

Forty-seven Year Changes in Vegetation at the Apostle Islands: Effects of Deer on the Forest Understory

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ABSTRACT: White-tailed deer (*Odocoileus virginianus* Zimmerman) have been labeled a keystone herbivore in forests of the midwestern United States, particularly as deer have increased over the past century due to forest fragmentation, reduction of natural predators, reduced hunting, and mild winters. Deer browsing in the Apostle Islands National Lakeshore has had a pronounced effect on formerly large continuous patches of reproductive Canada yew (*Taxus canadensis* Marshall). In order to compare understory plant communities in 2005 to those at sites sampled in 1958, we resurveyed 32 forest sites on islands that remained free of deer throughout this period, on islands that retained deer, and on islands that gained or lost deer. Multivariate analyses reveal that deer have strong effects on the type of change in the forest understory. Plant communities on sites with long-term deer pressure are becoming increasingly different from those on sites that have never had deer. Four new understory species were detected at these sites, two other species increased by more than 20%, while eight decreased by more than 20%. While grasses and sedges were favored on sites that maintained or gained deer, perennial forbs declined conspicuously on these sites. The recovery of understories on islands where deer were removed suggests that such actions can effectively restore suitable habitat conditions for certain species sensitive to deer herbivory.

Index terms: plant community change, *Taxus canadensis*, white-tailed deer

INTRODUCTION

Overabundance of white-tailed deer (*Odocoileus virginianus* Zimmerman) in the midwestern United States appears to be curtailing tree regeneration and shifting the density and composition of forest understory herb communities (Frelich and Lorimer 1985; Rooney and Waller 2003; Côté et al. 2004). Slow-growing forbs with single meristems, shade-tolerant shrubs, and tree seedlings are all vulnerable to deer; whereas other species may persist and even thrive. Ferns, grasses, sedges, and rushes have become more abundant in midwestern mixed coniferous-deciduous forests (Rooney and Waller 2003). This disruption of species composition may shift forests to an alternate path of succession (Côté et al. 2004).

In Wisconsin, scarce natural predators, mild winters, and the predominance of early successional forests have combined to dramatically increase the deer populations (Waller and Alverson 1997). Pre-European settlement deer population densities were lower than four per km², but rose to 9–14 deer per km² by the 1930s (Rooney and Waller 2003). Between 1962 and 1984, hunting succeeded in keeping winter deer densities on average 1% over goals set by Wisconsin Department of Natural Resources; but since the mid 1990s, averages have increased to 45%–55% over goal (Wisconsin Department of Natural Resources 2007). Deer browsing over the past fifty years has, in turn, acted to simplify plant

communities (Rooney and Waller 2003). In northern Wisconsin, areas lacking active deer hunting (e.g., protected parks and natural areas) showed a greater decline in native species than areas that allowed deer hunting (Rooney et al. 2002, 2004).

The Apostle Islands region in northern Wisconsin is an area where deer have been of great concern since the early 1900s (Beals et al. 1960; Balgooyen and Waller 1995; Allison 2006). Some of the islands close to the mainland have supported deer herds for hundreds of years, whereas some more remote islands never had deer. On other islands, deer have come and gone. The forests of many of the islands are characterized by a dense understory of Canada yew (*Taxus canadensis* Marshall), which is highly susceptible to herbivory by deer (Curtis 1959). Of woody plant species occurring on the islands, *Taxus* provides the most biomass within the deer browse zone (0.25–2 m height) and suffers the most browse (Smith 2007). Large continuous patches of reproductive yew are rare throughout its range, and yew cannot persist on islands with abundant deer (Allison 2006; Smith 2007). Hence the protection of yew in the Apostle Islands is a priority for area resource managers (Allison 2006).

Here, we investigate the 47-year changes that have occurred in the vegetation of forest stands on the Apostle Islands. We have baseline data from 1958 allowing us to investigate changes in forest vegetation. In 1958, Beals and Cottam (1960) sought

to characterize the vegetation of the region and to develop a deer browse pressure index (Beals et al. 1960). When they visited the Apostles, there were twelve islands with established deer herds. Currently, deer herds are present on five of the islands (National Park Service 2007).

By resurveying these sites 47 years later, we can determine the ways in which forest vegetation has changed, and how these changes may be related to the deer histories at those sites. In particular, we use these data sets to ask the following questions: (1) How have the plant communities at these sites changed over 47 years?; (2) Have communities experiencing different histories of deer occupation changed in different ways?; (3) Which plant species have increased or decreased on the islands over the last 47 years?; and (4) Do shifts in species abundances differ across sites with different deer histories?

We expect to observe greater changes in plant populations and communities at sites subject to continual deer pressure than at sites lacking deer. We expect species sensitive to deer browsing to change the most at sites with a history of deer occupation. In contrast, we expect browse-tolerant species to benefit from the competitive advantage afforded to them in areas of deer browse.

METHODS

Study Area

The Apostle Islands are a group of twenty-two islands situated in Lake Superior at the very northernmost tip of Wisconsin (Figure 1). Pre-settlement vegetation consisted primarily of upland mixed coniferous and deciduous forest, dominated by *Tsuga canadensis* (L.) Carrière, *Pinus strobus* L., *Acer saccharum* Marshall, *Betula alleghaniensis* Britton, and *Betula papyrifera* Marshall. Today, the understory is dominated by *Taxus canadensis* and *Acer spicatum* Lam., also with *Corylus cornuta* Marshall, *Ribes glandulosum* Grauer, and *Amelanchier* spp. Other parts of the islands are covered in boreal forests with *Picea glauca* (Moench) Voss,

Abies balsamea (L.) Mill., *Larix laricina* (Du Roi) K. Koch, *Thuja occidentalis* L., *Betula papyrifera* Marshall, and *Populus tremuloides* Michx. Soils of upland areas are mostly poorly drained clays, while other areas are covered in reddish sandy-clay till (Judziewicz and Koch 1993). The mean temperature for Madeline Island is 18.7 °C in July and -11.0 °C in January. Annual average precipitation is 84.3 cm (Kraft et al. 2007).

The region has been subjected to various degrees of human impact, beginning with a Native American settlement on Madeline and other islands, followed by French explorers, fur traders, fishing communities, and tourism. In the late 19th and early 20th centuries, most of the islands were logged for white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), yellow birch (*Betula allegheniensis*) and sugar maple (*Acer saccharum*), with frequent burning and mining. Lighthouses were built on five islands in the late 1800s, with portions of the adjacent forest reserved for firewood. These areas remain un-logged today and give an idea of the original vegetation (Judziewicz

and Koch 1993). In 1970, twenty of the islands were incorporated into a National Lakeshore along with 18 km of coastline along the Bayfield Peninsula. Madeline Island, which was not included, is the largest island and the only one to currently support a permanent human population (about 3000 people in summer). In 1986, the National Lakeshore was expanded to include Long Island, which extends off the north shore of Ashland County. In 2004, 80% of the Lakeshore was designated as federally protected wilderness (National Park Service 2007).

Deer became common by the late 1940s, and their abundance peaked in the mid-1950s. In the late 1960s, liberal hunting seasons and a series of severe winters reduced deer populations. Of the 21 islands, three (Outer, North Twin, and Raspberry) have never been reached by deer. The other islands have had different sizes of deer populations that have increased or decreased over time (Judziewicz and Koch 1993).

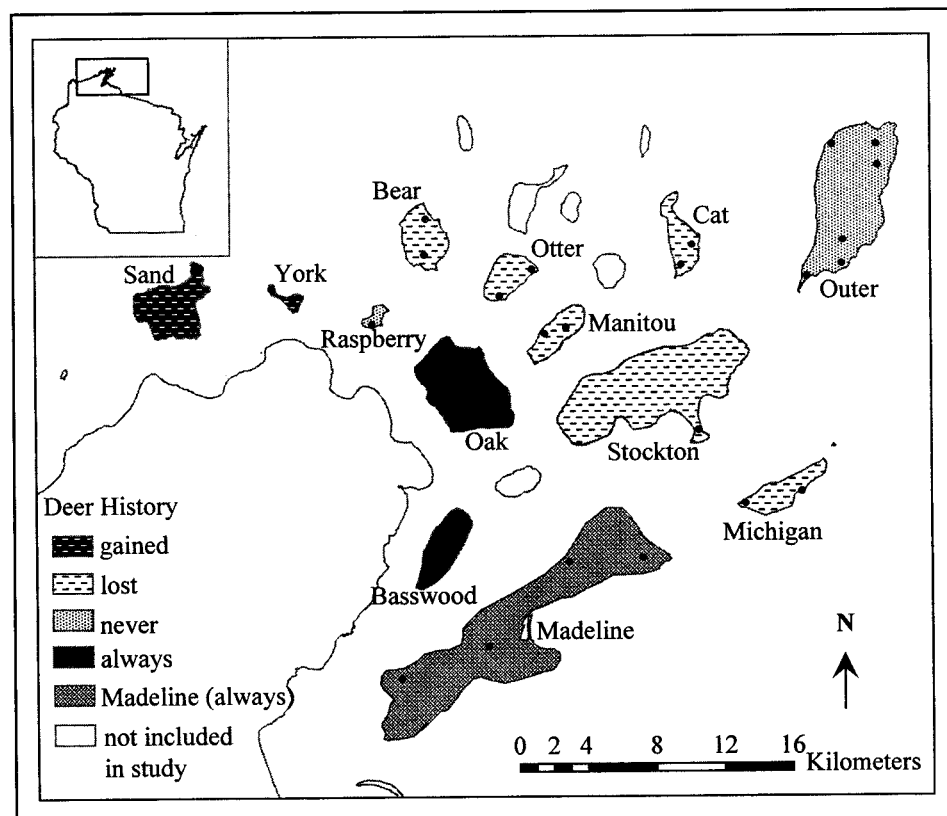


Figure 1. Map of deer history categories on the Apostle Islands, Wisconsin.

Site Selection

In 1958, Ed Beals and colleagues (Beals and Cottam 1960; Beals et al. 1960) surveyed 75 sites on 18 islands, with the criteria that each site should be free from recent human disturbance and situated within 4.05 ha of uniform topography. In 2005, we resampled 32 of these sites in conjunction with a separate study (Johnson et al. 2008). We selected a subset of sites from the original 75 to achieve adequate replication within several dominant habitat types (avoiding rare habitats) and to include sites among islands of various size and deer histories (Johnson et al. 2008). We do not have reliable information regarding deer densities at these sites during the two time periods, nor do we have reliable annual survey data to determine the year when deer invaded or were extirpated from the islands. Therefore, we defined four “deer history” groups based on the presence or absence of deer during the two sampling periods (Figure 1). We determined deer presence during these periods from aerial observations, browse studies, and harvest records (National Park Service 2007). Two islands (7 sites) remained free of deer throughout both sampling periods (“never”): Outer (6) and Raspberry (1). Controlled hunting eliminated deer from six islands (11 sites) that had deer in 1958 (“lost”): Bear (2), Otter (2), Manitou (2), Stockton (1), Michigan (2), and Cat (2). The two western islands (5 sites) are of special concern to park personnel (Allison 2006) as they were recently invaded by deer (“gained”): Sand (4) and York (1). Two islands in the National Lakeshore had a substantial deer population during both sampling years (“always”): Oak (4 sites) and Basswood (1). Madeline Island (4 sites) had deer in both time periods, but was treated as a separate category as it is likely impacted by the village of La Pointe and Madeline Island Airport, and because it is not part of the National Lakeshore.

Field Methods

We relocated the sites using the original maps and site descriptions from Beals and Cottam’s (1960) study. We sampled trees using the point-centered-quarter method

(Cottam and Curtis 1956) at 10 points along four 135 m transects spaced 30 m apart (40 points total). At alternate points (20 total), Beals and Cottam (1960) listed the presence of all herb, shrub, and tree seedling species present in a 1 m² quadrat. The 2005 sampling protocol was identical to that of Beals and Cottam (1960), except that we intensified sampling of the ground layer by placing 1 m² quadrats at all 40 points. Transects were placed according to a random starting point and direction, but adjusted to maintain a buffer of at least 25 m from the forest edge. In both sampling periods, observers surveyed the area covered by the transects and noted the presence of any species that did not fall within any quadrat. We gathered island characteristics such as island size and kilometers of shoreline from park documents (National Park Service 2007), and determined site-specific characteristics such as elevation and distance to mainland from topographic maps.

Data Analyses

To ensure adequate comparisons between the historical and present day data sets, we first matched species lists by updating the nomenclature from 1958 and by lumping some taxa that the historical surveys did not identify to species (*Carex*, *Dryopteris*, *Solidago*, and *Sorbus*). The final combined list of understory species contained 209 ground layer taxa (146 herbaceous, 41 shrub, and 22 tree seedling).

We used rarefaction curves (Colwell 2005) to fairly compare understory species richness in the ground layer despite the unequal sample sizes (20 quadrats in 1958 vs. 40 quadrats in 2005). We conducted sample-based analyses and transformed the x-axis to number of individuals sampled before making the comparison. We inferred a significant change in species richness when the 95% confidence intervals of the two rarefaction curves did not overlap.

To identify significantly increasing or decreasing understory species, we used single classification *G*-tests and replicated tests for goodness of fit (*G*-Tests; Sokal and Rohlf 1995) using both sites and

deer history groups as replicates. *G*-tests are non-parametric and do not require a balanced sample size between groups. The single-classification *G*-statistic tests for a change in a particular species at a given site. Replicated goodness of fit tests were applied to all sites at once. The G_{total} statistic for a species tests for changes in frequency in either direction across all sites. The G_{pooled} statistic combines data from all sites, testing for overall net increases or decreases in quadrat frequency. It will detect systematic regional shifts even if shifts within individual sites are not significant. The *G*-test for heterogeneity (G_{het}) determines whether a species responds similarly over all sites or the four deer history groups. We also conducted this test on understory species grouped by guilds (annual forbs, perennial forbs, ferns, fern allies, grasses, sedges, and shrubs) to determine whether deer have affected plants of various growth forms in different ways. To ensure biological as well as statistical significance, we limited our analyses to species that were present in at least two sites and at least 20 total quadrats in either sample period and that increased or decreased by at least 20% relative to their initial frequency in 1958 (following Weigmann and Waller 2006). These criteria limited the *G*-test analyses to 46 of the original 209 understory species. We classified species as “increasers” or “decreasers” only if their changes were large enough and consistent enough to make both the G_{total} and G_{pooled} test statistics significant after Holm’s *P*-value correction for multiple hypothesis tests (Holm 1979).

We applied several multivariate methods to understand community level changes. Because of the unequal sampling intensity in the ground layer between the two time periods, multivariate analyses include only 20 of the 40 quadrats sampled in 2005 (every other quadrat). For three of the sites, missing 1958 datasheets from the last transect (5 quadrats) forced us to also exclude the corresponding transect for those sites in 2005. We then relativized the resulting community frequency data by dividing each species’ frequency by the total plant frequency sampled at that site to account for these unequal sample

sizes across sites.

For each site, we calculated overstory characteristics including density of trees, tree basal area per hectare, total basal area, richness of tree species, and a “climax adaptation value” (CAV; Curtis and McIntosh 1951; Curtis 1959; Rooney et al. 2004). Curtis (1959) assigned a CAV score to each tree species between 1 and 10, such that species with higher scores persist the most in late-successional forests. A mean CAV score for each stand was calculated by weighting each species’ CAV score by its relative basal area. We also calculated a shade adaptation value for the understory community at each site by weighting the shade tolerance index (Humbert et al. 2007) by the relative frequency of a species. This scale varies between 1 (very shade tolerant) and 9 (very intolerant). There were 100 species in our data set that did not have a shade tolerance value as reported by Humbert et al. (2007), but these rare species made up only 17% of the entire understory data set.

Within each deer history category, we computed the mean Bray-Curtis site similarity between the two sample years to determine the magnitude of change in the understory plant communities at sites over the 47-year time span. Significant differences in site similarities among these groups indicate different magnitudes of change under different deer browsing pressures. We assigned differences in species composition among deer history groups using the 1-way analysis of similarity (ANOSIM) significance test (Clarke and Green 1988; Clarke 1993) included in Primer V.6 software (Clarke and Gorley 2006). The ANOSIM *R*-statistic varies between 1 and -1: values greater than zero indicate two groups are distinct from each other; values near zero indicate that the groups are homogenous; and values near -1 are highly unlikely and indicate that similarities across groups are higher than within groups (Clarke 1993). The *R* statistic can be applied to all groups at once (Global *R*) and then broken down to study pairwise difference between groups.

We used non-metric multidimensional scaling from PC-Ord v.5 software (NMDS;

McCune and Mefford 1999) to ordinate the plot data and to visualize changes in the sites through time. We used the Bray-Curtis distance metric with random starting configurations to compute NMDS (McCune and Grace 2002). We related the resulting axes to several explanatory variables across sites. Some variables were common to all sites on the same island, such as island size, miles of shoreline, and shortest distance to mainland, while others were specific to each site, such as elevation and distance of the site to the mainland. We examined effects of overstory structure using tree density, basal area per hectare, tree richness, and CAV. Finally, we also addressed how summary characteristics of the understory community (abundance, richness, relative frequency of *Taxus*, and the mean shade adaptation value) were related to the ordination axes.

RESULTS

Sites that never had deer were the only group to show any change in understory species richness (Figure 2). These sites experienced a decline in species richness from 72 native (plus 1 exotic) species in 1958 to 59 native (plus 2 exotic) species in 2005 (Figure 2). Far more exotic species were detected in quadrats from Madeline Island (2 species in 1958 to 13 in 2005).

Across all sites, the number of species observed declines with the relative number of quadrats occupied by *Taxus* (modeling by Poisson regression: species observed = $\exp[3.32 - 1.76 * \text{relative } Taxus \text{ occupancy}]$, $P < 0.0001$). *Taxus* dominated sites without deer, but was rare at sites with deer in both sampling periods (Figure 3a). Sites that lost deer also experienced significant decreases in *Taxus* over the 47-year interval (paired t-test, $t_{10} = 2.45$, $P = 0.034$). *Taxus* increased slightly across sites that recently gained deer but this trend is not significant (Figure 3a).

Eight species significantly declined across all sites, two species increased, and one species (*Maianthemum racemosum*) colonized one or more of the islands at the National Lakeshore (Table 1). Four of these 11 species showed inconsistent change across islands with different deer histories, indicating differential responses to the presence of deer (Table 1). Sites surveyed at Madeline Island were colonized by three additional species (*Arisaema triphyllum*, *Calamagrostis canadensis*, and *Ranunculus acris*).

We also observed that plants of different guilds shifted their frequency in different ways depending on island history (Figure 4). Grasses and sedges increased at sites

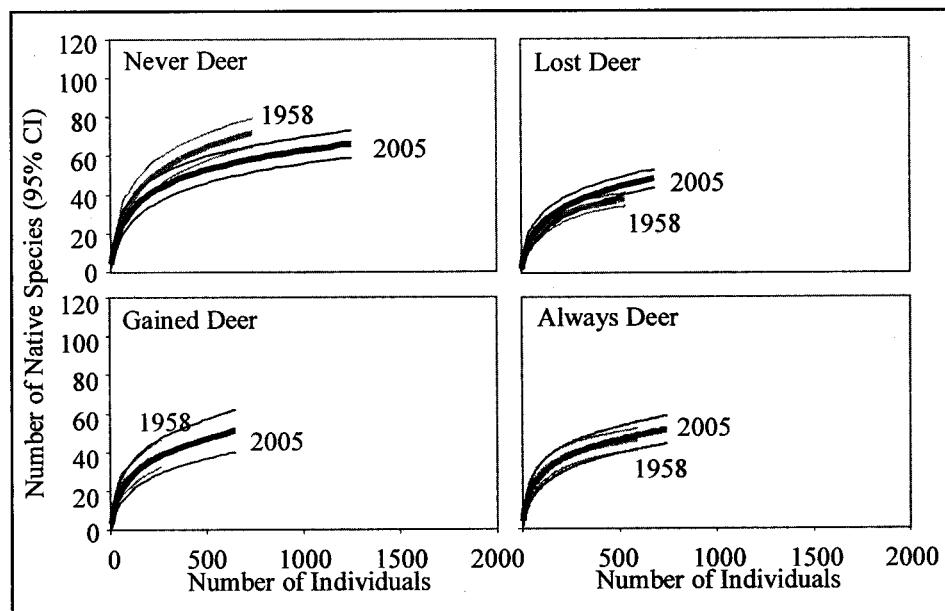


Figure 2. Rarefaction curves (with 95% confidence intervals) for the number of native species observed with increasing number of individuals sampled in 1958 and 2005.

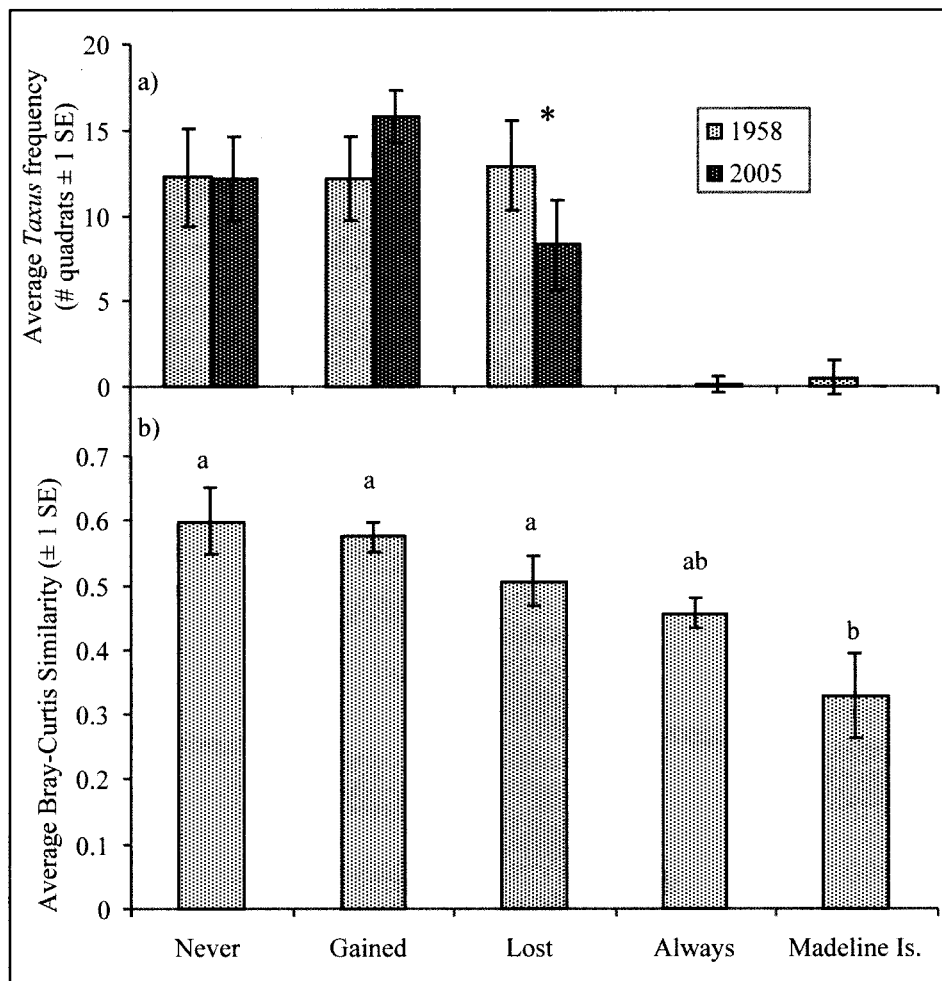


Figure 3. a) Changes in average site frequency of *Taxus canadensis*. To account for difference in sample size, only 20 quadrats were used for the 2005 data (see methods). In the “lost group,” there was a significant decrease (indicated with *) in the frequency of *Taxus* (paired t-test, $t_{10} = 2.45$, $P = 0.034$). There was no difference between years in any other deer history group. The abundance of *Taxus* in the “always” group was significantly lower than the other groups during both years (Kruskal-Wallis rank sum test, $K = 32.58$ on 4df, $P < 0.001$). b) Bray-Curtis site similarity between the two sampling periods averaged by deer history group ($F_{3,28} = 3.813$; $P = 0.02$). Categories showing the different letter label are significantly different ($P < 0.05$).

that gained deer whereas perennial forbs declined at these sites. Perennial forbs and shrubs declined significantly at sites that always had deer. Except for ferns and fern allies, all guilds had a significant G_{het} statistic, indicating that these plants respond differently to different deer histories.

The NMDS ordination reveals that understory plant communities on islands with a particular deer history show some clustering (Figure 5a). The one-way ANOSIM global test showed that deer history groups differ in understory composition in both sampling periods (1958: $R = 0.314$, $P = 0.005$; 2005: $R = 0.228$, $P = 0.005$). Two axes explained 85% of the variation found

in the understory community (axis-1 $r^2 = 0.54$, axis-2 $r^2 = 0.31$). The abundance of *Taxus* at a site was positively correlated with NMDS axis 1 ($r^2 = 0.73$). The CAV score for the overstory community at a site was negatively correlated with NMDS axis 2 ($r^2 = 0.65$). All other environmental variables tested were not highly correlated with either axis ($r^2 < 0.30$). In particular, the shade adaptation value for the community of understory species at a site was not highly correlated with either axis 1 ($r^2 = 0.27$) or axis 2 ($r^2 = 0.18$).

Though the CAV score for the overstory was highly correlated with an axis in the NMDS plot, anova analyses revealed that

neither CAV nor the understory shade tolerance index differed significantly among sites in the four deer histories in either time period. These metrics also did not differ between the two time periods among these groups.

Rates of change in understory plant composition for these sites in the national lakeshore did not differ significantly, and all of these sites changed less (showed higher similarity between the two time-periods) than sites on Madeline Island (Figure 3b). However, amounts of change at sites that always had deer did not differ significantly from changes observed at sites on Madeline Island.

The NMDS ordination showing vectors of change translated to the origin (Figure 5b) illustrates that the direction of change in ordination space differs among sites occupying islands with different deer histories within the National Lakeshore. The direction of each vector in each group is generally consistent along axis 1, except for the “never” group, which has vectors pointing in both directions as well as vectors indicating a very low degree of change. Figure 5c shows the average vector for each group along with standard error ellipses. This graphic makes clear that the groups changed in significantly different ways (except for the “lost” and “always” groups).

The effect of deer on plant community composition can be examined more closely by comparing two deer history groups at each sampling period using pairwise ANOSIM. Plant communities at sites that recently gained deer and sites that always had deer differed significantly in 1958 ($R = 0.756$, $P = 0.008$) as well as in 2005 ($R = 0.776$; $P = 0.008$; Figure 6a). Sites that lost deer and sites that always had deer had different plant assemblages in 1958, despite both having deer at that time ($R = 0.472$; $P = 0.009$; Figure 6b). Though sites in the “always” and “never” groups were significantly different in both time periods, this difference had become more extreme by 2005 ($R = 0.458$, $P = 0.006$) than it was in 1958 ($R = 0.336$, $P = 0.015$; Figure 6c). Sites that recently gained deer resembled sites in

Table 1. Plant species change over 47 years across the 28 sites included in the Apostle Islands National Lakeshore (Madeline Island excluded). Species included increased or decreased by > 20% of 1958 quadrat (quad) frequency and had significant values for both G_{pooled} and G_{total} statistics. The G -test for heterogeneity (G_{het}) tests whether changes were heterogeneous across all the deer history groups. A significant value for G_{het} indicates inconsistent changes. Madeline Island was colonized by three additional species (*Arisaema triphyllum*, *Calamagrostis canadensis*, and *Ranunculus acris*).

Species name	Guild	1958 Quad Freq ^a (# sites)	2005 Quad Freq ^a (# sites)	% Change ^b	Signif G_{het} ?
"Increasers"					
<i>Maianthemum racemosum</i>	perennial forb	0 (0)	47 (7)	Detection ^c	NA
<i>Dryopteris</i> sp.	fern	78 (18)	269 (22)	72	no
<i>Trientalis borealis</i>	perennial forb	86 (17)	269 (26)	56	yes
"Decreasers"					
<i>Aralia nudicaulis</i>	perennial forb	83 (13)	82 (18)	-50	yes
<i>Streptopus lanceolatus</i>	perennial forb	79 (14)	59 (13)	-63	no
<i>Lycopodium annotinum</i>	fern ally	22 (19)	15 (7)	-66	no
<i>Acer spicatum</i>	shrub	277 (25)	163 (22)	-71	yes
<i>Aster macrophyllus</i>	perennial forb	70 (8)	36 (7)	-74	no
<i>Diervilla lonicera</i>	shrub	22 (3)	11 (4)	-75	yes
<i>Viola blanda</i>	perennial forb	37 (11)	18 (8)	-76	no
<i>Galium triflorum</i>	perennial forb	17 (8)	5 (2)	-85	no

^a Quadrat frequencies listed are the number of quadrats in which each plant was observed. In total, 625 quadrats were sampled in 1958 and 1250 quadrats were sampled in 2005. G -tests are non-parametric and do not require a balanced sample size between groups.

^b Percent change for each species is based on changes in relative frequency to account for the uneven quadrat number in each sample period. The relative frequencies were calculated using only sites where a species was observed in both sample periods.

^c On one site on Outer Island, *Maianthemum racemosum* was not recorded in any quadrat, but was detected as present elsewhere in the site.

the "never" group in 1958 ($R = -0.016$, $P = 0.465$; Figure 6d) and remained similar in 2005 ($R = 0.061$, $P = 0.256$; Figure 6d). Sites that had deer but later lost them had significantly different plant community compositions relative to sites that never had deer in 1958 ($R = 0.273$; $P = 0.012$, Figure 6e). However, by 2005 these two groups converged in community composition ($R = 0.026$, $P = 0.313$).

DISCUSSION

Plant communities on the Apostle Islands have changed over the past 47 years. The nature of these changes reflects many forces including that island's history of occupation by deer. Herbivory by deer

is altering plant communities on these islands, most noticeably by reducing the abundance of *Taxus canadensis* (Allison 2006; Smith 2007).

The correlation of sites' mean CAV with NMDS axis 2 suggests succession is occurring on these islands. However, islands with different histories of deer occupation do not differ in mean CAV or mean understory shade adaptation values, suggesting that these groupings represent similar successional stages. The other possible environmental variables we examined (island size, distance from mainland, elevation, tree density, basal area per hectare, and tree richness) were not correlated with either of the NMDS axes that described most of the variation in the understory

herb community. Yet sites that differed in deer history had distinct communities as shown by the global R statistic. Thus, although succession clearly affects individual sites, deer are having an even more pronounced effect on vegetation across the Apostle Islands.

Native species richness was highest at sites that never had deer, but still declined between 1958 and 2005 (Figure 2). This may reflect the dominant role of *Taxus canadensis* in the ecosystem. Canada yew often grows in dense thickets which can prevent the growth of other species (Judziewicz and Koch 1993). Our analyses showed fewer native species at sites with higher *Taxus* frequency (also seen by Balgooyen and Waller 1995). *Taxus* was virtually absent

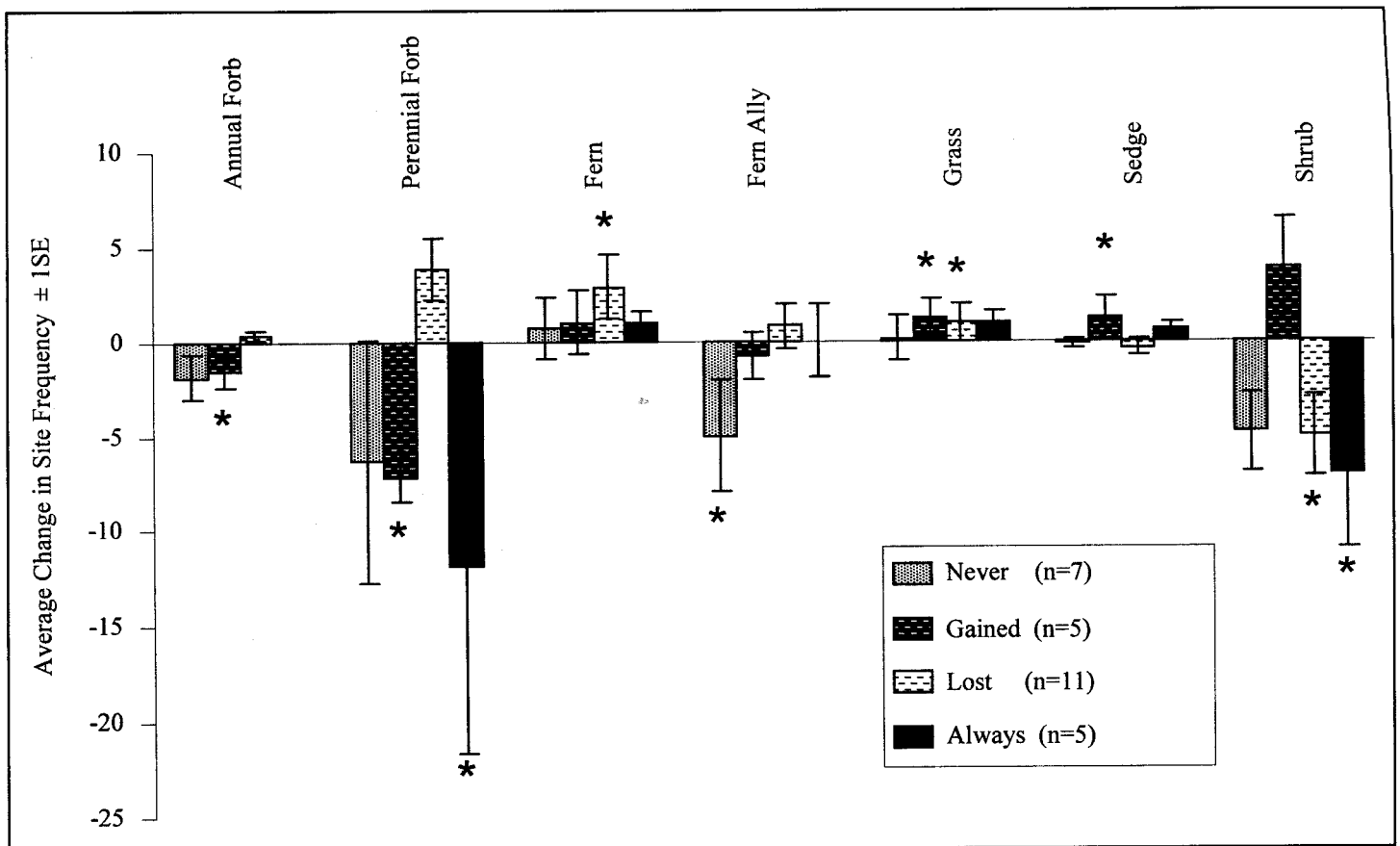


Figure 4. Average change in site frequency (number of quadrats at a site) of plant guilds for sites from the national lakeshore in each deer history category. A “*” indicates that a guild significantly increased or decreased at sites in the given deer category (single classification G -test, after Holm’s P -value correction for multiple hypothesis tests). All guilds (except for ferns and fern allies) responded differently to different deer history groups (significant G_{het} values). Standard error bars are included, but may not necessarily indicate the same results obtained by the non-parametric G -tests.

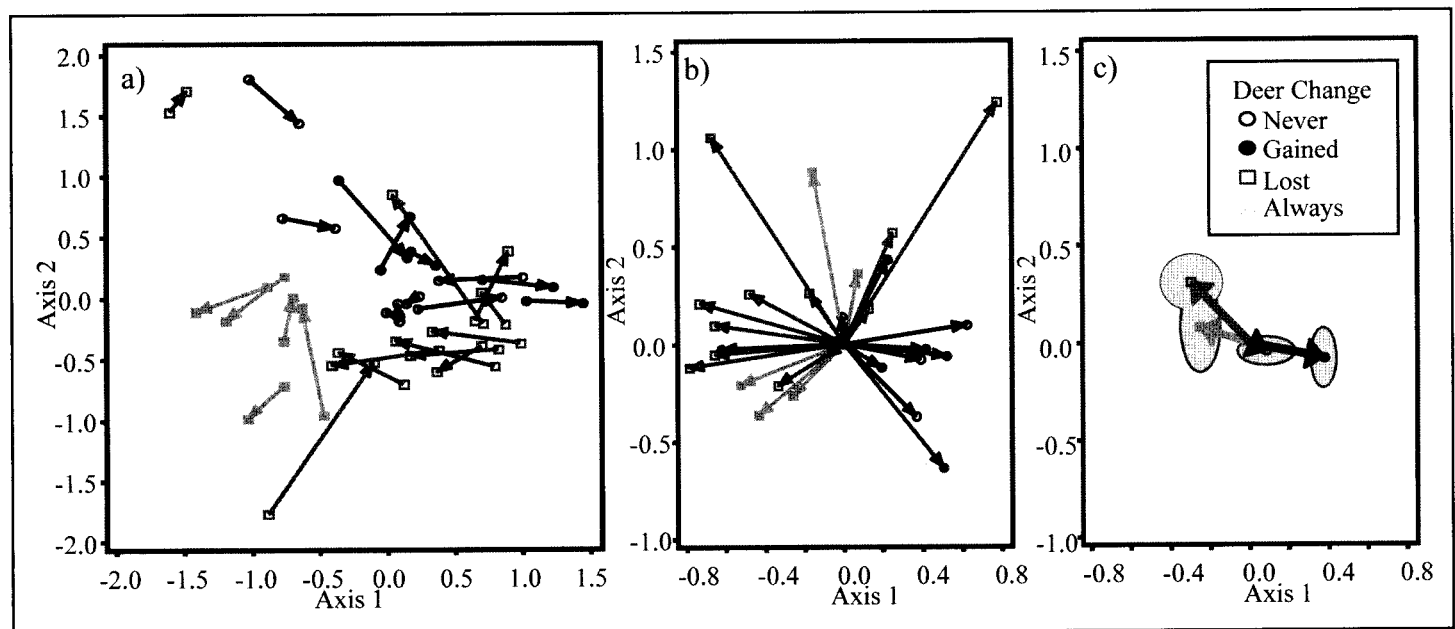


Figure 5. NMDS ordination of site data by deer history category. Only sites included in the national lakeshore are included. Figure 5a includes arrows connecting sites showing shifts in understory plant community composition between 1958 and 2005. Figure 5b shows the arrows translated to the origin to visualize the direction and magnitude of change at a site regardless of starting position. Figure 5c shows the mean translated vector for each deer history category, with an ellipse denoting the standard error in both axis 1 and axis 2.

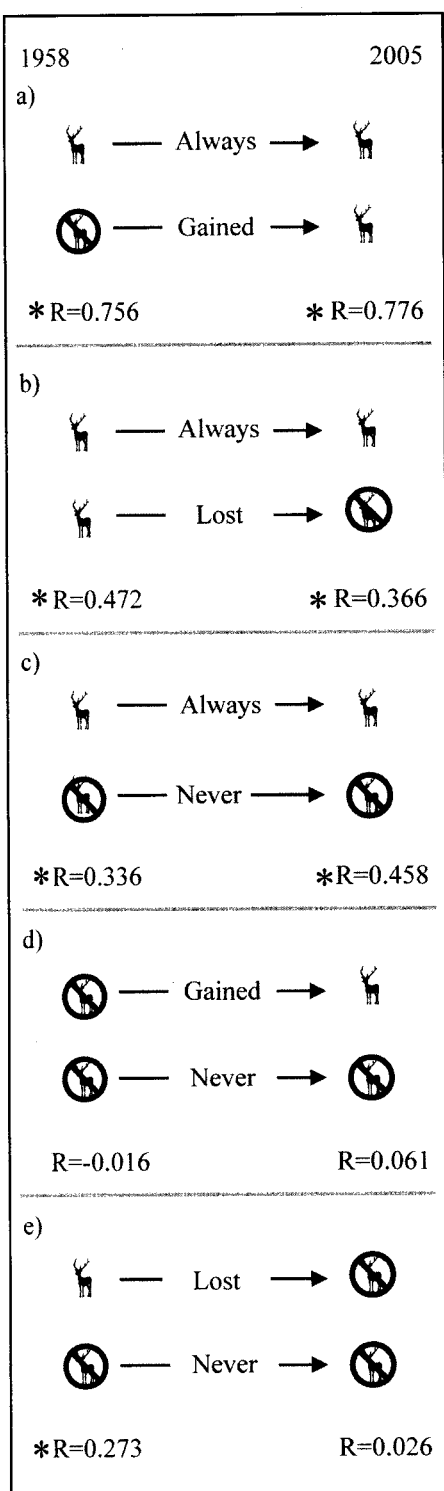


Figure 6. Degree of dissimilarity between the understory plant communities at sites from the national lakeshore in selected deer history categories at each sampling period, using the ANOSIM pairwise R statistic. The R statistic varies between 1 and -1; values greater than zero indicate two groups are distinct from each other, values near zero indicate that the groups are homogenous; values near -1 are highly unlikely and indicate that similarities across groups are higher than within groups. Figure 6a shows the difference between

at sites with constant deer pressure (Figure 3a). This absence of *Taxus* on Madeline Island may also have contributed to the increase in exotic species there.

Many shifts in species frequency on the Apostle Islands mirror changes occurring on the Wisconsin mainland. Four species that decreased on the Apostle Islands also decreased on the mainland of northern Wisconsin: wild sarsaparilla (*Aralia nudicaulis* L.), twisted-stalk, (*Streptopus lanceolatus* (Aiton) Reveal), large-leaved aster (*Aster macrophyllus* L.), and northern bush-honeysuckle (*Diervilla lonicera* Mill.; Weigmann and Waller 2006). Jack-in-the-pulpit (*Arisaema triphyllum* L.) has increased strongly in northern Wisconsin since 1950 (Weigmann and Waller 2006) and was detected on sites in Madeline Island in 2005 though not in 1958. American starflower (*Trientalis borealis* Raf.) has also increased significantly both on the Apostle Islands and in Northern Wisconsin generally.

The large decline in the abundance of perennial forbs at sites with deer (Figure 4) matches results from several other studies that have also found declining herb diversity and abundance in heavily browsed mixed coniferous-deciduous forest stands (Balgooyen and Waller 1995; Rooney 1997; Rooney and Waller 2003). More than half of the eight declining species were perennial forbs (Table 1). Grasses and sedges increased at sites that gained deer, again matching widespread increases in the region and implicating deer as a driver (see citations in Rooney and Waller 2003). Only ferns and fern allies did not change heterogeneously across islands with different deer histories. Thus, deer appear to be generally affecting the abundances of many plant species over time.

sites with and without deer at both time periods. Using only the 1958 data, we used ANOSIM to compare sites with deer (pooling "always" and "lost" sites, since both of these categories had deer in 1958) to sites without deer (pooling "never" and "gained" sites). Similarly, using data from 2005, we compared sites with deer (pooling "always" and "gained") data to sites that did not have deer (pooling "lost" and "never" sites). Figures 6b-6e shows the R -statistic for each year for each pair of deer history groups. Stars indicate an R -value is significant at the 5% level after Holm's P -value correction for multiple hypothesis tests.

Sites from islands with different deer histories support distinct types of vegetation undergoing different types of change (Figure 5c). Sites on Basswood and Stockton Islands, which had deer populations in both sampling periods, are clustered on the ordination, indicating that the understory plant communities on these islands are similar. Sites on islands that have lost deer are also clustered. This is not surprising, considering that the islands within each category are closer to each other geographically and are a similar distance from the mainland.

The difference between plant communities in sites that always had deer and sites that never had deer increased over time, suggesting divergent trajectories of community change on these two sets of islands. Understory plant communities at sites that have lost deer now resemble sites that never had deer (despite differences in 1958). This suggests that eradicating deer from an island can allow the plant community to recover to conditions similar to sites without deer. Killmaster et al. (2007) similarly found signs of plant community recovery as soon as one year after a significant reduction in deer density at a Georgia state park. In contrast, Balgooyen and Waller (1995) found that certain sensitive species, such as *Clintonia borealis* (Aiton) Raf., recover slowly from the impacts of deer grazing. While our results suggest that recovery is possible, this community measure of recovery is general and tends to not weigh rare or sensitive species heavily.

The plant communities on sites that lost deer were distinct from sites that always had deer, despite both groups having deer in 1958 (Figure 6). If these differences reflect different initial deer densities on the islands, we should be careful in using islands that always had deer as "controls" to compare with sites that lost deer. Sites that never had deer and sites that recently gained deer (on Sand and York Islands) were matched in the sense that their plant communities did not significantly differ in 1958. Even in 2005, plant communities on Sand and York Islands better resembled those on islands that have never had deer than they did communities on islands with consistent deer pressure (Oak and Bass-

wood). This result suggests that impacts of deer on these plant communities have just begun or may take some time to be detected.

The results presented here are complex. Clearly, the distribution of deer within and among the Apostle Islands reflects many factors, including proximity to the mainland, distance from other islands, accessibility of the shoreline, and characteristics of the vegetation. The result of this "natural experiment" is an uneven distribution of sites that differ in deer history, perhaps confounding some of the results presented here. Large scale, long-term controlled studies of the effects of deer herbivory on understory plant communities are desirable, but they prevent practical challenges that will need to be overcome.

CONCLUSION

Forest understory plant communities on the Apostle Islands have changed over the last 47 years, often reflecting the impacts of deer herbivory. Deer strongly affected changes in the forest understory and particularly reduced the dominant shrub *Taxus canadensis*. While succession is occurring at these sites, the effects of deer are more pronounced. Species-specific shifts at the Apostle Islands are consistent with other studies documenting changes on the Wisconsin mainland. Plant communities on sites with long-term deer pressure continue to diverge from those on sites that have never had deer. However, eliminating deer on some islands appeared to return the plant community to conditions similar to those on islands lacking deer.

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