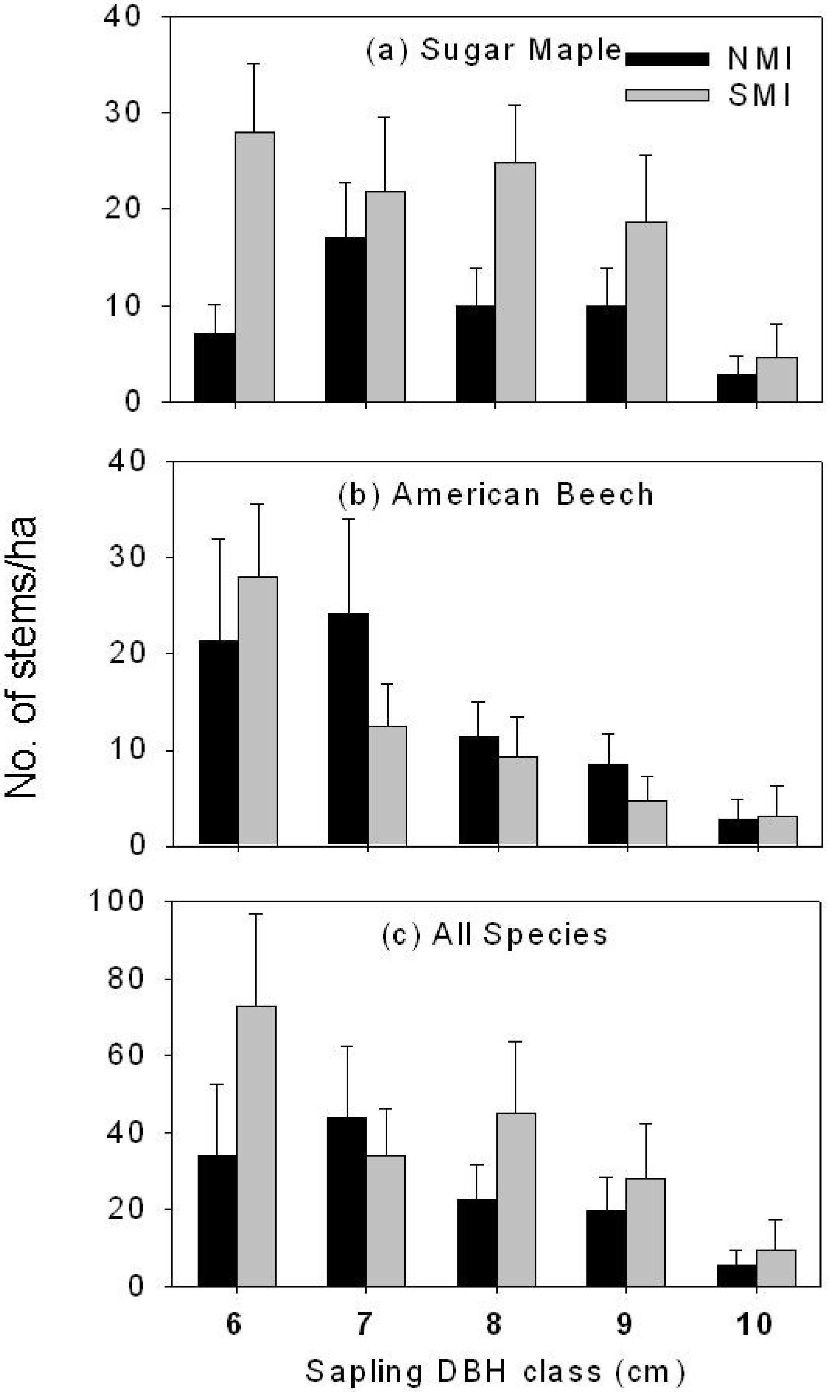

Figure 4*. Mean ± SE for large diameter tree saplings across plots on North and South Manitou Islands.*

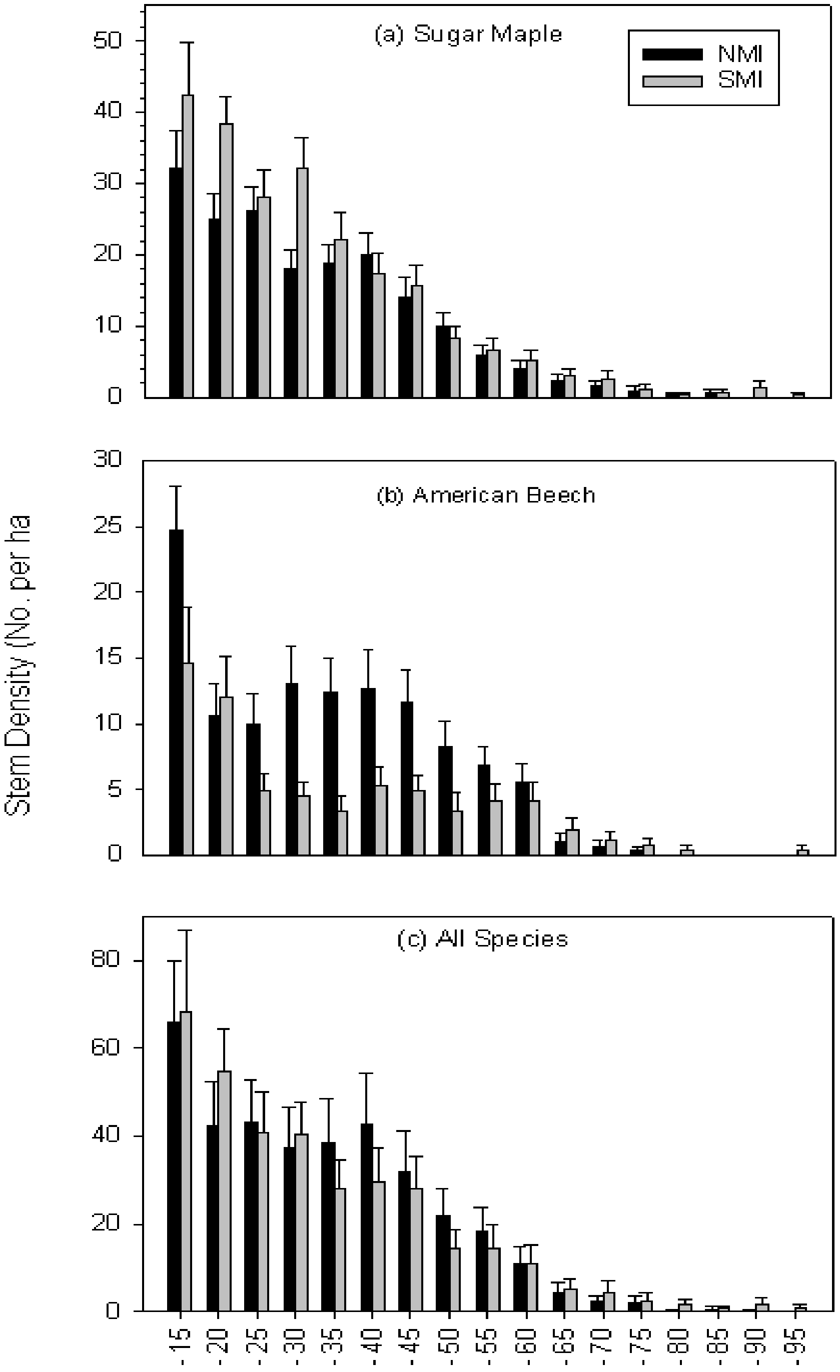

***Figure 5**. Diameter distributions (mean ±SE) for trees in northern hardwood forest on North and South Manitou Islands.*

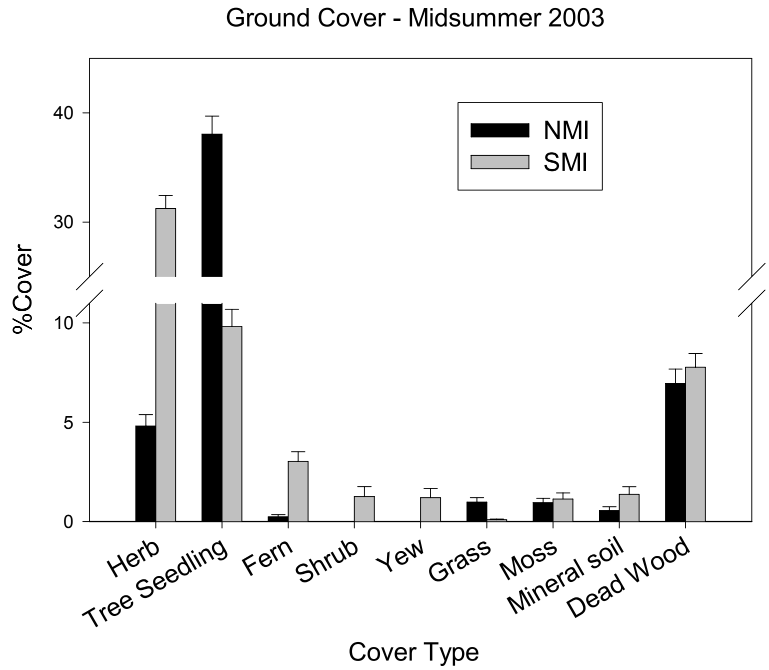

Figure 6. *Percent ground cover in mature second growth northern hardwood forest on North and South Manitou Islands. Tree seedling cover was estimated for all seedlings woody stems < 1.8 m tall.*

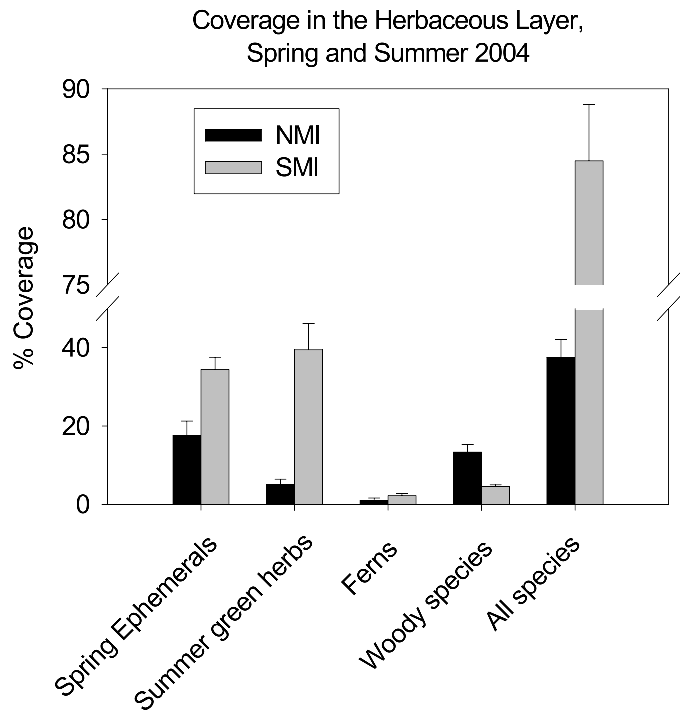

Figure 7. *Herbaceous layer percent cover in mature second growth northern hardwood forest on North and South Manitou Islands. Tree seedling cover was estimated for all woody stems < 1 m tall.*

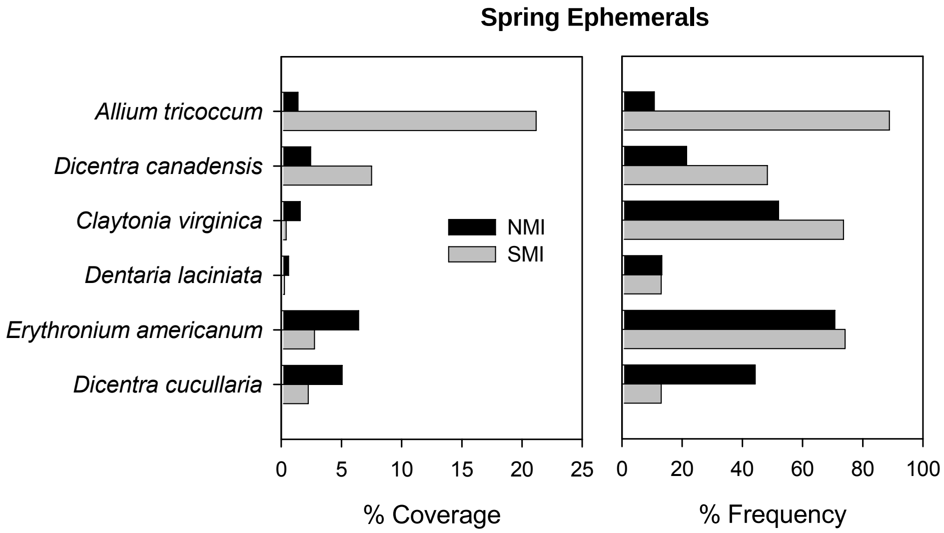

Figure 8. *Percent coverage and frequency (quadrat level) for spring ephemeral forest herbs on North and South Manitou Islands. Species are ranked by mean in quadrat level frequency between the two islands for six species that occurred in at least one percent of quadrats.*

Forest Herbs and Understory Shrubs

Comparing NMI and SMI northern hardwood forests, we found profound differences in the relative frequency and/or abundance of many species of forest herbs and shrubs (Figures 8, 9, and 10 and Appendices 2, 3 and 4) as well as major differences in the total amount of forest floor covered by herbs versus tree seedlings (Figure 6 and 7).

Many of these differences are consistent with what one would expect given known browse preferences of deer. Our data on shrubs and herbs suggest that some species have been functionally extirpated from NMI (e.g., *Taxus canadensis*, *Acer spicatum*, *Viburnum acerfolium*, *Ribes cynosbati*, *Caulophyllum thalictroides*, and *Uvularia grandiflora*). This means that while a few individuals may remain in protected microsites, the functional role of these plants has been greatly reduced or eliminated from the forest ecosystem. Many palatable herb species that do remain on NMI (e.g., *Allium tricoccum and Arisaema triphyllum*) are far less abundant than on SMI. In midsummer (late June and July, 2003 survey, Figure 6), understory herbaceous plants cover only 5% of the forest floor on NMI compared to 35% (41% in 2004 survey) of the forest floor on SMI.

There is some evidence of recovery since the mid 1980's, however. In particular, the frequency and cover of spring ephemeral herb species on NMI (18% cover, measured in mid May, 2004) now approaches that found on SMI (34% cover). *Eyrthronium americanum* (trout lily) actually had higher average cover and was encountered asfrequently on NMI as on SMI (Figure 8). Of the spring ephemerals, only *Allium tricoccum* (wild leek) appears not to have recovered substantially on NMI. Also, several summer green herb species that Hazlett (1985) reported as absent from NMI (e.g., *Actaea pachypoda*, *Sanguinaria canadensis*, *Smilacena racemosa*, and *Thalictrum dioicum*) now occur at low, but detectable, frequencies (Figure 9).

Trillium grandiflorum, in particular, has recovered substantially on NMI, with both average cover and frequency approaching that found on SMI. A handful of summer green herbs were actually more common on NMI, but most species had much lower cover and were far less abundant on NMI, with average total cover of summer green herbs on NMI being only 5% compared to 31% (39% 2004 survey) for SMI.

Shrubs and some understory tree species have also recovered slowly on NMI. Several species that were encountered on sampling plots on SMI were not present on NMI sampling plots, including *Taxus canadensis* (Canada yew), *Sambucus canadensis* (elderberry), and *Acer* *spicatum* (mountain maple) (Figure 10, Appendix 1) Only two woody species that regularly grow and reproduce in the forest understory, *Acer pennsylvanicm* (striped maple) and *Ostrya virginiana* (ironwood), were more common on NMI than on SMI, and deer generally avoid both of these species.

The slow recovery of the summer green herb and shrub communities on NMI may be in part due to competition with vigorous advance regeneration of American beech and sugar maple. As pointed out previously, densities of small saplings (primarily American beech) are much higher on NMI than on SMI. Additionally, the abundance of seedlings (defined here as trees less than 1.8m tall) is much greater on NMI (Figure 2.8), with midsummer (late June and July, 2003 survey) percent cover for seedlings on NMI at 38% vs. 10% for SMI.

The total woody and herbaceous midsummer plant cover (< 1.8 m, 2003 survey) in the herbaceous layer on NMI is 44% compared to 46% for SMI, suggesting that growing space is equally occupied on the two islands. Apparently advance regeneration of overstory tree species, with a ready seed source from reproductive canopy trees and absence of competition from perennial herbs and shrubs, has opportunistically taken over. Whether this is an ephemeral phenomenon, or represents an alternate dynamic equilibrium, is currently unclear.

In addition to large differences in frequency and percent coverage between the two islands, we also found interesting differences in herbaceous layer species richness, particularly for summer green herbs (Figure 11). While NMI had fewer summer green herb species than SMI, the magnitude of the differences between the two islands depended on the spatial scale at which it was measured. NMI had on average 81% fewer species per 1-m^2 sampling quadrat than SMI, whereas at the whole island scale (400 1-m^2 quadrats) NMI had just 31% fewer species. This pattern suggests relatively more clumped species distributions and/or lower species evenness on NMI compared to SMI. However, calculation of Simpson's index of evenness ($E_{1/D}$) indicates a somewhat more even species distribution for NMI summer green herbs ($E_{1/D}$ = 0.438) relative to SMI ($E_{1/D}$ = 0.359), though the difference was not statistically significant (Student's t = -1.44, df = 18, p = 0.167). We found no differences in evenness between the two islands when all species (spring ephemerals, summer green herbs, and woody species) were considered, either.

We did find evidence of a greater degree of clumping on NMI, with the majority of species for which it was possible to estimate a dispersion index (Green's coefficient of dispersion, G_c) (Krebs 1999) showing a more clumped dispersion pattern on NMI than SMI (see Appendix 5). Moreover, differences in the degree of dispersion between the two islands depended on the spatial scale at which we measured dispersion. For example, *Trillium grandiflorum* showed a markedly more clumped pattern on NMI relative to SMI when dispersion was measured at an island level spatial scale (i.e., across transects). However, at a smaller spatial scale, that of quadrats within transects, G_c values for *T. grandiflorum* indicated more or less equal levels of clumping between the two islands. Additionally, we found a general pattern across all species of greater within-transect relative to between-transect clumping on SMI. Nevertheless, G_c values for species on SMI were generally smaller, indicating a more random and less clumped dispersion pattern, at both within- and between-transect spatial scales. Across transects, 18 of 22 herb species were more clumped on NMI, 1 was more clumped on SMI, and 3 species showed more or less equal levels of clumping between the islands (X^2 = 23.5, df = 2, p < 0.001). Across quadrats within transects, the pattern was similar, with 15 species demonstrating higher clumping on NMI, 5 species with higher clumping on SMI, and 1 species showing equal levels of clumping (X^2 = 12.6, df = 2, p < 0.002).

Careful study of dominance-diversity curves (Whittaker plots, after Whittaker 1965) for the two islands (Figure 12) does reveal further differences in the distributions of species abundances (e.g., degree of dominance) that a simple index of evenness does not, however. Curves for both islands resemble the characteristic S-shape of a lognormal distribution of species relative abundance. However, the overall shape of the two curves more strongly suggest Hubbell's (2001) asymmetric zero-sum multinomial distribution, particularly as predicted by a neutral community model that assumes dispersal limitation. This may have important implications for restoration and for testing models of community assembly, in that neutral theory emphasizes the importance of stochastic relative to deterministic processes. If chance and history play dominant roles in determining community structure and dynamics, restoration may play a more important role in determining the future state of the islands' biodiversity.

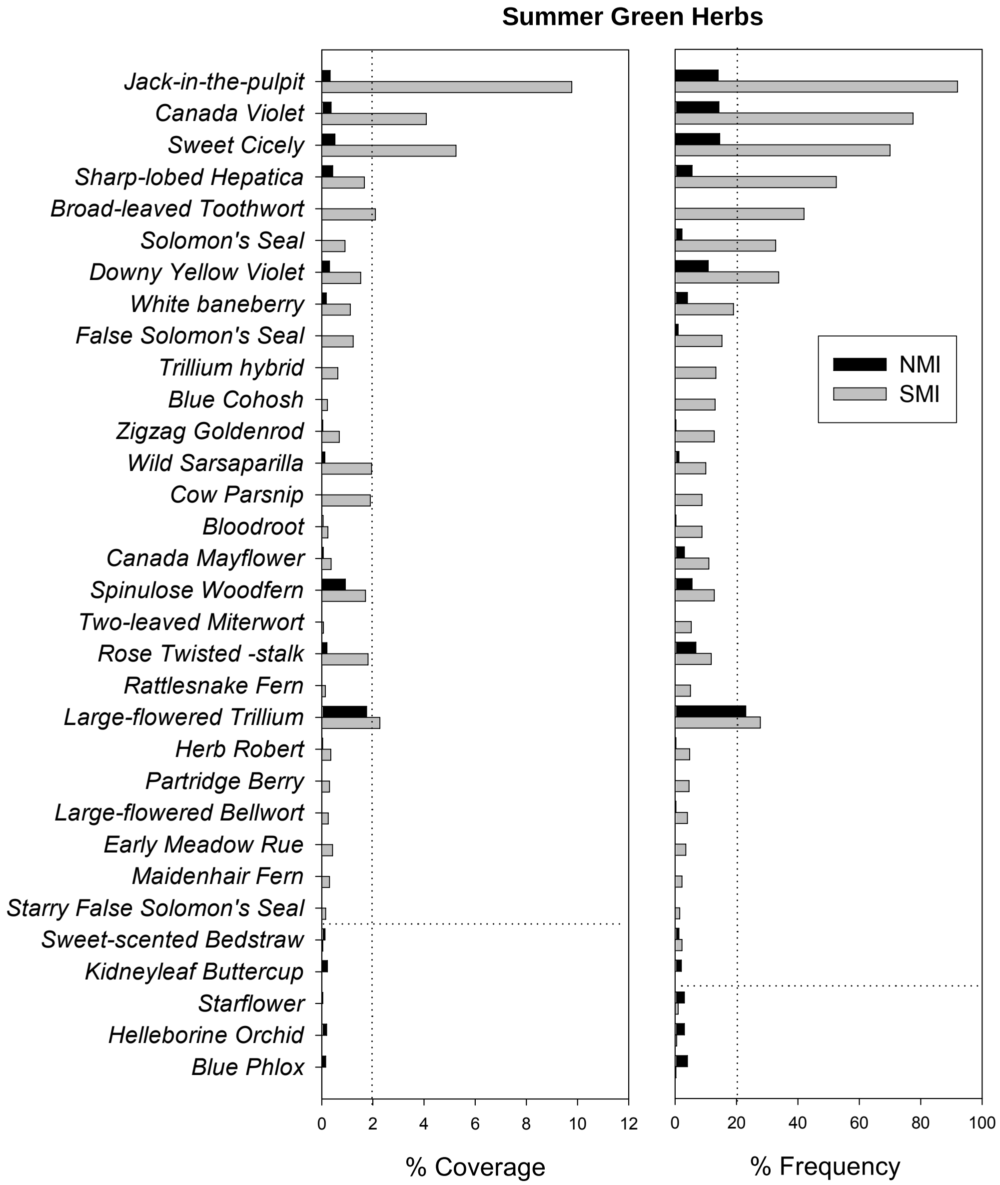

Figure 9. *Percent coverage and frequency (quadrat level) for summer green forest herbs on North and South Manitou Islands. Species are ranked by mean difference in quadrat level frequency between the two islands for 33 species that occurred in at least one percent of quadrats.*

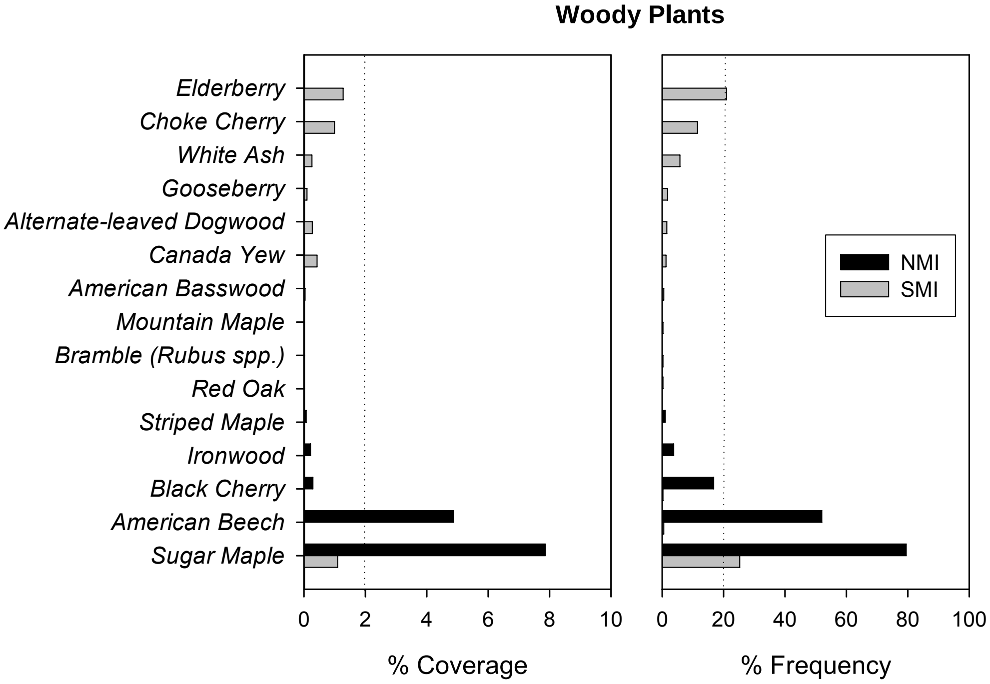

Figure 10. *Percent coverage and frequency (quadrat level) for woody plants (height ≤ 1 m) on North and South Manitou Islands. Species are ranked by mean difference in quadrat level frequency between the two islands for 15 species that occurred in at least one percent of quadrats.*

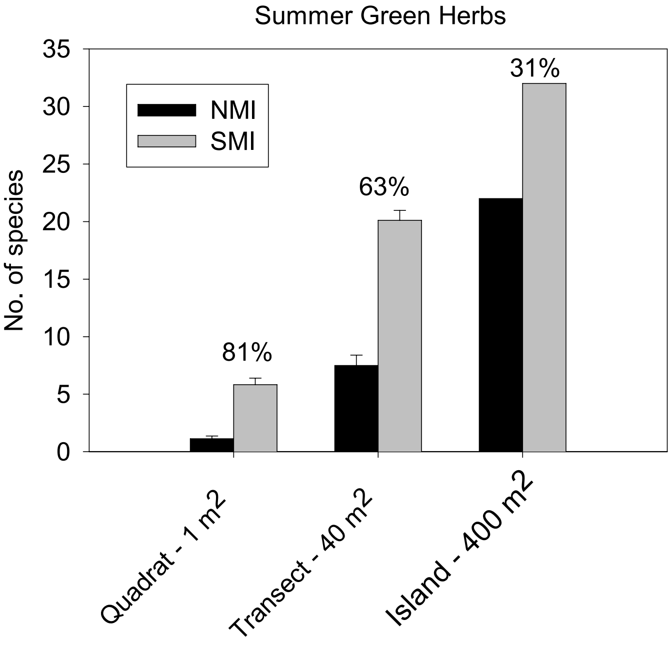

Figure 11. *Herbaceous layer species richness (mean ± SE) in mature second growth northern hardwood forest on North and South Manitou Islands. Average richness is shown at three spatial scales. Numbers above bars represent the percentage decrease in richness on NMI relative to SMI.*

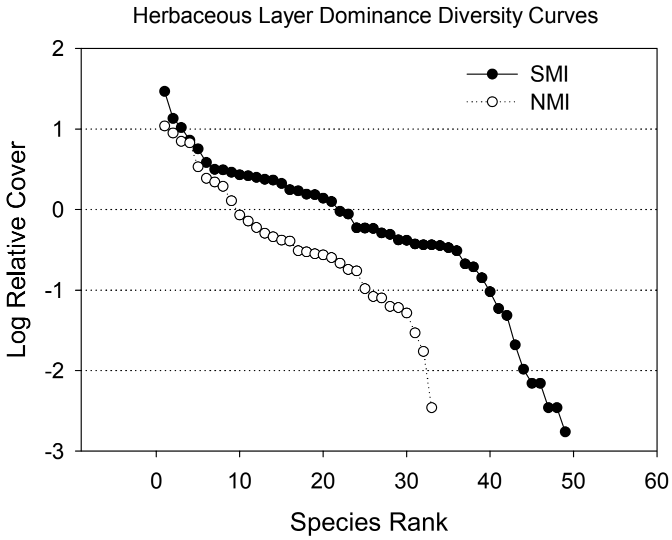

Figure 12. *Herbaceous layer dominance-diversity curves (Whitaker plots) for mature second growth northern hardwood forest on North and South Manitou Islands.*

Conclusion

Studies of entire herb communities recovering from historic, chronic overbrowse by white-tailed deer or other ungulates are extremely rare (although see Webster et al. 2005). Exclosure studies, while common, do not allow assessment of recovery at an appropriate scale (i.e., whole community or stand level vs. plot level). Exclosures provide an effective means of documenting deer impacts on plant communities primarily in the early stages of overbrowse, before local extirpation of preferred or browse intolerant species. Long-term, chronic herbivory often results in loss of species from large areas (Leopold 1938, Côté et al. 2004) as evident in this and other studies (e.g., Webster 2005). Many forest herbs are dispersal limited (Ehrl and Eriksson 2000), with little ability to recolonize an area if source populations are distant or dispersal must occur a across a relatively hostile matrix. Thus for locally extirpated, dispersal limited herb species, exclosures are of limited utility in documenting either browse impacts or recovery from browse. In such cases, comparison with an appropriate reference system(s), such as SMI, is necessary to provide a suitable baseline for recovery.

Comparison of the forest understory and herbaceous layers on the two islands indicate that recovery from intense, chronic browse on NMI may take decades to proceed appreciably. Forest herb communities, in particular, are slow to respond to reduced deer densities. Sustained browse levels were great enough on NMI to severely alter ecosystem trajectory and cause biotic impoverishment of island forest communities, particularly forest herbs. Since NPS took over management of the island, some recovery is evident and the deer that remain on NMI, while likely inhibiting recovery of some plant species, do not appear to be continuing to erode the island's biotic integrity (as indexed by species richness, number of plant extirpations, etc.). However, the role of this introduced ungulate in shaping current forest ecosystem processes, especially with regard to the recovery of understory plant communities, is not well understood and warrants further study.

Although deer do exhibit selective browsing when resources are abundant (Strole and Anderson 1992), Seagle and Liang (1997) suggested that overabundant deer can lower availability of vegetative browse to a point where deer become generalists and all species are equally utilized. Such a switch from a selective to nonselective foraging strategy likely occurred on NMI, at least for deer foraging in the forest understory (see Case and McCullough 1987).

Even unpalatable beech leaves were conspicuously browsed, and it seems likely that most if not all forest herbaceous species were heavily browsed, with some populations declining to the point where they became barely detectable or were eliminated entirely (Hazlett 1985, 1988). Thus population recovery may not reflect selective browsing in the past so much as the suite of factors which have limited recovery since deer numbers were reduced to their current levels. However, even if the overabundant deer of the past browsed all herbs more-or-less equally, current selective foraging patterns by deer may have differential impacts on recovery rates of different understory species, depending on palatability. Deer may avoid woody species in favor of foraging on more palatable forest herbs. Under this scenario, even a relatively low density of deer might be capable of suppressing many herb species made rare by intense browse in the past. This could result in an alteration of competitive dynamics between different forest understory species or species' guilds, producing an alternate dynamic trajectory (sensu Augustine et al. 1998's "alternate stable states") where tree seedlings and saplings maintain dominance over herbs into the foreseeable future.

We believe that the shrub and herbaceous plant communities have and will continue to recover much more slowly than the understory tree community. While the composition of established understory trees was almost certainly altered by past deer browse, current low rates of deer browse are unlikely to continue to have a profound impact. As evidence of this, tree seedling abundance is actually higher for some browse sensitive species (e.g., *Acer saccharum*) on NMI than on SMI. Thus trees seem to be coming back unassisted, likely due to a steady seed rain from the reproductively mature overstory.

In contrast, understory shrubs and herbaceous plants that were greatly reduced in abundance or locally extirpated, do not have a locally abundant seed source, and thus recovery may be seed limited. Factors that may limit herb and shrub recovery include: 1) resource competition with tree seedlings and saplings, 2) lack of and/or competition for suitable germination microsites, 3) pollen or pollinator limitations, 4) seed predation, 5) herbivory by deer or other animals, and 6) life history traits that predispose understory plants to slow dispersal and slow growth. More than one of these factors may interact in complex ways to limit growth, dispersal and thus population recovery. A better understanding of the processes that limit growth, reproduction and dispersal of forest herbs would be helpful for future restoration of this component of NMI's forests.

In this paper, we have highlighted structural and functional components of the forests on NMI that were likely most impacted by chronic overbrowse. Given sufficient time, unmanipulated ecological succession may continue to move the islands' forests toward the desired condition, whatever that may be (e.g., mid-19th century). On the other hand, some of the conditions documented in this study that are the result of past deer browse may not be ameliorated by decades or even centuries of natural succession.

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Appendix 1. Importance values for all tree species sampled within tree plots during 2003 survey, sorted in descending order of combined importance values on the two islands.

		Relative Frequency		Relative Density		Relative Dominance		Importance Values	
Scientific Name	**Common Name**	NMI	SMI	NMI	SMI	NMI	SMI	NMI	SMI
Acer saccharum	Sugar Maple	38.21	42.96	49.67	65.12	46.16	58.70	44.68	55.59
Fagus grandifolia	American Beech	30.75	28.52	32.39	18.90	33.45	22.34	32.20	23.25
Fraxinus americana	White Ash	0.00	13.38	0.00	9.29	0.00	13.21	0.00	11.96
Prunus serotina	Black Cherry	8.66	0.70	4.44	0.22	8.58	0.65	7.23	0.52
Betula alleghaniensis	Yellow Birch	6.57	3.87	3.59	1.51	3.26	1.42	4.47	2.27
Tsuga canadensis	Eastern Hemlock	3.28	2.82	3.40	1.51	0.98	1.50	2.56	1.94
Ostrya virginiana	Ironwood	4.78	2.82	2.27	1.62	0.51	0.12	2.52	1.52
Tilia americana	American Basswood	2.39	2.11	1.23	0.65	2.25	1.12	1.96	1.29
Betula papyrifera	White Birch	2.99	1.41	1.23	0.65	1.45	0.62	1.89	0.89
Populus grandidentata	Bigtooth Aspen	0.90	0.00	1.23	0.00	1.87	0.00	1.33	0.00
Acer rubrum	Red Maple	0.60	0.00	0.28	0.00	0.35	0.00	0.41	0.00
Quercus rubra	Red Oak	0.30	0.00	0.09	0.00	0.81	0.00	0.40	0.00
Prunus virginiana	Choke Cherry	0.00	0.70	0.00	0.32	0.00	0.09	0.00	0.37
Pinus strobus	White Pine	0.30	0.00	0.09	0.00	0.32	0.00	0.24	0.00
Juglans nigra	Black Walnut	0.00	0.35	0.00	0.11	0.00	0.23	0.00	0.23
Cornus alternafolia	Alternate-leaved Dogwood	0.00	0.35	0.00	0.11	0.00	0.00	0.00	0.15
Populus tremuloides	Quaking Aspen	0.30	0.00	0.09	0.00	0.00	0.00	0.13	0.00

Appendix 2. Frequency of herbaceous plant species encountered within plots during 2003 surveys, sorted in descending order of occurrence frequency on South Manitou Island. Data represent all herbs observed within the 8-m radius tree plots, not the 1-m2 quadrats nested within tree plots. Spring ephemerals and some early summer green herbs are under-represented, particularly for South Manitou, because sampling was conducted in midsummer.

Scientific Name	Common Name	Species Code	North Manitou Island	South Manitou Island
Arisaema triphyllum	Jack-in-the-pulpit	ARTR	51.43	100.00
Hepatica acutiloba	Sharp-lobed Hepatica	HEAC	48.57	100.00
Viola sp.	Violet	VIOL	71.43	100.00
Allium tricoccum	Wild Leek	ALTR	74.29	96.88
Osmorhiza claytoni	Sweet Cicely	OSCL	77.14	96.88
Actaea pachypoda	White Baneberry	ACPA	8.57	90.63
Polygonatum pubescens	Solomon's Seal	POBI	68.57	87.51
Dryopteris spinulosa	Spinulose Woodfern	DRSP	60.00	81.25
Sanguinaria canadensis	Bloodroot	SACA	25.71	78.13
Smilacene racemosa	False Solomon's Seal	SMRA	17.14	75.00
Dryopteris marginalis	Marginal Wood Fern	DRMA	11.43	68.75
Botrychium virginianum	Rattlesnake Fern	RAFE	17.14	68.75
Trillium grandiflorum	Large-flowered Trillium	TRGR	82.86	65.63
Caulophyllum thalictroides	Blue Cohosh	CATH	0.00	56.25
Maianthemum canadense	Wild Lily of the Valley	MACA	34.29	56.25
Solidago flexicaulis	Zigzag goldenrod	SOFL	8.57	56.25
Galium sp.	Bedstraw	GASP	22.86	53.13
Ribes sp.	Gooseberry	RISP	0.00	53.13
Mitchella repens	Partridgeberry	MIRE	14.29	46.88
Streptopus roseus	Rose Twisted-stalk	STRO	11.43	46.88
Uvularia grandiflora	Large-flowered Bellwort	UVGR	0.00	43.75
Heracleum maximum	Cow-parsnip	HEMA	0.00	40.63
Mitella diphylla	Bishop's Cap	MIDI	0.00	40.63
Taxus canadensis	Canada Yew	TACA	0.00	40.63
Thalictrum dioicum	Meadow Rue	THSP	14.29	53.13
Geranium robertianum	Herb Robert	GERO	45.71	25.00
Adiantum pedatum	Maiden-hair Fern	MHFE	2.86	21.88
Aralia nudicaulus	Wild Sarsaparilla	ARSP	2.86	15.63
Aralia racemosa	Spikenard	ARRA	0.00	12.50
Anemone quiquefolia	Wood Anemone	ANQU	0.00	9.38
Dentaria laciniata	Cut-leaf Toothwort	DELA	8.57	6.25
Smilacene trifolia	Three-leaved False Solomon's Seal	SMTR	0.00	6.25
Acer spicatum	Mountain Maple	ACSP	0.00	3.13
Aralia hispida	Bristly Sarsaparilla	ARHI	2.86	3.13
Clintonia borealis	Clintonia, Corn Lily	CLBO	0.00	3.13
Dentaria diphylla	Toothwort	DEDI	5.71	3.13
Equisetum sp	Horsetail	EQSP	5.71	3.13
Panax quinquefolius	Ginseng	PAQU	0.00	3.13
Sagittaria latifolia	Broad-leaved Arrowhead	SALA	0.00	3.13
Vitus sp.	Wild Grape	VISP	0.00	3.13
Lycopodium sp.	Club Moss	CLMO	5.71	0.00
Dicentra canadensis	Squirrel Corn	DICA	28.57	0.00
Erythronium americanum	Trout Lily	ERAM	17.14	0.00
Galium asprellum	Rough Bedstraw	GAAS	11.43	0.00
Galium triflorum	Fragrant Bedstraw	GATR	5.71	0.00
Phlox divaricata	Blue Phlox	PHDI	20.00	0.00
Onoclea sensibilis	Sensitive Fern	SEFE	2.86	0.00
Senecio obovatus	Roundleaf Ragwort	SEOB	2.86	0.00
Stellaria sp	Chickweed	STSP	2.86	0.00
Taraxacum officnale	Common Dandelion	TAOF	2.86	0.00
Trientalis borealis	Starflower	TRBO	22.86	0.00
Viola canadensis	Canada Violet	VICA	17.14	0.00
Viola pubescens	Downy Yelow Violet	VIPU	5.71	0.00

Appendix 3. Means ± SE for herbaceous layer percent frequency in northern hardwood forests on North and South Manitou Islands, summarized for 2004 for surveys.

		Frequency - % of quadrats		**Frequency - % of sites**	
Scientific Name	**Common Name**	NMI	SMI	NMI	SMI
Spring Ephemerals					
Allium tricoccum	Wild Leek	10.75	88.89	60	100
Claytonia virginica	Spring Beauty	52.00	73.61	100	100
Dentaria laciniata	Cut-leaved Toothwort	13.25	13.06	70	89
Dicentra canadensis	Squirrel Corn	21.50	48.33	60	89
Dicentra cucullaria	Dutchman's Breeches	44.25	13.06	90	78
Erythronium americanum	Trout-lily	70.75	74.17	100	100
Summer Green Herbs					
Actaea pachypoda	White baneberry	4.00	19.00	40	90
Aralia nudicalus	Wild Sarsaparilla	1.25	10.00	20	30
Arisaema tripyllum	Jack-in-the-pulpit	14.00	92.00	50	100
Caulophyllum thalictroides	Blue Cohosh	0.00	13.00	0	90
Clintonia borealis	Bead-lily	0.00	0.75	0	10
Dentaria diphylla	Broad-leaved Toothwort	0.00	42.00	0	100
Epipactus helleborine	Helleborine Orchid	3.00	0.50	50	20
Galium lanceolatum	Wild Licorice	0.00	0.50	0	20
Galium triflorum	Sweet-scented Bedstraw	1.25	2.25	30	50
Geranium robertianum	Herb Robert	0.25	4.75	10	50
Hepatica acutiloba	Sharp-lobed Hepatica	5.50	52.50	30	100
Heracleum maximum	Cow Parsnip	0.00	8.75	0	60
Maianthemum canadense	Canada Mayflower	3.00	11.00	60	80
Mitchella repens	Partridge Berry	0.00	4.50	0	50
Mitella diphylla	Two-leaved Miterwort	0.00	5.25	0	60
Osmorhiza claytoni	Sweet Cicely	14.50	70.00	60	90
Phlox divaricata	Blue Phlox	4.00	0.25	20	10
Polygonatum pubescens	Solomon's Seal	2.25	32.75	40	100
Prenanthes alba	White Lettuce	0.00	0.50	0	20
Ranunculus abortivus	Kidneyleaf Buttercup	2.00	0.00	20	0
Sanguinaria canadensis	Bloodroot	0.25	8.75	10	70
Smilacene racemosa	False Solomon's Seal	1.00	15.25	40	90
Smilacene stellaria	Starry False Solomon's Seal	0.00	1.50	0	20
Solidago caesia	Ble-stemmed Goldenrod	0.25	0.25	10	10
Solidago flexicaulis	Zigzag Goldenrod	0.25	12.75	10	90
Streptopus roseus	Rose Twisted -stalk	6.75	11.75	60	100
Thalictrum dioicum	Early Meadow Rue	0.00	3.50	0	60
Trientalis borealis	Starflower	3.00	1.00	20	10
Trillium erectum x *flexipes*	Trillium hybrid	0.00	13.25	0	90
Trillium grandiflorum	Large-flowered Trillium	23.00	27.75	90	100
Uvularia grandiflora	Large-flowered Bellwort	0.25	4.00	10	50
Viola canadensis	Canada Violet	14.25	77.50	60	100
Viola pubescens	Downy Yellow Violet	10.75	33.75	50	90
Ferns					
Adiantum pedatum	Maidenhair Fern	0.00	2.25	0	20
Botrychium virginianum	Rattlesnake Fern	0.00	5.00	0	40
Dryopteris spinulosa	Spinulose Woodfern	5.50	12.75	40	90
Onoclea sensibilis	Sensitive Fern	0.50	0.00	20	0
Grass/sedge	Grass/sedge	11.75	1.50	60	30
Woody Plants					
Acer pennsylvanicum	Striped Maple	1.00	0.00	30	0
Acer saccharrum	Sugar Maple	79.50	25.25	100	100
Acer spicatum	Mountain Maple	0.00	0.25	0	10
Cornus alternafolia	Alternate-leaved Dogwood	0.00	1.50	0	20
Fagus grandifolia	American Beech	52.00	0.50	100	10
Fraxinus americana	White Ash	0.00	5.75	0	90
Ostrya virginiana	Ironwood	3.75	0.00	20	0
Prunus serotina	Black Cherry	16.75	0.25	60	10
Prunus virginiana	Choke Cherry	0.00	11.50	0	70
Quercus rubra	Red Oak	0.25	0.00	10	0
Ribes sp.	Ribes sp.	0.00	1.75	0	50
Rubus sp.	Rubus sp.	0.00	0.25	0	10
Sambucus pubens	Elderberry	0.00	21.00	0	100
Taraxacum officnale	Dandelion	0.25	0.00	10	0
Taxus canadensis	Canada Yew	0.00	1.25	0	30
Tilia americana	American Basswood	0.00	0.50	0	10

Appendix 4. Means ± SE for herbaceous layer percent frequency in northern hardwood forests on North and South Manitou Islands, summarized for 2004 for surveys.

		North Manitou Island			South Manitou Island		
Scientific Name	**Common Name**	Mean		SE	Mean		SE
Spring Ephemerals							
Allium tricoccum	Wild Leek	1.40	±	0.78	21.18	±	2.38
Claytonia virginica	Spring Beauty	1.58	±	0.40	0.42	±	0.05
Dentaria laciniata	Cut-leaved Toothwort	0.62	±	0.27	0.26	±	0.07
Dicentra canadensis	Squirrel Corn	2.44	±	1.11	7.50	±	2.27
Dicentra cucullaria	Dutchman's Breeches	5.07	±	1.80	2.25	±	0.71
Erythronium americanum	Trout-lily	6.43	±	1.33	2.77	±	0.48
Summer Green Herbs							
Actaea pachypoda	White baneberry	0.18	±	0.09	1.12	±	0.26
Aralia nudicalus	Wild Sarsaparilla	0.13	±	0.11	1.95	±	1.79
Arisaema tripyllum	Jack-in-the-pulpit	0.33	±	0.24	9.78	±	1.46
Caulophyllum thalictroides	Blue Cohosh	0.00	±	0.00	0.22	±	0.06
Clintonia borealis	Bead-lily	0.00	±	0.00	0.05	±	0.05
Dentaria diphylla	Broad-leaved Toothwort	0.00	±	0.00	2.10	±	0.66
Epipactus helleborine	Helleborine Orchid	0.20	±	0.14	0.01	±	0.01
Galium lanceolatum	Wild Licorice	0.00	±	0.00	0.01	±	0.00
Galium triflorum	Sweet-scented Bedstraw	0.13	±	0.11	0.04	±	0.02
Geranium robertianum	Herb Robert	0.04	±	0.04	0.36	±	0.32
Hepatica acutiloba	Sharp-lobed Hepatica	0.43	±	0.24	1.67	±	0.27
Heracleum maximum	Cow Parsnip	0.00	±	0.00	1.90	±	1.34
Maianthemum canadense	Canada Mayflower	0.06	±	0.02	0.37	±	0.10
Mitchella repens	Partridge Berry	0.00	±	0.00	0.30	±	0.16
Mitella diphylla	Two-leaved Miterwort	0.00	±	0.00	0.07	±	0.03
Osmorhiza claytoni	Sweet Cicely	0.52	±	0.33	5.25	±	0.86
Phlox divaricata	Blue Phlox	0.16	±	0.10	0.00	±	0.00
Polygonatum pubescens	Solomon's Seal	0.02	±	0.01	0.91	±	0.26
Prenanthes alba	White Lettuce	0.00	±	0.00	0.01	±	0.01
Ranunculus abortivus	Kidneyleaf Buttercup	0.22	±	0.22	0.00	±	0.00
Sanguinaria canadensis	Bloodroot	0.06	±	0.06	0.24	±	0.07
Smilacene racemosa	False Solomon's Seal	0.01	±	0.01	1.23	±	0.63
Smilacene stellaria	Starry False Solomon's Seal	0.00	±	0.00	0.15	±	0.15
Solidago caesia	Ble-stemmed Goldenrod	0.05	±	0.05	0.00	±	0.00
Solidago flexicaulis	Zigzag Goldenrod	0.05	±	0.05	0.69	±	0.27
Streptopus roseus	Rose Twisted -stalk	0.20	±	0.12	1.81	±	0.97
Thalictrum dioicum	Early Meadow Rue	0.00	±	0.00	0.43	±	0.16
Trientalis borealis	Starflower	0.04	±	0.04	0.02	±	0.02
Trillium erectum x *flexipes*	Trillium hybrid	0.00	±	0.00	0.64	±	0.15
Trillium grandiflorum	Large-flowered Trillium	1.76	±	0.83	2.28	±	0.54
Uvularia grandiflora	Large-flowered Bellwort	0.00	±	0.00	0.26	±	0.10
Viola canadensis	Canada Violet	0.37	±	0.17	4.09	±	0.49
Viola pubescens	Downy Yellow Violet	0.30	±	0.17	1.52	±	0.48
Ferns							
Adiantum pedatum	Maidenhair Fern	0.00	±	0.00	0.30	±	0.25
Botrychium virginianum	Rattlesnake Fern	0.00	±	0.00	0.14	±	0.09
Dryopteris spinulosa	Spinulose Woodfern	0.93	±	0.65	1.72	±	0.59
Onoclea sensibilis	Sensitive Fern	0.01	±	0.01	0.00	±	0.00
Grass/sedge	Grass/sedge	0.35	±	0.16	0.06	±	0.04
Woody Plants							
Acer pennsylvanicum	Striped Maple	0.08	±	0.04	0.00	±	0.00
Acer saccharrum	Sugar Maple	7.86	±	1.93	1.10	±	0.31
Acer spicatum	Mountain Maple	0.00	±	0.00	0.00	±	0.00
Cornus alternafolia	Alternate-leaved Dogwood	0.00	±	0.00	0.27	±	0.22
Fagus grandifolia	American Beech	4.87	±	1.38	0.01	±	0.01
Fraxinus americana	White Ash	0.00	±	0.00	0.26	±	0.08
Ostrya virginiana	Ironwood	0.22	±	0.15	0.00	±	0.00
Prunus serotina	Black Cherry	0.29	±	0.12	0.00	±	0.00
Prunus virginiana	Choke Cherry	0.00	±	0.00	1.00	±	0.39
Quercus rubra	Red Oak	0.00	±	0.00	0.00	±	0.00
Ribes sp.	Ribes sp.	0.00	±	0.00	0.10	±	0.06
Rubus sp.	Rubus sp.	0.00	±	0.00	0.01	±	0.01
Sambucus pubens	Elderberry	0.00	±	0.00	1.28	±	0.29
Taraxacum officnale	Dandelion	0.00	±	0.00	0.00	±	0.00
Taxus canadensis	Canada Yew	0.00	±	0.00	0.43	±	0.30
Tilia americana	American Basswood	0.00	±	0.00	0.04	±	0.04

Appendix 5. Green's coefficient of dispersion for herbaceous layer species on North and South Manitou Islands.

		Transects		Quadrats within transects	
Scientific Name	Common Name	**NMI**	**SMI**	**NMI**	**SMI**
Spring Ephemerals					
Allium tricoccum	Wild Leek	0.309	0.014	0.409	0.035
Claytonia virginica	Spring Beauty	0.062	0.009	0.236	-0.026
Dentaria laciniata	Cut-leaved Toothwort	0.193	0.078	0.257	0.414
Dicentra canadensis	Squirrel Corn	0.207	0.102	0.194	0.093
Dicentra cucullaria	Dutchman's Breeches	0.125	0.111	0.298	0.384
Erythronium americanum	Trout-lily	0.043	0.033	0.092	0.043
Summer Green Herbs					
Actaea pachypoda	White baneberry	0.247	0.040	0.426	0.193
Aralia nudicalus	Wild Sarsaparilla	0.796	0.791	0.779	0.326
Arisaema tripyllum	Jack-in-the-pulpit	0.508	0.022	0.093	0.030
Caulophyllum thalictroides	Blue Cohosh	--	0.042	--	0.385
Clintonia borealis	Bead-lily	--	--	--	0.883
Dentaria diphylla	Broad-leaved Toothwort	--	0.097	--	0.193
Epipactus helleborine	Helleborine Orchid	0.495	--	0.605	--
Galium triflorum	Sweet-scented Bedstraw	0.731	0.072	0.825	0.759
Geranium robertianum	Herb Robert	--	0.768	--	0.475
Hepatica acutiloba	Sharp-lobed Hepatica	0.304	0.025	0.377	0.079
Heracleum maximum	Cow Parsnip	--	0.457	--	0.623
Maianthemum canadense	Canada Mayflower	0.126	0.036	0.737	0.540
Mitella diphylla	Two-leaved Miterwort	--	0.077	--	0.411
Mitchella repens	Partridge Berry	--	0.165	--	0.556
Osmorhiza claytoni	Sweet Cicely	0.396	0.014	0.436	0.072
Phlox divaricata	Blue Phlox	0.438	--	0.213	--
Polygonatum pubescens	Solomon's Seal	0.146	0.082	-0.172	0.147
Ranunculus abortivus	Kidneyleaf Buttercup	0.975	--	0.461	--
Sanguinaria canadensis	Bloodroot	1.000	0.033	1.000	0.305
Smilacene racemosa	False Solomon's Seal	0.000	0.252	1.000	0.452
Smilacene stellaria	Starry False Solomon's Seal	--	0.934	--	0.348
Solidago flexicaulis	Zigzag Goldenrod	--	0.143	--	0.554
Streptopus roseus	Rose Twisted -stalk	0.323	0.284	0.448	0.494
Thalictrum dioicum	Early Meadow Rue	--	0.069	--	0.813
Trientalis borealis	Starflower	0.761	--	0.622	0.228
Trillium erectum x *flexipes*	Trillium hybrid	--	0.042	--	0.463
Trillium grandiflorum	Large-flowered Trillium	0.224	0.054	0.327	0.227
Uvularia grandiflora	Large-flowered Bellwort	--	0.042	--	0.687
Viola canadensis	Canada Violet	0.204	0.014	0.370	0.043
Viola pubescens	Downy Yellow Violet	0.303	0.087	0.076	0.221
Ferns					
Adiantum pedatum	Maidenhair Fern	--	0.396	--	0.448
Botrychium virginianum	Rattlesnake Fern	--	0.287	--	0.653
Dryopteris spinulosa	Spinulose Woodfern	0.493	0.105	0.648	0.397
Onoclea sensibilis	Sensitive Fern	0.333	--	1.000	--
Woody Plants					
Acer pennsylvanicum	Striped Maple	0.282	--	0.820	--
Acer saccharrum	Sugar Maple	0.060	0.077	0.077	0.323
Cornus alternafolia	Alternate-leaved Dogwood	--	0.439	--	0.462
Fagus grandifolia	American Beech	0.080	--	0.216	--
Fraxinus americana	White Ash	--	0.075	--	0.620
Ostrya virginiana	Ironwood	0.468	--	0.279	--
Prunus serotina	Black Cherry	0.164	--	0.198	--
Prunus virginiana	Choke Cherry	--	0.109	--	0.455
Ribes sp.	Ribes sp.	--	0.255	--	0.979
Sambucus pubens	Elderberry	--	0.052	--	0.447
Taxus canadensis	Canada Yew	--	0.315	--	1.000