National Park Service
U.S. Department of the Interior

Natural Resource Stewardship and Science

The Challenging Past and Precarious Future of Canada Yew (*Taxus canadensis*) in the Apostle Islands National Lakeshore

Natural Resource Report NPS/APIS/NRR—2021/2251

ON THIS PAGE
Robust yew understory
Photograph courtesy of Matthew J. Widen

ON THE COVER
Canada yew arils
Photograph courtesy of Matthew J. Widen

The Challenging Past and Precarious Future of Canada Yew (*Taxus canadensis*) in the Apostle Islands National Lakeshore

Natural Resource Report NPS/APIS/NRR—2021/2251

Sarah E. Johnson*, Jordan S. Mead, Matthew J. Widen, Emily E. Leonard

Natural Resources Department
Northland College
1411 Ellis Avenue
Ashland, Wisconsin 54806
* *Primary contact: sjohnson@northland.edu*

April 2021

U.S. Department of the Interior
National Park Service
Natural Resource Stewardship and Science
Fort Collins, Colorado

The National Park Service, Natural Resource Stewardship and Science office in Fort Collins, Colorado, publishes a range of reports that address natural resource topics. These reports are of interest and applicability to a broad audience in the National Park Service and others in natural resource management, including scientists, conservation and environmental constituencies, and the public.

The Natural Resource Report Series is used to disseminate comprehensive information and analysis about natural resources and related topics concerning lands managed by the National Park Service. The series supports the advancement of science, informed decision-making, and the achievement of the National Park Service mission. The series also provides a forum for presenting more lengthy results that may not be accepted by publications with page limitations.

All manuscripts in the series receive the appropriate level of peer review to ensure that the information is scientifically credible, technically accurate, appropriately written for the intended audience, and designed and published in a professional manner.

This report received formal peer review by subject-matter experts who were not directly involved in the collection, analysis, or reporting of the data, and whose background and expertise put them on par technically and scientifically with the authors of the information.

This report is available in digital format from the Natural Resource Publications Management website. If you have difficulty accessing information in this publication, particularly if using assistive technology, please email irma@nps.gov.

Please cite this publication as:

Johnson, S. E., J. S. Mead, M. J. Widen, and E. E. Leonard. 2021. The challenging past and precarious future of Canada yew (*Taxus canadensis*) in the Apostle Islands National Lakeshore. Natural Resource Report NPS/APIS/NRR—2021/2251. National Park Service, Fort Collins, Colorado. https://doi.org/10.36967/nrr-2285336.

NPS 633/175245, April 2021

Contents

Contents (continued)

Page

Figures

Figures (continued)

Page

Tables

Page

Photographs

Executive Summary

Forest understories on many of the Apostle Islands are unique due to the extensive distribution and abundance of Canada yew (*Taxus canadensis*), a robust evergreen shrub. When available, "yew" is a preferred food source for the white-tailed deer (*Odocoileus virginiana*). Historically, deer were less abundant in the "north woods" region near the Apostle Islands National Lakeshore (APIS) until widespread logging and fires that occurred with Euro-American settlement opened up habitat favorable to deer. APIS, a Lake Superior archipelago, has partially served as a refuge for yew, isolating it from the impacts of browsing deer. Yet, not all islands have escaped the influence of this herbivore. Variations in the spatial coverage of yew among the islands are reflective of deer histories and other elements of past land uses.

Some islands experienced irruptive deer densities in the 1940s and 1950s, and others more recently in the 2000s. The impacts of deer on yew have been well-documented throughout its range by numerous studies, including several studies focused on the Apostle Islands and its varied deer history. To sustain yew and other fragile ecological components of the islands, resource managers have actively harvested deer on islands that experienced high abundance of deer (i.e., Rocky and Stockton in the 1950s and more intensive culling activities on Sand and York in the 2000s). As outlined by the park's Harvestable Species Plan (National Park Service 2014), managers divided the islands into zones so that a subset of islands are managed to maintain historic low presence or absence of deer (Zone 1 islands), and other islands (Zone 2) are managed to allow for deer at or below pre-Euro-American settlement densities (ca. 10/mi^2).

In 1991–1992, a study of island vegetation was conducted by Emmet Judziewicz, and he recorded the abundance and distribution of yew among 18 islands. We used his data to determine the 22-year changes and current status in the abundance and distribution of yew on these islands, and to assess yew changes in the context of island history, related to deer and their management since the 1950s. The varied and active management of deer on the islands provides us with a natural "living laboratory" in which we can study yew dynamics.

We observed steep declines in average cover of yew on several Zone 1 islands including Sand (−28.4%), York (−26.8%), Ironwood (−30.9%), and Cat islands (−25.1%). Despite these declines, yew cover on these islands is still currently higher than on some of the Zone 2 islands with a record of heavy deer activity in the 1950s. Declines on Sand and York (both Zone 1 islands) are explainable by the high numbers of deer recorded there in the 2000s. Observed signs of browsing activity may explain declines of yew on Cat and Ironwood, but this needs to be further investigated to ascertain deer presence.

Our results suggest that yew may be recovering, albeit very slowly, in patches among some islands. A notable area of recovery included Outer Island (+13.3%), a Zone 1 island with a history of fire on the southern half of the island. Recovery of yew also occurred on Zone 2 islands including throughout South Twin Island (+15.9%), on Bear Island (+6.9%) especially at the north tip, and in scattered patches on Manitou (+6.3%), Stockton (+2.2%), Hermit (+2.7%), and Rocky Island (+3.5%). Except for Outer Island, where deer have been absent or transient in low numbers, cover of

yew on these "recovering" islands remains at levels lower than islands that have not historically had deer populations. Where deer have persisted on Oak and Basswood islands, yew does not appear to be recovering.

We conclude the following:

- Our observations of steep declines in yew on some islands over the past 22 years reflect the foresight and conclusions of past researchers—"yew and deer are not compatible";
- Recovery of yew is possible on islands without persistent and high deer densities, but rates of recovery are much lower than rates of loss when deer densities exceed a sustainable level; and
- Deer (and possibly snowshoe hare, *Lepus americanus*) appear to be present and are browsing yew and other woody species on several islands where they were presumed absent.

We recommend that:

- Deer populations on Sand and York islands continue to be closely monitored and managed at low numbers to improve the chances for yew recovery in highly impacted patches;
- Cat and Ironwood islands be closely monitored for deer and other factors that may explain declines since the 1990s;
- Other islands should continue to be monitored regularly and managed for deer in accordance with the park's 2014 Harvestable Species Plan;
- Yew abundance among the islands should be monitored to determine if patterns of decline on some islands continues, and to determine if recovery on other islands continues (and at what rates); and
- Park managers should consider and potentially monitor additional and additive forces of change in yew vigor, such as insect pests, earthworm invasions, and climate change.

Acknowledgments

The National Park Service provided funding, and we thank J. Van Stappen, P. Burkman, D. Cooper, and other Apostle Islands National Lakeshore personnel for logistical support. We thank E. Judziewicz for his impressive survey of the island flora in the 1990s, making our analyses of change in yew possible. C. May, A. Kirschbaum, and A. DeRose provided GIS assistance. E. Mudrak offered statistical advice. S. Sanders, T. Gostomski, G. Smith, S. Windels, and K. Frerker reviewed the report and provided helpful comments and edits that much improved the final report.

Introduction

Canada yew (*Taxus canadensis* Marshall) is a low-growing, evergreen shrub that was historically abundant in the Great Lakes region (Windels and Flaspohler 2011). Walking in northern forests today, one might assume Canada yew only persists as a small, scattered shrub primarily present along ravine faces or on forested rock outcrops. Yet, those who travel to certain Great Lakes islands learn that Canada yew does exist in some places as a tall (sometimes up to 4 m) shrub that easily dominates the understory vegetation in cool, moist forests. The apparent loss of this species in many forest understories has been attributed to population spikes of ungulate browsers and intensive logging and burning that occurred with Euro-American settlement (Windels and Flaspohler 2011). Despite the production of alkaloids usually implicated in anti-herbivore defense, white-tailed deer browse yew, lending yew the nickname “deer candy” among botanists. Indeed, the deer-yew relationship is a truly tenuous one, and it has been boldly declared that deer and Canada yew are not compatible (Allison 2006).

The Apostle Islands National Lakeshore (APIS) provides park managers and researchers with a unique opportunity to study the distribution, status, and trends of Canada yew across islands with different histories of deer habitation, logging, and fire. Previous research at APIS noted significant influences of deer on island vegetation and in particular Canada yew (e.g., Beals et al. 1960, Judziewicz and Koch 1993, Balgooyen and Waller 1995, Allison 2006, Mudrak et al. 2009). Irruptions of deer in the 1940s and 1950s resulted in the near extirpation of yew from some islands. This also marked the beginning of a period of active deer management that included liberal quotas and incentives to reduce deer populations on the Apostle Islands in the 1950s and 1960s. Following these peak harvests, a series of long, cold winters was also key to reducing the deer herds (National Park Service 2014). Deer have been actively managed in the lakeshore in collaboration with the WDNR’s Deer Management Unit (DMU) plan for DMU79 since 1985 (Figure 1). In response to threats posed by high deer densities to sensitive vegetation on the islands, resource managers at APIS divided the islands into two zones for deer management (National Park Service 2014). Zone 1 is comprised of 11 islands that historically supported no-to-very few deer (Figure 1). Exceptions in this category are Sand and York islands, which experienced rapid increases in numbers in the 2000s. The management goal for Zone 1 islands (which encompass 36% of the park’s land acreage) is to maintain the historical status of deer to protect sensitive vegetation. The nine Zone 2 islands are managed to maintain deer levels at or below pre-European deer densities in northwestern Wisconsin (3.86 deer/km^2; Dahlberg and Guettinger 1956). Zone 2 islands have historically experienced extreme fluctuations in deer densities.

Ongoing efforts to protect Canada yew bring to bear questions that focus both on the current status and on long-term rates of change in yew, as well as how any observed changes might inform management efforts in the park. Mudrak et al. (2008) studied vegetation change using the 50-year data set of Ed Beals (Beals and Cottam 1960), but the number of forest plots was relatively low and plot placement was not designed specifically to explore changes in Canada yew across the islands. Judziewicz, however, conducted a very thorough survey of forest vegetation across all islands, and provided high resolution data on Canada yew’s distribution within the archipelago.

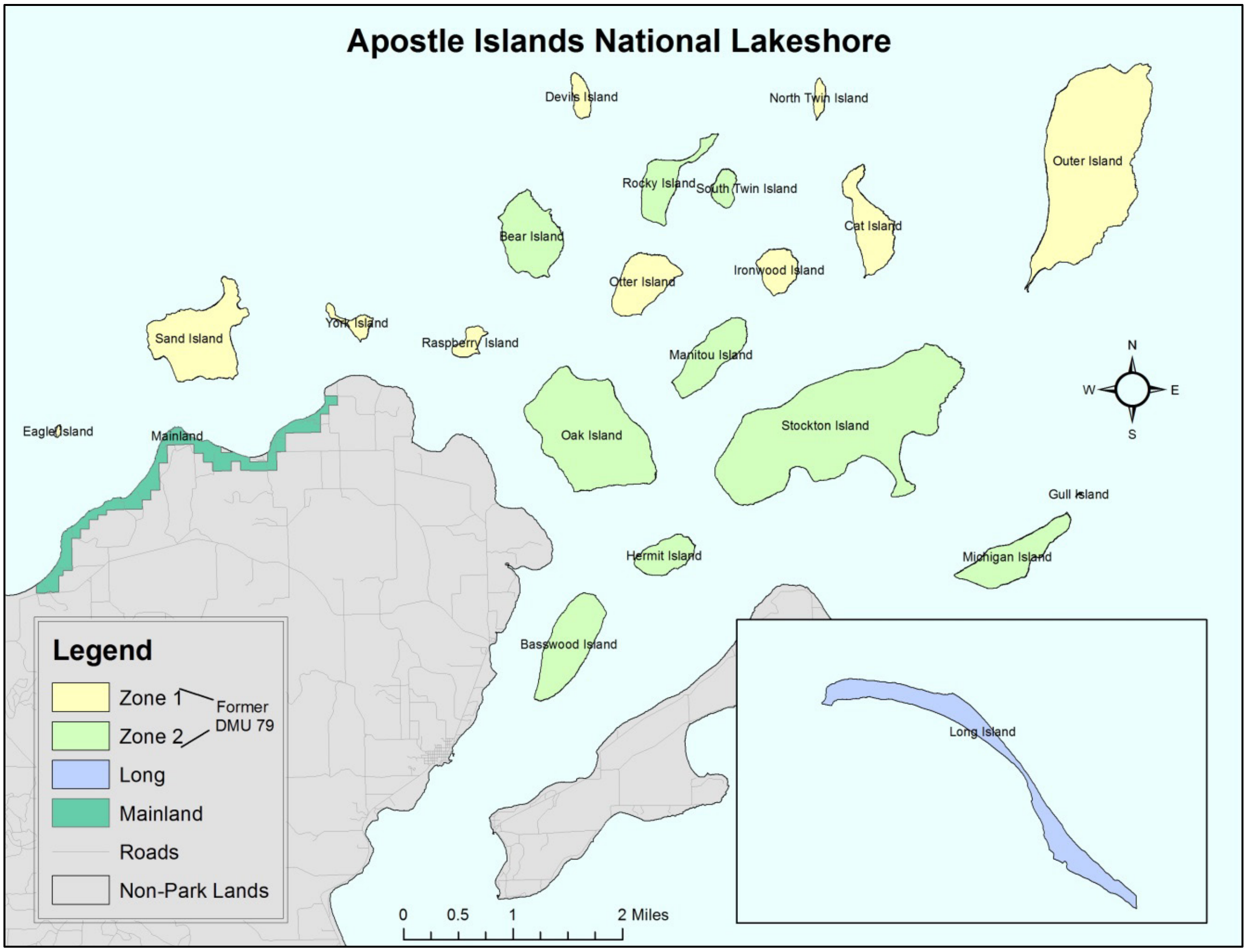


Figure 1. State deer management units and NPS deer management zones in the Apostle Islands, Wisconsin. Detailed information on deer management in the park is discussed in the park's Harvestable Species Plan (National Park Service 2014).

Judziewicz was originally focused on community-level vegetation data for the development of a flora for the Apostle Islands (Judziewicz and Koch 1993), but he singled out Canada yew for collection of percent cover and height data. A high-resolution map included in Judziewicz and Koch (1993) demonstrates that Canada yew was quite dominant on many of the islands, especially those lacking a long history of deer habitation. The map also indicates that yew's distribution on some islands (e.g., Outer Island) reflects logging and fire history.

In the 22 years since Judziewicz's extensive vegetation surveys across the archipelago, Canada yew may have advanced in its recovery from the 1950s era of irruptive deer densities (i.e., Rocky Island) and early logging and burning activities (i.e., southern end of Outer, Hermit and Stockton islands). Theoretically, with growth rates of 39–197 cm^2/year for small-to-large plants (Allison 2006), recovery should be observable after 22 years. For example, Rocky Island deer numbers were among the highest in the islands in the 1950s before intensive management efforts and harsh winters essentially removed all deer by the late 1960s. Percent cover of yew on Rocky 20–25 years later was relatively low among the islands at 0.4% in 1991/1992. Now, ca. 50 years post-peak deer pressure,

with sustained low deer numbers since, is yew on the trajectory of recovery? What implications do the trends on Rocky Island have for recovery potential of yew on other islands where recent high deer densities likely resulted in significant declines in stature and abundance of yew?

In 2013, we reestablished the sampling grid used by Judziewicz and Koch (1993) and employed compatible sampling methods to evaluate the status and change in yew across the Apostle Islands archipelago over the 21-year time span. By employing spatial and temporal methods of studying change in Canada yew in relation to deer management zones and deer densities, we aim to infer potential losses and/or recovery of yew populations among the islands. Specifically, our objectives are to:

1. Document the spatial distribution, abundance, and stature of Canada yew on 18 of the Apostle Islands,
2. Quantify any changes in Canada yew abundance on the islands between 1991/1992 and 2013, and
3. Assess how the status or changes in abundance of Canada yew varies between islands managed for no deer (Deer Management Zone 1 islands) and islands with a past history of periods of higher deer numbers and which are managed to have deer at or below the pre-Euro-American estimated density of <3.86 deer/km2 (Zone 2 islands).
4. Document evidence of herbivory on Canada yew and other woody plants in 2013.

Methods

Study Species

Canada yew (*Taxus canadensis* Marsh.), member of the Taxaceae family, is a sprawling (usually <2 m) to erect (up to 4 m) evergreen shrub found in the understories of forests in northeastern North America and the Great Lakes region. Fossilized yew structures suggest that yew colonization shortly followed glacial retreat throughout this region, and was likely present before and during glaciation via refugia habitats (Windels and Flaspohler 2011). It is monoecious, but seed production is usually sparse (especially when deer are present; Allison 2006), and spreading by layering is the dominant form of reproduction. A thorough review of this species is available elsewhere (Windels and Flaspohler 2011).

Study Area

The Apostle Islands are a group of 22 islands in western Lake Superior extending outward from Wisconsin's Bayfield peninsula (46°42′–47°05′ N, 90°24′–91°03′ W) (Figure 2), 21 of which fall within the jurisdiction of the National Park Service as the Apostle Islands National Lakeshore, established in 1970. In 2004, Congress designated 80% of the national lakeshore as the Gaylord Nelson Wilderness. Island size varies from 1-ha Gull Island to 4,087-ha Stockton Island (Judziewicz and Koch 1993). The islands have had a varied history of land-use, including traditional harvesting by the Ojibwe people and later an intense period of Euro-American logging, slash fires, quarrying, homesteading, and fishing. Reserve areas created around island light stations protected some forests from being cut, leaving behind stands of old-growth forest amid the second-growth forest most typically found on the islands (Judziewicz and Koch 1993). The predominant forest types on the islands are mesic and wet-mesic mixed coniferous and northern hardwood forests dominated by *Acer saccharum* Marshall (sugar maple), *Betula alleghenensis* Britton (yellow birch), *Thuja occidentalis* L. (white cedar), and *Tsuga canadensis* (L.) Carrière (hemlock), but a boreal forest element consisting primarily of *Abies balsamea* (L.) Miller (balsam fir) mixed with *Populus tremuloides* Michaux (trembling aspen), *Betula papyrifera* Marshall (paper birch) and occasionally *Picea glauca* (Moench) A. Voss (white spruce) occurs in some locations (Sanders and Grochowski 2012). Today's forests contain relatively more deciduous species than the hemlock and *Pinus strobus* L. (white pines) that were once more frequent (Judziewicz and Koch 1993). Precambrian sandstone bedrock underlies glacial deposits of clay and sandy-clay till, most of which are poorly-drained. Mean precipitation is 84.3 cm, annual snowfall is 187.7 cm, and mean temperatures reach 18.7ºC in July and −11.0°C in January for nearby Madeline Island (1971–2000 normals, Wisconsin State Climatology Office). Islands further away from the mainland, such as Outer Island, are consistently cooler than islands closer to the mainland.

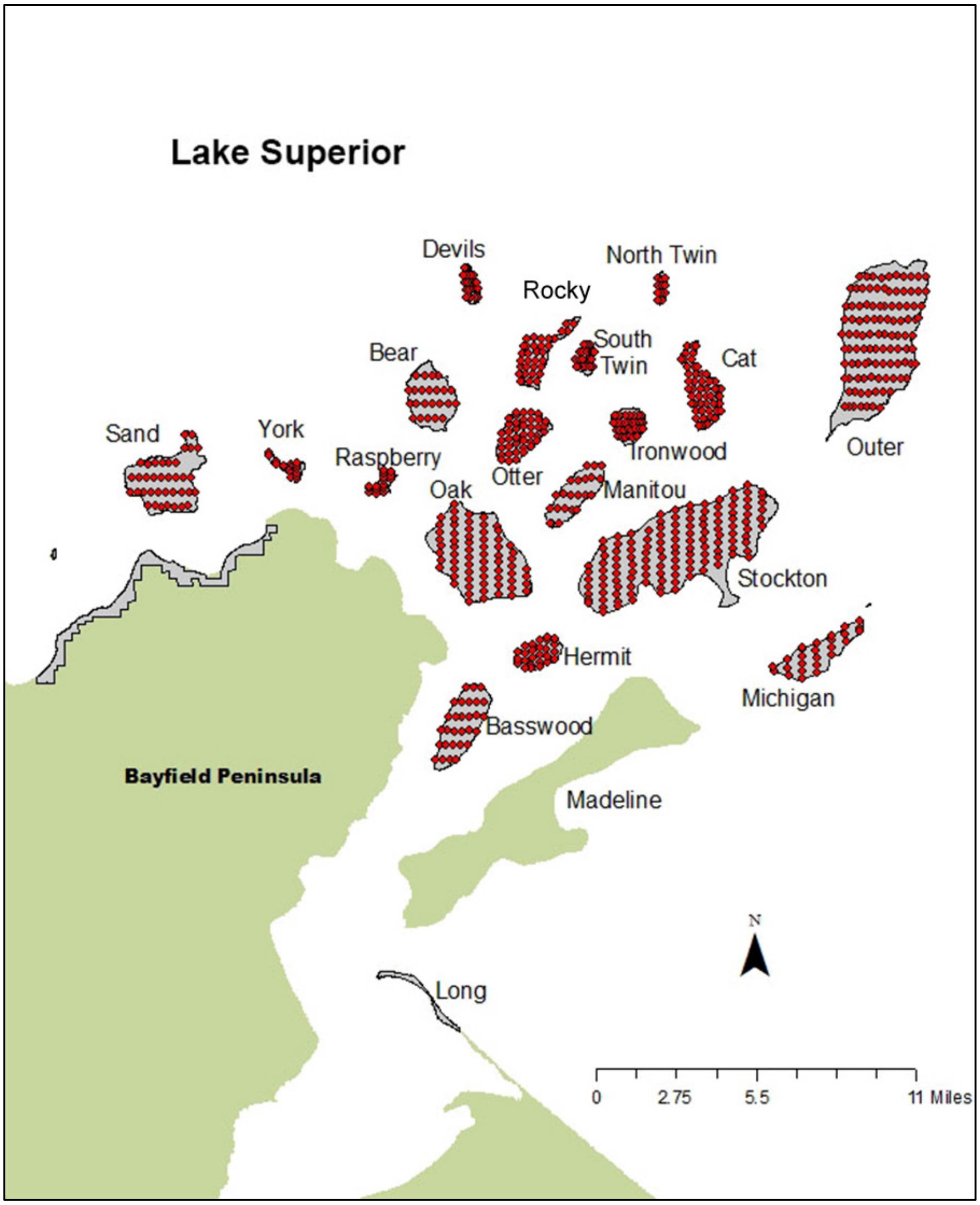


Figure 2. The location and orientation of plots (*red circles*) surveyed along transects on 18 islands within Apostle Islands National Lakeshore, 2013. No plots were placed on Long, Eagle, or Gull Islands, nor the mainland unit. Grey polygons represent National Park Service land.

Field Methods

We conducted field surveys of Canada yew distribution and abundance on 18 of the Apostle Islands (Figure 2) during summer 2013. Our sampling protocol balanced the need to: 1) be comparable to the plot design used by Judziewicz and Koch (1993) for reliable estimates of changes in yew abundance, 2) collect adequate data on the distribution of yew across the islands, and 3) be efficient and be completed within a single field season. To meet the goal of efficiency, we designed a sampling scheme that was half of the intensity of Judziewicz's two-summer survey in the 1990s. For purposes of fair comparisons in analyses, we sub-sampled the 1990s data (Figure 3).

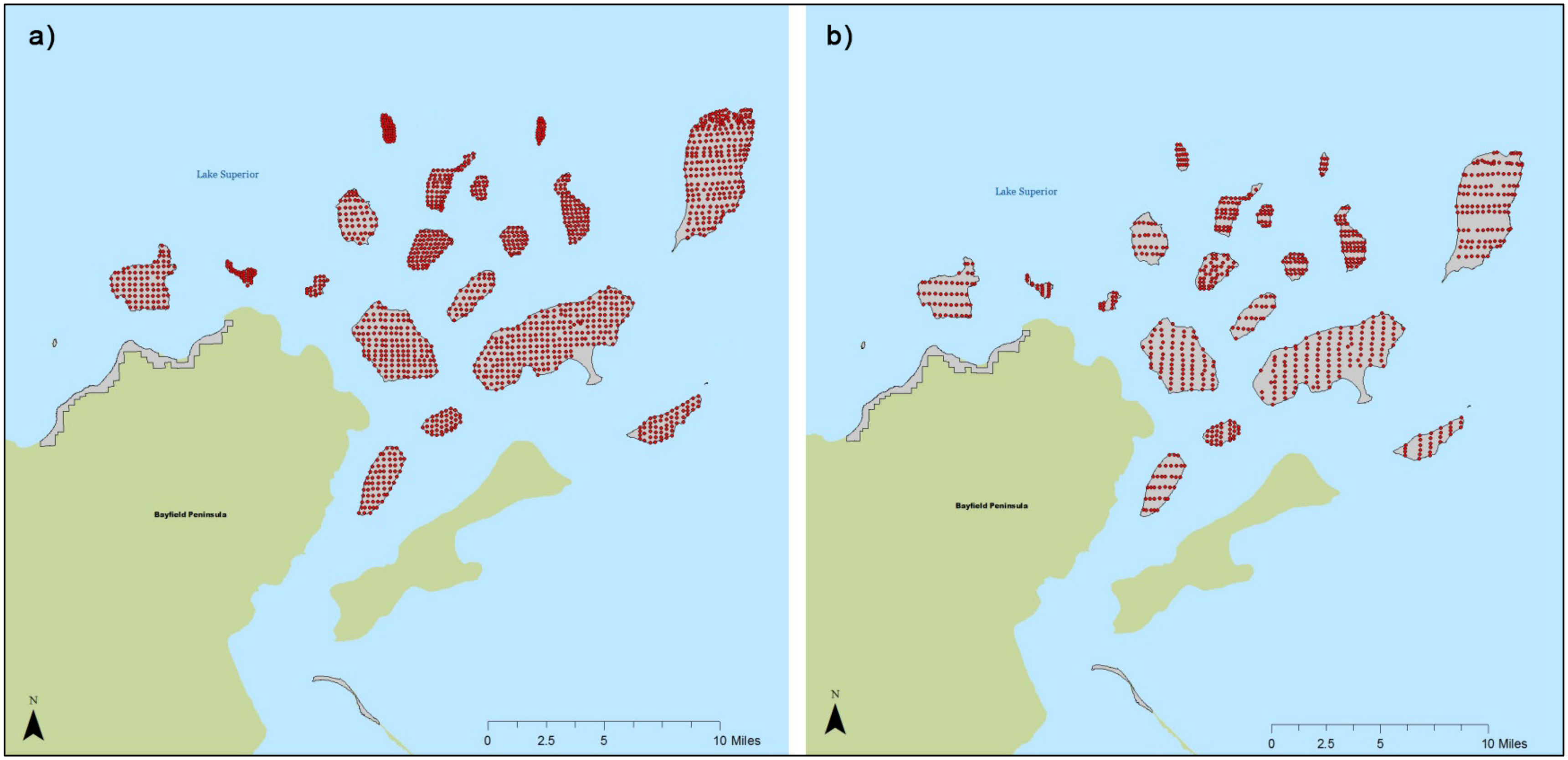


Figure 3. The location and orientation of plots surveyed along transects on 18 of the Apostle Islands in the 1990s (*a*), and a subset of those plots that best matched the location of plots surveyed in 2013 (*b*). The Apostle Islands National Lakeshore is located in northern Wisconsin off the tip of the Bayfield Peninsula in Lake Superior.

Transect and plot layout

Judziewicz and Koch (1993) surveyed 1,424 forest plots along compass-line transects with spacing between plots and transects varying by island size and physiography. For the present work, we surveyed 706 plots using a plot spacing that was approximately half the intensity of the 1990s survey. We separated transects by either 400 m or 800 m and plots by either 200 m or 400 m along each transect (Table 1).

Table 1. Transect spacing (m), plot spacing (m), and the number of plots surveyed on each island 1991/1992 and in 2013, grouped by Deer Management Zones. Zone 1 = low-to-no deer history, Zone 2 = low-to-high deer history. More transects and plots were surveyed in the 1990s, but the plot numbers presented in this table represent a sub-sample of transects to more equitably compare to 2013 data.

Island	Deer Management Zone	Transect Spacing (m)	Plot Spacing (m)	1991/1992 Plot #	2013 Plot #
Basswood	2	800	400	34	30
Bear	2	800	400	27	20
Cat	1	400	200	59	52
Devils	1	400	200	21	22
Hermit	2	400	200	33	26
Ironwood	1	400	200	28	29
Manitou	2	800	400	22	22
Michigan	2	800	400	27	26
North Twin	1	400	200	11	11
Oak	2	800	400	73	67
Otter	1	400	200	42	39
Outer	1	800	400	114	113
Raspberry	1	400	200	14	16
Rocky	2	400	200	45	34
Sand	1	800	400	47	37
South Twin	2	400	200	19	21
Stockton	2	800	400	121	124
York	1	400	200	19	17

We used GIS to overlay the proposed locations of plots onto aerial photographs and used these, along with a compass and Trimble Juno GPS, as a guide for establishing the survey points in the field. We positioned transects in the same orientation as what was traveled by Judziewicz and Koch in the

1990s, which was most often the short axes of islands (e.g., east–west transects instead of north–south on Outer Island), and we used measured pacing (two steps per pace) to approximate our distance between plots along transects. To be efficient, two crew members worked individually on alternate transect lines.

Yew surveys and browse assessments

In 1991/1992, E. Judziewicz recorded species lists within 0.01-ha circular plots (5.6 m radius) and noted the percent cover and height range of Canada yew (Judziewicz and Koch 1993). In 2013, we also used 0.01-ha circular plots; we estimated percent cover, measured the maximum stem height (cm) of the tallest individual, and measured the average stem height representative of the majority of stems of Canada yew within plots. Because Judziewicz's data on height ranges appeared to be rough estimates, we assumed for analysis purposes that the upper end of these ranges were on par with our maximum height data. Because of the differences in how these data were obtained, sampling error could bias our interpretations. However, maximum heights did not significantly differ between time periods, suggesting that any differences in yew height between deer management zones should be real effects. Between plots, we recorded the presence or absence (within 1 m radius) of Canada yew at each measured pace along transects.

Within each 0.01-ha plot, we recorded the presence or absence of deer (*Odocoileus virginianus*) or hare (*Lepis americanus*) browse on the Canada yew and associate woody species. Stems with sharp, angular cuts were recorded as hare browse, and stems with horizontal and usually rough-cut tips were considered browsed by deer, similar to methods that Johnson applied when collaborating on browse survey protocols for the Great Lakes Inventory and Monitoring Network (Waller et al. 2009). Our confidence for distinguishing between hare and deer browse was high for larger diameter twigs and if the browse was recent. Identifying browsed twigs in the field can be a challenge, however, especially if the browsed twig is not fresh or if it has a small diameter. Twigs can abort in development, adding to the challenge of identifying the cause of stunted, broken, or grazed branches. Data on the identity of browsers should be interpreted with caution, as some sample error is inherent in distinguishing between deer vs hare browse on the smallest diameter yew branches. Further, the crew observed a few instances of needle leaves having been stripped off of branches of yew, and it is unclear what animal is responsible for stripping needles, whether it be hare, deer, rodents, insects, or other stressors that could induce leaf dropping (Windels and Flaspohler 2014; Windels, pers. comm.). Although we did not have a formal method established for looking for deer evidence other than deer-browsed stems, we did note any signs of deer (e.g., scat, deer tracks and informal trails, rubs, and live animals) if they were obvious. We made notes on the general health of the yew and any standout features within every plot and at the scale of each transect.

Historical Land Survey Records

We investigated the potential use of historical land survey records for documented presence of Canada yew on the Apostle Islands in the 1800s. We accessed these records digitally (http://digicoll.library.wisc.edu/SurveyNotes/) and read through numerous records before determining that the surveyors for the Apostle Islands were not very specific in their record-keeping. Surveyors elsewhere have been noted to have referred to Canada yew as "ground hemlock" (Van

Deelen et al. 1996), but surveyors for the Apostle Islands merely mention an “evergreen understory.” This “evergreen understory” undoubtedly included Canada yew, but it could also have included regenerating tree species such as balsam fir, white cedar, hemlock, spruce (*Picea glauca* and *P. mariana*), or pines (*Pinus strobus* or *P. resinosa*). Therefore, we did not proceed with using these data to infer the distribution of Canada yew prior to the historic cutover by Euro-American settlers. We mention it here because park managers asked us to look into this, and it is frequently questioned by researchers if Canada yew coverage could be detected from the survey records on the islands.

Statistical and Geospatial Analyses

Contemporary Canada yew status

To address our first objective, we estimated the percentage of Canada yew presence on each island at two scales. At the transect-scale, we calculated the frequency of yew occurrence along transects and converted this to a percent occurrence (number of paces where found divided by total transect length × 100). These data were tabulated to compare Canada yew percent occurrence among islands and to compare these transect-level data with the presence of yew calculated at the 0.01-ha plot level. Using plot-level data on Canada yew, we computed the mean (± 1 SE) percent cover and maximum height for each island and plotted these by deer management zone.

Temporal change in Canada yew

To address our second objective, we compared the distribution and abundance of yew in 2013 with that in 1991/1992 collected by Judziewicz and Koch (1993). Their survey methods were more extensive, so we subsampled their georeferenced plots that best approximated the location of transects we sampled in 2013. Similar to the 2013 data, we tabulated the mean (± 1 SE) for percent cover and maximum height (largest value listed in size range) of the 1990s Canada yew for each island. To assess 22-year changes in the percent cover and maximum height of Canada yew, we conducted separate restricted maximum likelihood (REML) mixed-model linear analyses with time period, deer management zone, and the interaction of these terms included as fixed effect variables. Random effects variables included island and transect (nested within island). The inclusion of deer management zone in this model was to address our third objective. Using the logit transformation and the addition of the smallest non-zero value to the numerator and denominator of the logit function, we transformed percent cover of Canada yew to meet assumptions of linearity, equality of variances, and normally distributed residuals (Warton and Hui 2011).

Spatial interpolation of Canada yew status and change

To further assess changes in Canada yew abundance and distribution, we applied geospatial analyses. Plot-level percent cover data were entered into ArcMap10.1 to spatially analyze the extent of deer browse and to examine yew health on each island. Using the Spatial Analyst tool in ArcGIS, we interpolated the 2013 abundance of yew between plots using Inverse Distance Weighting (IDW) with a pixel size of 10 and a power of three to best approximate our plot size. We performed this process separately for each island prior to creating a mosaic data set to merge the islands into a single raster. Using the subsample of 1990s transects and plots that best approximated the locations of plots we sampled in 2013, we repeated the IDW and merging process to interpolate Canada yew percent cover on islands in the 1990s. To determine 22-year changes in yew, we used the Spatial Analyst Raster

Calculator tool to subtract the interpolated 1991/1992 raster values from the 2013 raster values. This provided us with a map displaying decline and growth of yew on each of the islands on a scale stretching from 100% loss to 100% gain of yew cover. We repeated this entire process for data on maximum height of Canada yew.

Results

Contemporary Yew Distribution Among Islands Relative to Deer Management Zones

The presence of Canada yew was consistently high among islands in Deer Management Zone 1 (no-to-low deer history) compared with Zone 2 (low-to-high deer history) islands. By recording the presence or absence of Canada yew at each pace along transects (approximately every 1.5 m), we observed yew present at >75% of paces on all Zone 1 islands and only on 33% of paces on Zone 2 islands (Table 2). Relative abundance of yew among islands was similar between the 0.01-ha circular plots and the presences recorded at paced distances along transects, suggesting that plots approximated yew distribution well. Yew presence within the 0.01-ha plots did skew slightly higher than what was estimated with the line intercept coverage along transects, so the patchy distribution of yew may be best characterized by larger surface area plots than a line intercept approach to characterize yew at both local and island-scale extents (Table 2).

Using the 0.01-ha plot-level data collected on Zone 1 islands, all but Devils Island had yew present within >75% of plots, but at 50% plot presence Devils Island still had a notable yew presence (Table 2, Figure 4). The percentage of browsed plots on Ironwood Island seems high given that there are not multiple lines of evidence suggesting deer on that island (Figure 4). The field notes had sparse information about patterns of browse observations, nor were other signs of deer indicated. Nevertheless, but both crew members independently coded those plots as having deer browse. This suggests that follow-up browse surveys should be done on Zone 1 islands.

Of the Zone 2 islands, only Bear, Manitou, Michigan, and South Twin have a yew presence comparable to Zone 1 Islands. Basswood and Oak Island plots did not contain yew in 2013 (Figure 4), but its sparse presence was recorded along transects on Oak Island (Table 2).

Percent cover of yew ranged from 0% to 100% cover among plots on the islands, reflecting a patchy distribution. The greatest mean percent cover observed in 2013 was on Raspberry and North Twin islands, and the lowest cover on Basswood and Oak islands (Table 2, Figure 5). Mean percent cover was distinctly greater among Zone 1 islands (43.3 ± 5.8 SE) than Zone 2 (8.3 ± 3.4 SE) islands, except for Michigan Island (30.8 ± 6.5 SE), which is comparable to some Zone 1 islands (Figure 5).

Table 2. Percentage of plots and transect lengths covered by *Taxus canadensis* and the percentage of plots with any evidence of deer or hare-browsed branches of *T. canadensis* or other woody species among 18 of the Apostle Islands in 2013. Zone refers to deer management zones identified by park managers, with Zone 1 = low-to-no deer history and Zone 2 = low-to-high deer history.

Island	Zone	% Plots Yew Present	% Transect Meters Yew Present	Mean % Yew Cover in Plots	% of Plots with Deer Browse on Yew	% of Plots with Hare Browse on Yew	% of Plots with Deer Browse on Non-Yew Species
Cat	1	86.0	71.3	28.8 (4.3)	38.0	12.0	6.0
Devils	1	50.0	56.7	26.6 (7.5)	0.0	4.6	0.0
Ironwood	1	86.7	68.0	29.4 (5.1)	50.0	0.0	3.3
North Twin	1	100.0	100.0	65.3 (9.9)	0.0	45.5	0.0
Otter	1	87.8	79.0	48.8 (5.8)	2.4	2.4	0.0
Outer	1	85.4	68.3	48.3 (3.4)	15.5	0.0	27.2
Raspberry	1	93.8	99.6	72.9 (7.5)	0.0	0.0	6.3
Sand	1	94.6	79.1	27.0 (4.8)	56.8	0.0	2.7
York	1	76.5	75.8	41.2 (8.5)	41.2	0.0	5.9
Zone 1 Average	**–**	**84.5 (4.9)**	**77.5 (4.8)**	**43.3 (5.8)**	**22.7 (7.9)**	**7.2 (5.0)**	**5.7 (2.8)**
Basswood	2	0.0	0.0	0.0	0.0	0.0	13.8
Bear	2	65.2	53.3	7.4 (2.6)	0.0	0.0	0.0
Hermit	2	42.3	25.9	3.0 (1.0)	3.9	0.0	23.1
Manitou	2	59.1	40.3	7.8 (2.6)	0.0	0.0	4.6
Michigan	2	73.1	61.9	30.8 (6.5)	42.3	0.0	26.9
Oak	2	0.0	0.1	0.0	0.0	0.0	10.5
Rocky	2	47.1	32.4	8.7 (3.9)	0.0	0.0	0.0
South Twin	2	80.0	61.1	18.0 (3.3)	0.0	5.0	0.0

Table 2 (continued). Percentage of plots and transect lengths covered by Taxus canadensis and the percentage of plots with any evidence of deer or hare-browsed branches of T. canadensis or other woody species among 18 of the Apostle Islands in 2013. Zone refers to deer management zones identified by park managers, with Zone 1 = low-to-no deer history and Zone 2 = low-to-high deer history.

Island	Zone	% Plots Yew Present	% Transect Meters Yew Present	Mean % Yew Cover in Plots	% of Plots with Deer Browse on Yew	% of Plots with Hare Browse on Yew	% of Plots with Deer Browse on Non-Yew Species
Stockton	2	39.5	15.7	2.7 (0.4)	10.1	0.0	27.9
Zone 2 Average	**–**	**45.1 (9.7)**	**32.3 (8.0)**	**8.3 (3.4)**	**6.3 (4.6)**	**0.6 (0.6)**	**11.9 (3.9)**

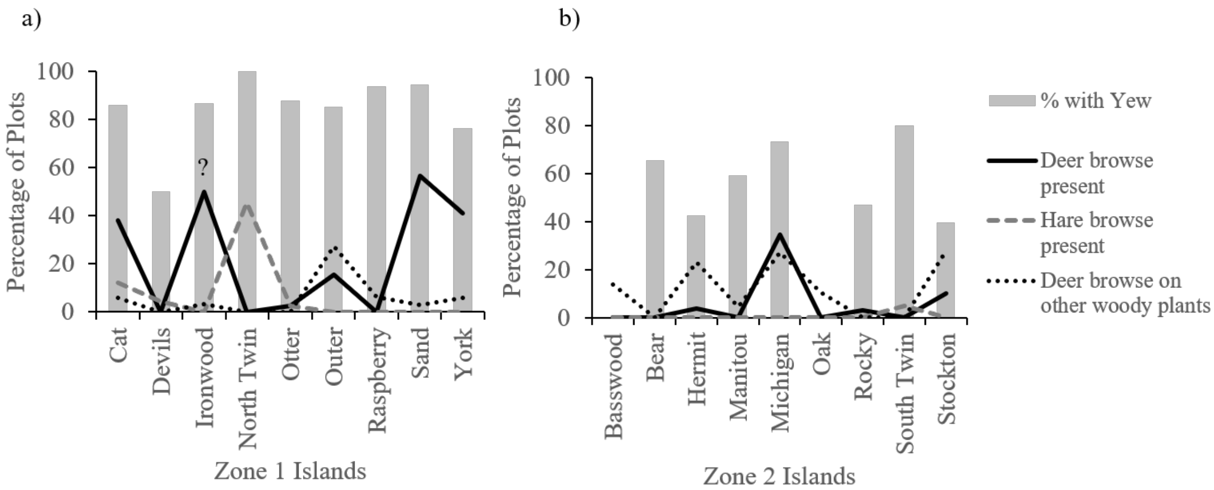


Figure 4. Percentage of plots with *Taxus canadensis* (Canada yew) and percentage with probable browse by deer or hare on Canada yew or other woody species among 18 Apostle Islands grouped by deer management zone. Zone 1 islands = low-to-no deer history (*a*), Zone 2 islands = low-to-high deer history (*b*). Question mark for Ironwood Island refers to an unusually high percentage of browsed plots despite there be not being multiple lines of evidence of deer on the island. However, both crew members independently coded those plots as having deer browse.

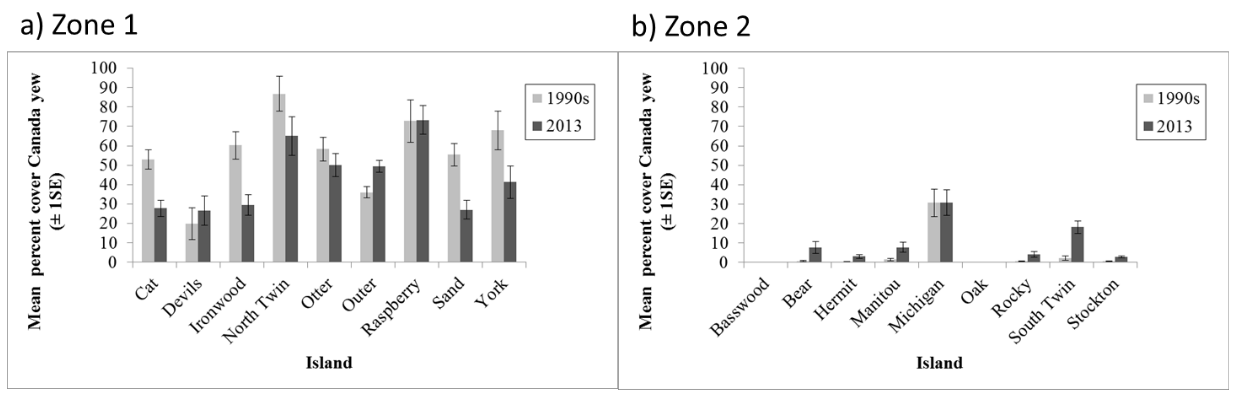


Figure 5. Mean (± 1 SE) percent cover of *Taxus canadensis* (Canada yew) in plots measured in the 1990s and in 2013 on 18 of the Apostle Islands, grouped by Deer Management Zone. Zone 1 = low-to-no deer history, Zone 2 = low-to-high deer history.

Status and Change in Canada Yew Abundance

Plot-level analysis of change in abundance

Zone 1 islands had, on average, 19-times more Canada yew cover than Zone 2 islands in the 1990s and 7.47-times more cover in 2013 (Figure 6). This change in cover over time and between zones was significant (Table 3) and accounted for 54% of the variation in yew cover among the islands. Steep declines in yew cover were observed on Sand (−28.4), Ironwood (−30.9), Cat (−25.1), and York (−26.8) —all are Zone 1 islands. Yew cover increased on Zone 1 islands including Outer (13.4) and Devils (6.8). Some Zone 2 islands experienced slight increases in yew, increasing from an average of 4.1% (± 3.3 SE) cover in the 1990s to 8.3% (± 3.4 SE) cover in 2013. Among Zone 2 islands, South Twin experienced the greatest increase in yew from the 1990s to 2013 (+15.9; see Figure 5).

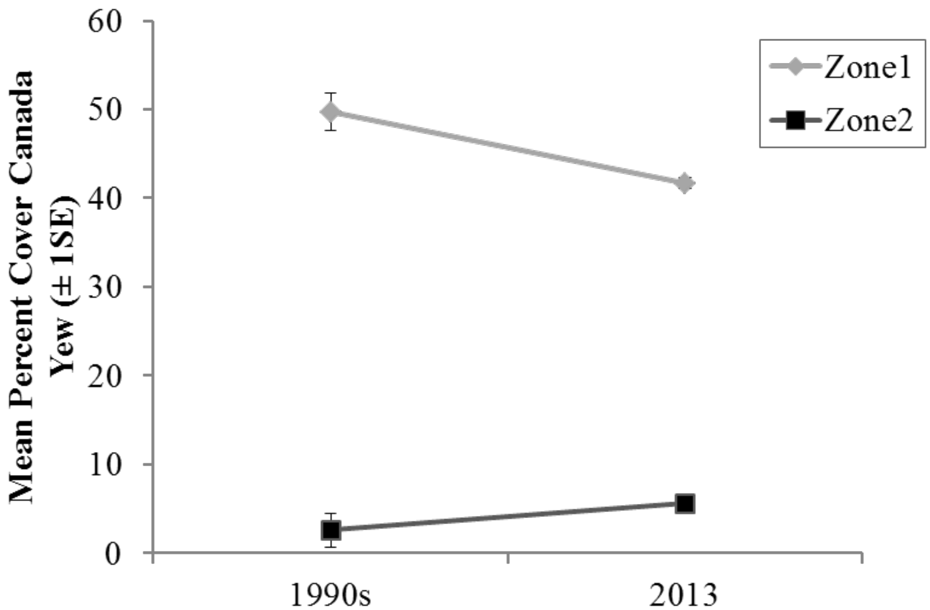


Figure 6. Mean percent cover of Canada yew (± 1 SE) between the 1990s and 2013, and between Deer Management zones (Zone 1 = low-to-no deer history, Zone 2 = low-to-high deer history) on the Apostle Islands.

Table 3. Results of REML analysis with % cover Canada yew (logit-transformed) fitted with two fixed effects variables: year (1990s and 2013) and Deer Management Zone (1 and 2), and the interaction between year and zone, and with the random effect variables island and transect nested within island. The model explained 54% of the variance in yew cover (R^2 adjusted). Asterisk (*) indicates statistically significant values.

Source	df (denominator)	F	P
Year	1395	1.85	0.18
Zone	15.08	47.37	**<0.0001***
Year*Zone	1395	32.95	**<0.0001***

The tallest yew observed in both time periods was on North Twin Island (Figure 7), with the tallest plant recorded in 2013 at 413 cm tall. The tallest plant recorded in the 1990s on North Twin was 274 cm. There was no significant difference between time periods in the mean maximum height of Canada yew, but regardless of time period, Zone 1 islands consistently had significantly taller yew than Zone 2 islands (Table 4, Figure 8). The REML model accounted for 48% of the variation in maximum yew height. Despite no overall significant difference in maximum yew height over time, some islands do appear to have gained in yew height (North Twin, Outer, Rocky, Bear, Hermit, Manitou, South Twin, and Stockton), while others such as Cat and Ironwood appear shorter in stature now than in the 1990s (Figure 7). Some of this variation in height could reflect biases in sample methodology between time periods.

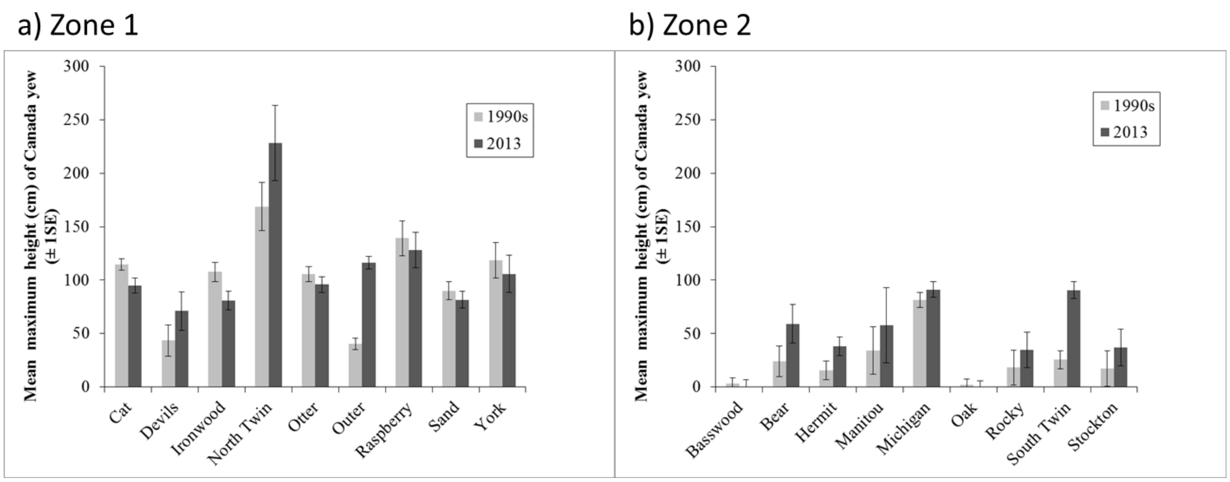


Figure 7. Mean (± 1 SE) maximum height of *Taxus canadensis* in plots measured in the 1990s and in 2013 on 18 of the Apostle Islands, grouped by Deer Management Zone (Zone 1 = low-to-no deer history, Zone 2 = low-to-high deer history). There were no statistical differences in yew height between time periods.

Table 4. Results of REML analysis with maximum height of Canada yew (cm) fitted with two fixed effects variables: year (1990s, 2013) and Deer Management Zone (1 and 2), and the interaction between year and zone, and with island incorporated as a random variable. The model explained 48.2% of the variance in yew cover (R2 adjusted). Asterisk (*) indicates statistically significant values.

Source	df (denominator)	F	P
Year	1391	51.50	**<0.0001***
Zone	15.01	21.01	**<0.001***
Year*Zone	1391	0.36	0.55

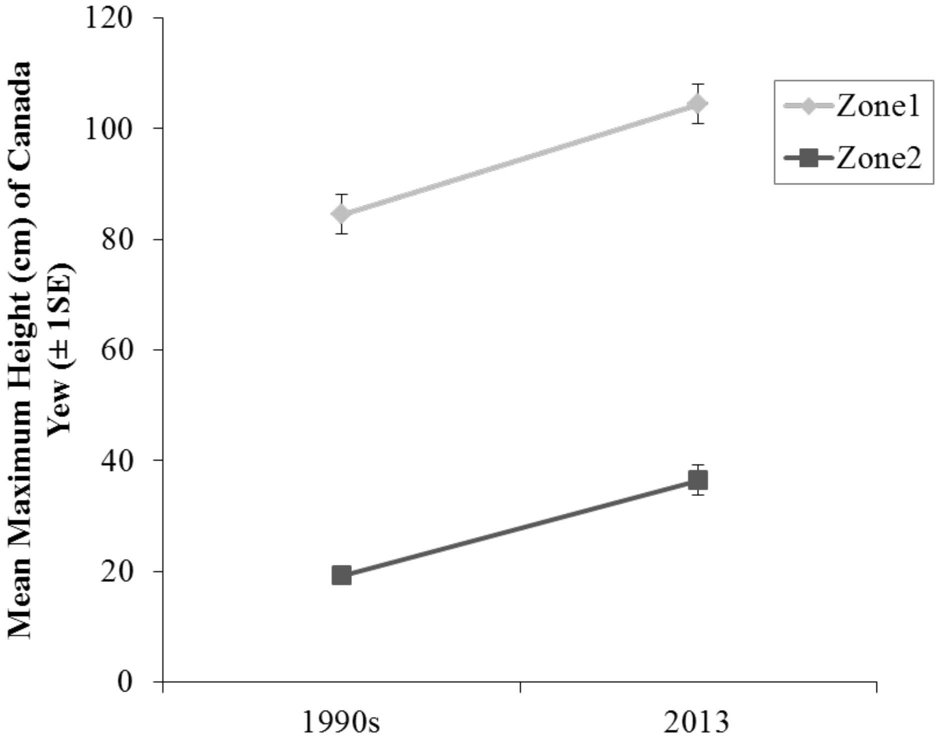


Figure 8. Mean maximum height (cm) of Canada yew (± 1 SE) between the 1990s and 2013, and between Deer Management zones (Zone 1 = low-to-no deer history, Zone 2 = low-to-high deer history) in the Apostle Islands.

Judziewicz and Koch (1993) presented a detailed assessment of a gradient in yew abundance on Outer Island, so we presented a comparable assessment here. As in 1991/1992, yew cover decreased on the south end compared to the north end of Outer (Figure 9). It was fairly common for plots on the south end of Outer Island to have <10% yew cover in the 1990s, but in 2013 there were only a few plots with <10% cover (Figure 10). Increases in yew presence and coverage among plots elsewhere among the islands were also noticeable (Figure 10).

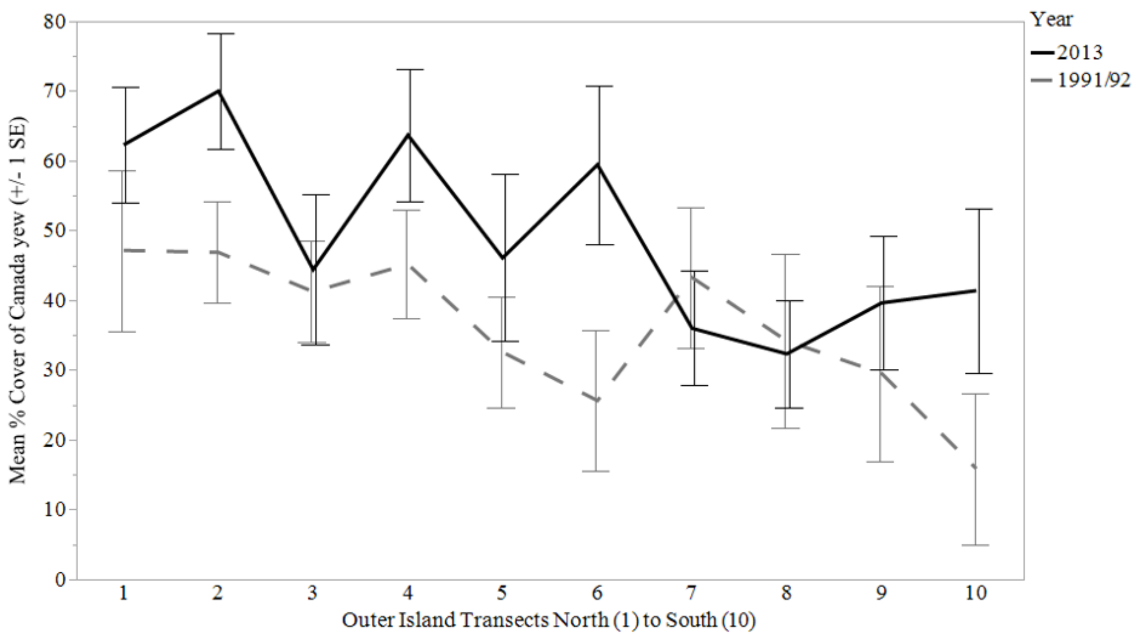
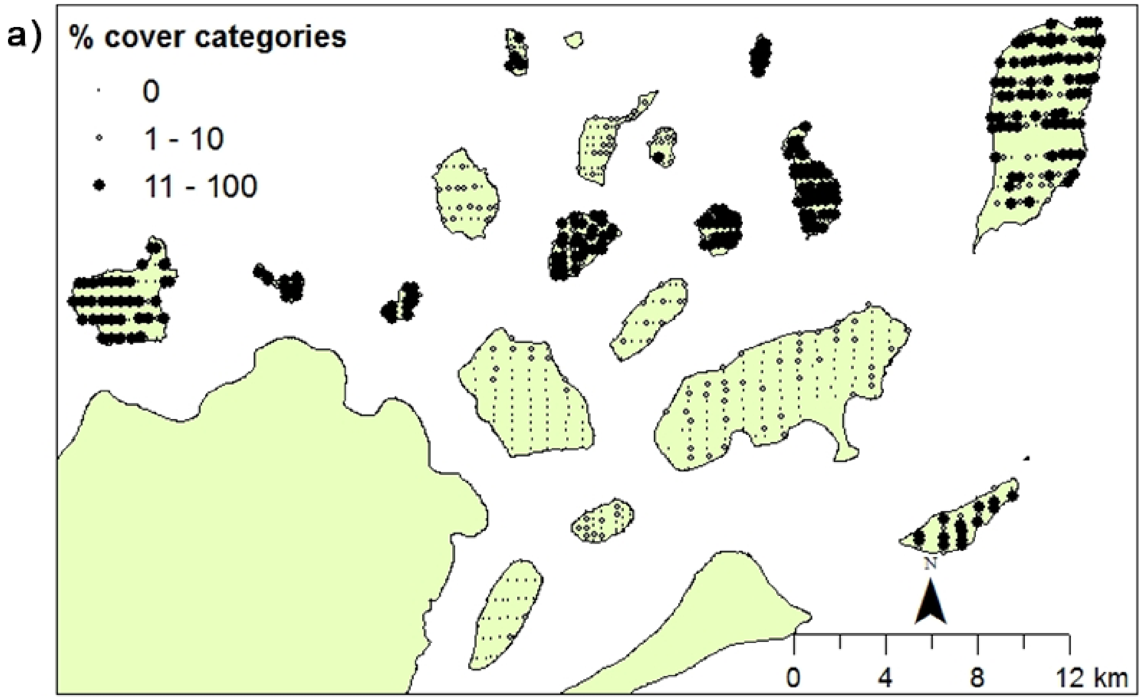


Figure 9. Mean percent cover (± 1 SE) of Canada yew measured in plots distributed among ten transects surveyed from the north end (transect 1) to the south end (transect 10) of Outer Island in the Apostle Islands. Here, the 2013 data and 1991/1992 data are plotted together to show general trends in yew cover across the island, but it is helpful to know that these transect locations were not permanent and so transect placement may vary somewhat between time periods.



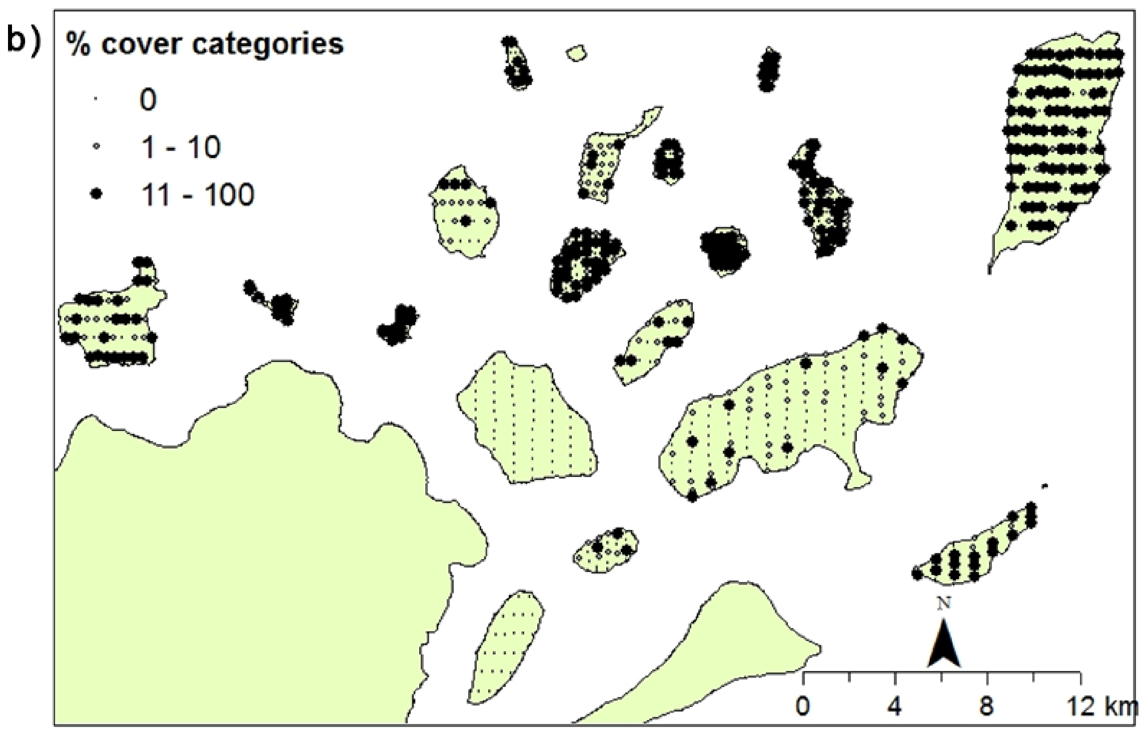


Figure 10. Distribution of Canada yew that was present at more and less than 10% cover in 1991/1992 (*a*) and in 2013 (*b*) in the Apostle Islands. See Figure 2 for island names.

Geospatial analysis of change in Canada yew abundance

Interpolated maps of percent cover and height of Canada yew illustrate the spatial variation in these metrics within and among islands for each time period, and the change in these metrics from 1991/1992 to 2013 (Figures 11–16). Sand and York Islands were already known to have had significant damage to yew due to high deer densities in the early to mid-2000s. The impact of deer is apparent by the large patches of declines in yew cover on these two islands close to the mainland, and to a lesser extent declines in maximum height (Figures 13 and 16). Patchy declines in yew cover and stature are also indicated on these maps for other islands that historically had a significant population of Canada yew, including Cat, Ironwood, and parts of Otter and Outer.

Recovery of yew is evident on some of the islands (Figures 13 and 16). Yew appears to be recovering throughout much of Outer Island (though the patchy pattern is unexplainable), on the north end of Bear Island, in a northern portion of Manitou Island, and throughout South Twin especially on the east side. Slight increases are also noted in small patches on Rocky, Hermit, Stockton, and Michigan islands.

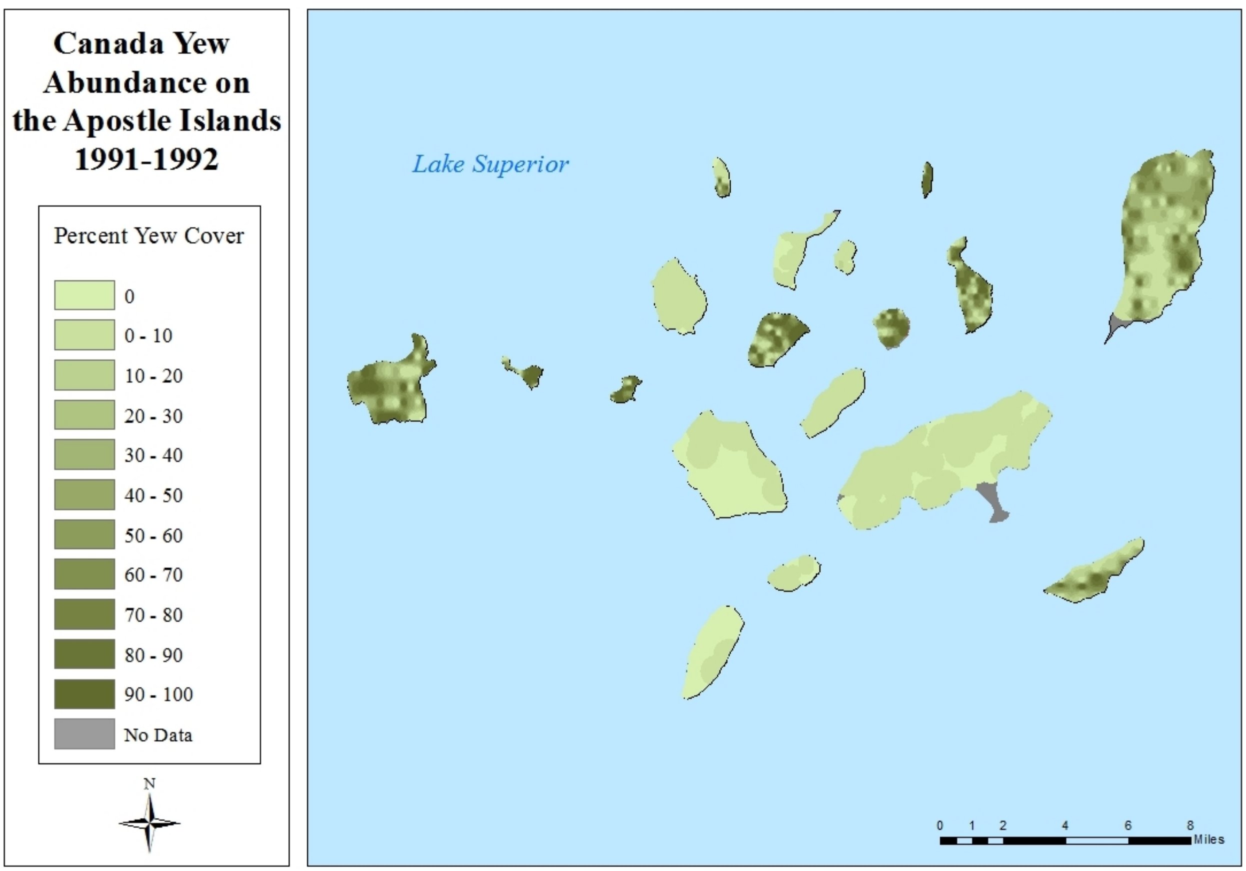


Figure 11. Interpolated percent cover of Canada yew on 18 of the Apostle Islands in the 1990s. See Figure 2 for island names.

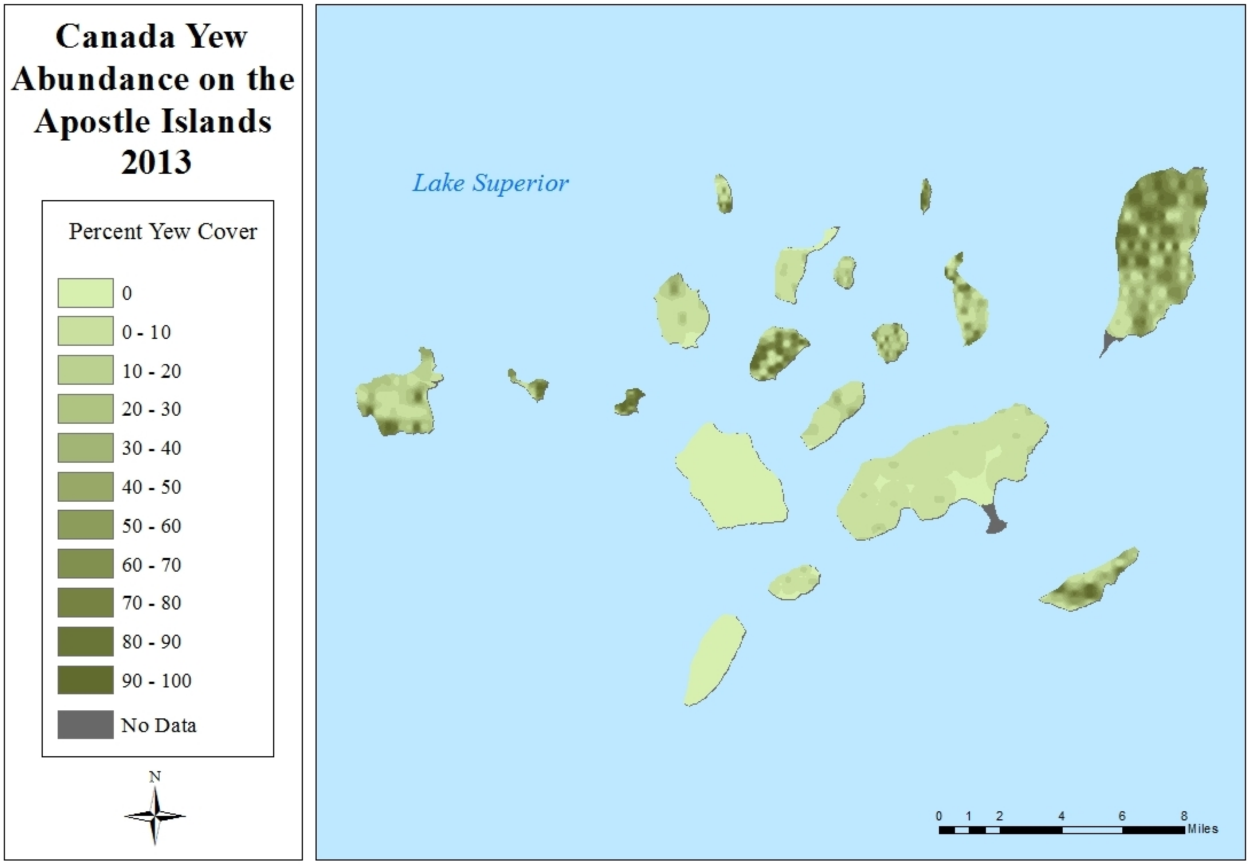


Figure 12. Interpolated percent cover of Canada yew on 18 of the Apostle Islands in 2013. See Figure 2 for island names.

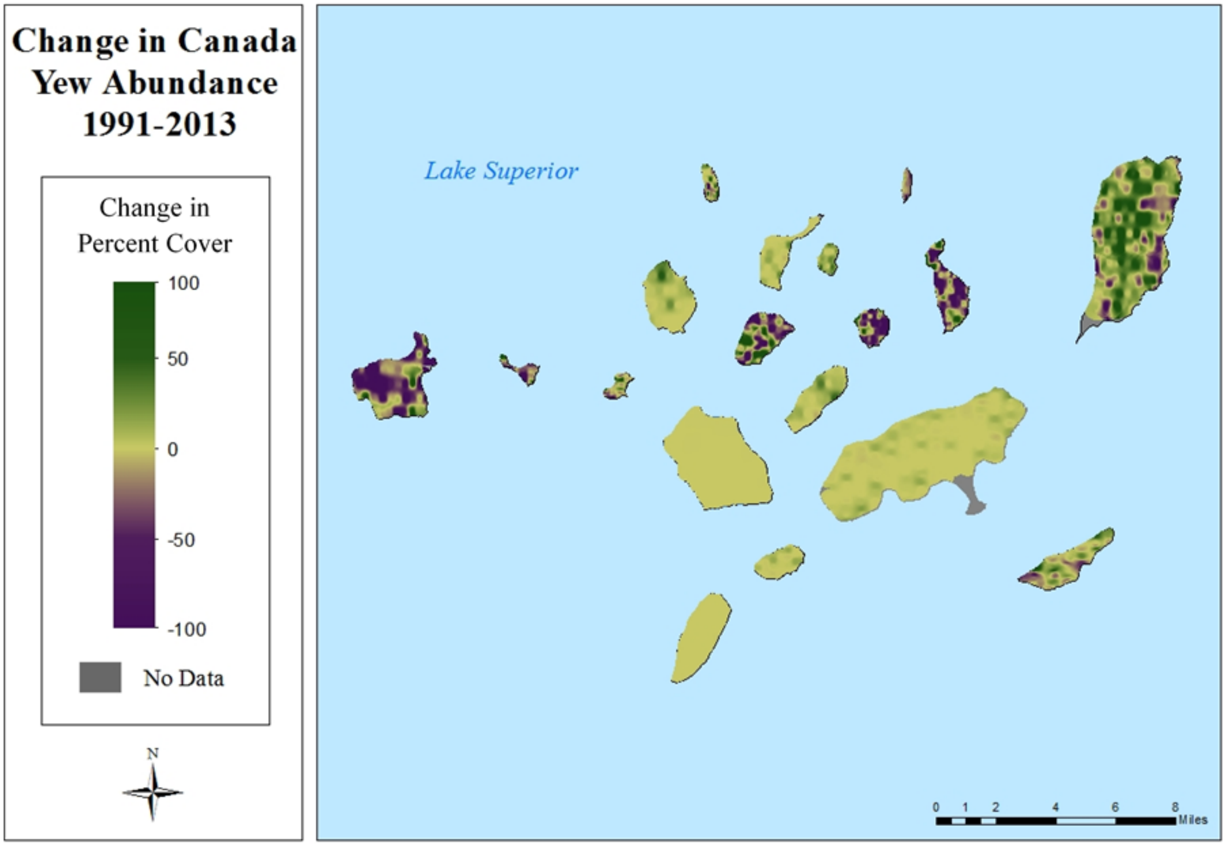


Figure 13. Change in the interpolated percent cover of Canada yew on 18 of the Apostle Islands, calculated as the difference between 2013 and 1990s interpolated values. Green = increase in Canada yew cover, purple = loss in Canada yew cover. See Figure 2 for island names.

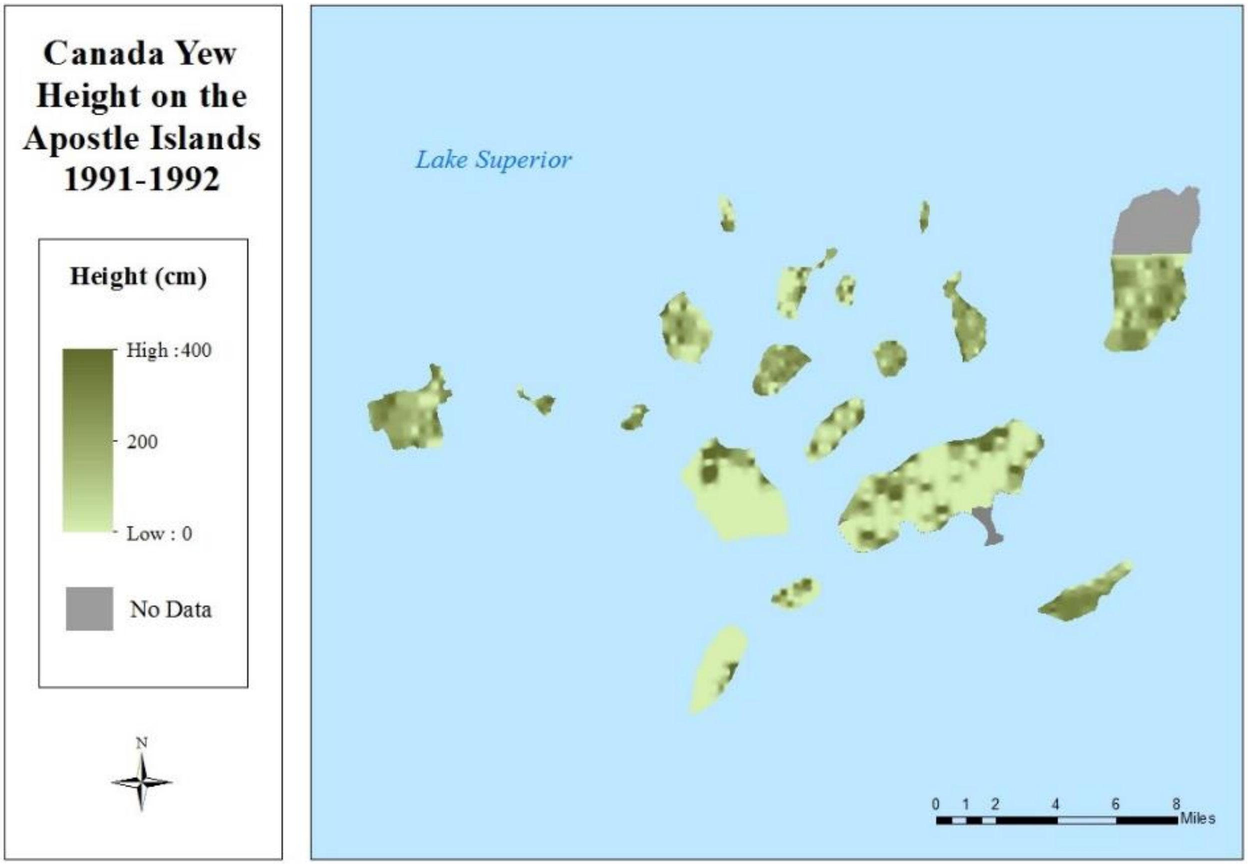


Figure 14. Interpolated height (cm) of Canada yew on 18 of the Apostle Islands in the 1990s. Height data were not recorded in plots at the north end of Outer Island or on the Stockton tombolo (shown in gray). See Figure 2 for island names.

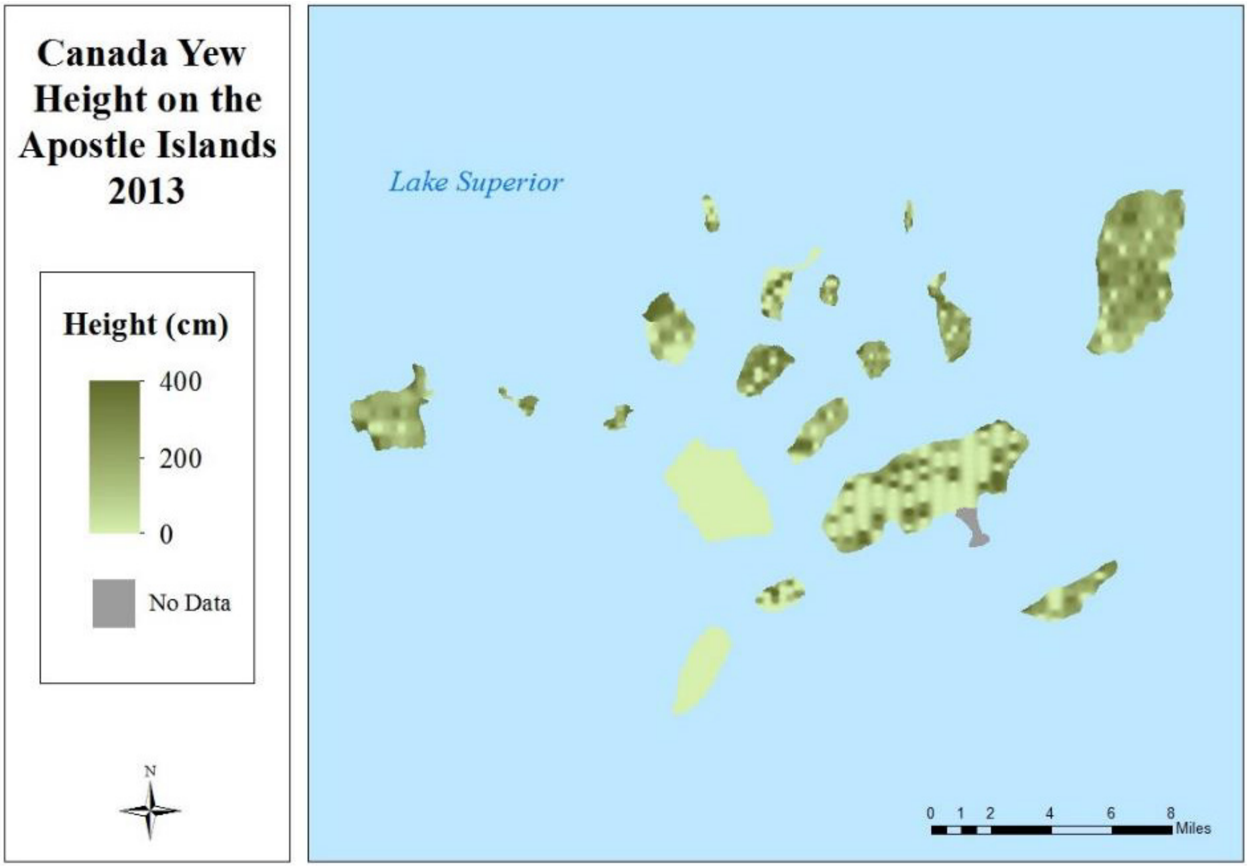


Figure 15. Interpolated percent cover of Canada yew on 18 of the Apostle Islands in 2013. See Figure 2 for island names.

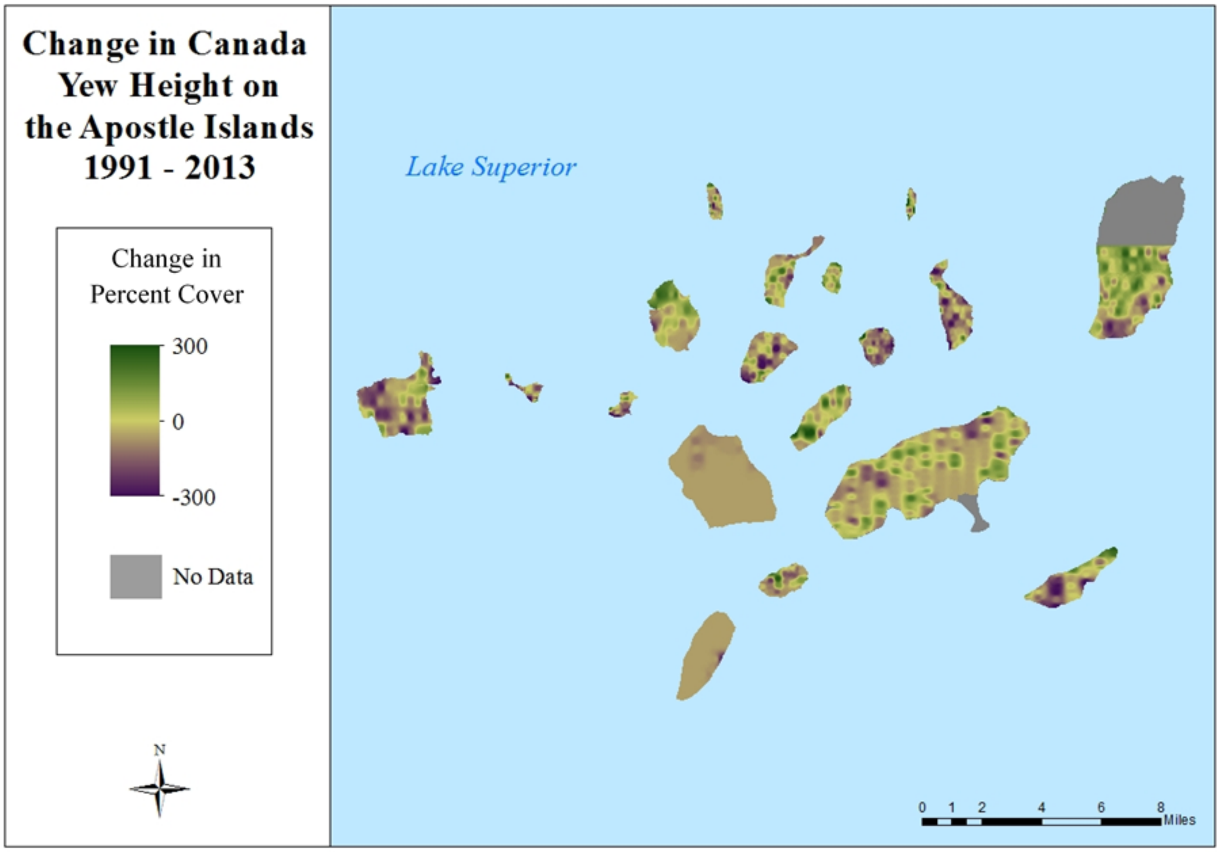


Figure 16. Change in the interpolated percent cover of Canada yew on 18 of the Apostle Islands, calculated as the difference between 2013 and the 1990s interpolated values. Maximum height data were missing for the northern end of Outer Island and the Stockton tombolo in the 1990s, precluding an analysis of change there. Green = increase in Canada yew cover, purple = loss in Canada yew cover. See Figure 2 for island names.

Herbivory Among Islands

Zone 1 islands have a history of low-to-no deer presence, but our field documentation of evidence of possible deer activity indicates that deer may be occupying some of these islands. Due to difficulties in identifying browse on small diameter branches of Canada yew and due to a range of patterns in branch damage observed by the crew, we cautiously present these data with browser identified. Our crew was trained on how to differentiate between deer and hare browse, and they often noted seeing both on islands. The crew recorded in their field notes observations of branches of Canada yew with stripped off leaves, but only in 13 plots. In eight of those plots, we could not be certain if the damage was due to by one of our target herbivores (deer or hare), so we excluded those eight plots from browse assessments. Sand Island had the highest proportion of plots with recorded deer browse activity on Canada yew (i.e., browsed stems, stripped stems). Half of the plots on Ironwood Island had evidence of browsing, as documented independently by two crew members working on different transects, but the field notes did not describe browsing impacts as severe or noteworthy. York, Cat, and Michigan had the next highest number of plots with browsed yew (see Figure 4). Browsing activity was observed on yew in >10% of plots on Outer and Stockton islands, and less frequent

browsing activity was recorded on yew on Hermit and Otter islands (see Table 2 and Figure 4). Deer browse activity on non-yew species was recorded in >10% of plots on several Zone 2 islands and in >10% of plots on only Outer Island among Zone 1 islands (see Table 2). Snowshoe hare occupy some of these islands and are apparently browsing on yew sometimes, with the highest frequency of hare activity occurring on North Twin Island (see Table 2).

Island-by-Island Observations and Recommendations

Zone 1 islands

Cat Island

Cat Island had consistently low deer densities in the late 1950s–1960s, after which it was largely thought to have lost deer (National Park 2014). In 2013, two crew members independently noted signs of deer presence. These signs included freshly browsed twigs of yew, cedar, hemlock, and mountain maple, and tall skeletonized yew with branches stripped to ground level. The crew did not record signs of scat or rubs. Hare browse was also indicated here (Photo series 1), thus it is possible that some stripped yew branches could be attributed to hare. However, the overall evidence does strongly suggest that deer have recently been present on Cat Island. These impacts on Cat island are not yet as pervasive as on Sand Island, but this balance can easily shift if the deer population is left unchecked.

Photo series 1. Animal trail (*left*), hare-browsed stem of deciduous species (*center*), and relatively short-statured yew (*right*) on Cat Island.

Being that this is one of the islands where we observed obvious declines in yew cover since the 1990s, we strongly advise early and frequent monitoring of this island. While browse sign was frequent and some patches of yew were shorter in stature, tall and robust patches of yew persist throughout much of this large island. Most of the plots where we observed browsing impacts are in the "neck" of Cat Island and just north and south of the neck (Figure 13).

Devils Island

Yew is fairly abundant, but its presence is scattered on Devils Island (50% of plots). Here, it tends to be absent or less abundant beneath the dense boreal canopies and mid-stories of spruce and balsam fir. We observed some leaves stripped from yew branches, but this was most often at the bottom of

the yew suggesting that this activity may be due to grazing by snowshoe hares. Devils Island has the largest snowshoe hare population in the archipelago (Erik Olson, personal communication), so follow-up monitoring may be warranted to determine if hare are responsible for this damage or if it could be rodents or insects.


Photo series 2. Patchy but robust yew (*left*) and fleshy cones, or arils, (*right*) present on deer-free Devils Island.


Photo series 3. Robust yew understory with expansive coverage (*left*), including in the wilderness zone camping area at the south end of Devils Island (*right*).

<u>Ironwood Island</u>

Yew is frequently present and healthy on Ironwood Island, but signs emerged in 2013 suggesting that deer may be impacting the yew in some places here. Both crew members independently observed signs of skeletonized yew on the island and browsing in 50% of the plots. One plot contained branches of yew that had been stripped of its leaves. The crew did not record signs of scat, trails, or deer rubs. It is possible that some damage could be hare related. Most of the browse sign was on the southern end of the island north of the sandspit. A biological technician for the park spent a limited number of hours looking for signs of deer here in July 2014, but he noted no sign of deer. This information, coupled with our observations of lower percent cover of yew in 2013 compared with

1990s, suggests that Ironwood should be monitored for increased deer activity in the future. During a visit in 2002, S. Windels and G. Smith observed deer pellets on the island (S. Windels, personal communication). We encourage the park staff to continue frequent monitoring to determine the status of deer on Ironwood Island.

North Twin Island
This old-growth forested island has never had documented deer presence, and our study supports this. The yew here is dense, delightfully tall (up to 6 m noted along transects), healthy, and unbrowsed by deer (Photo series 4). Hare, however, are present and their browsing is especially apparent on species along the rocky east shoreline (including the State threatened *Packera indecora*). We did observe stripped yew leaves a few times, but this is most likely due to hare or another small mammal or insect. On a visit to North Twin in 2013, the lead author (S. Johnson) observed a yew branch that had been girdled by hare. It appears that hare do not preferentially browse yew, but we advise monitoring the hare population here and elsewhere where hares may peak in abundance.

Photo series 4. A crew member is enveloped by yew (red circle), and signs of possible hare or microtine damage on yew on North Twin Island.

Otter Island
Yew is frequent and healthy, but it is not evenly distributed across Otter Island. White cedar is prevalent in the canopy and due to low recent deer pressure, it is regenerating very nicely and seemingly out-competing yew in some areas on the island. There is a history of low deer numbers on Otter Island prior to the 1970s and there is no obvious sign of current deer presence currently. One of our crew members did note two yew plants with single stripped branches each, but he specifically noted that this could also have been hare damage. Our spatial analysis of change in yew cover and stature indicates that Otter Island has undergone some declines that should continue to be monitored.

Photo 5. Yew understory of Otter Island.

Outer Island

Yew blankets much of the understory of the mixed-age to maturing hemlock-hardwood forests on Outer Island. Yew was only absent from 15% of 2013 plots, with it tapering out beneath the occasional dense patch of cedar and regenerating balsam fir. Percent cover within plots averaged 48% (see Table 2) and it was not uncommon to find some plots with nearly 100% coverage. Most upland hardwood forests among the islands tend to lack a dense yew understory, but at one point on Outer our crew noted "the nicest upland hardwood stand with yew I've seen" and "yew in a blanket on 100% of ground as far as I can see in each direction".

Outer Island does not have a documented history of deer presence, but evidence indicates that deer may now be present. Our crew fairly regularly documented signs throughout the island of browsed yew, mountain maple, sugar maple, hemlock, aspen, and red oak. In one case a crew member recorded in his field notes "yew heavily browsed beneath hemlock, almost skeletonized." Browsing by snowshoe hare was not indicated here and based on detailed descriptions of the browse in the one crew member's notes, we concluded that the observed browse damage is due to deer. The crew did not note signs of scat or deer rubs. Browse sign was indicated throughout the island, but most consistently it was located on the south end of the island 2.5–3 km north of the sandspit. In summer 2014 one of the co-authors (E. Leonard) observed what appeared to be a trail with deer prints near the sandscape, but we regret that no photos were taken. We do recommend future monitoring of deer presence and potential impacts on Outer Island. Since our fieldwork, deer were observed at eight

camera locations across Outer Island, but only during the summer months in 2018, suggesting that deer presence is so far for short periods of time (Erik Olson, personal communication).

Photo series 6. *Clockwise from left:* Robust yew beneath older forests on north end of Outer Island; robust yew beneath younger second-growth forest on Outer Island; and an example of the types of areas on the island lacking yew, such as beneath an evergreen canopy of thick balsam fir.

Raspberry Island

The small size of this island lends itself to a high proportion of edge habitat with stunted, thick balsam fir at edges and throughout. There are also many small gaps throughout the canopy and mountain maple is abundant. Yew is dense, tall, and frequent and its robust nature even beneath evergreen canopies of cedar and balsam likely reflects the more open nature of the canopy (Photo 7). While not alarming, we did note occasional browned and dead branches on some of the yew. The lack of deer presence on Raspberry Island despite its close proximity to the mainland is interesting and should not be taken for granted in case deer populations expand to this small island in the future. Most of the island is surrounded by steep sides, which may make it difficult for deer to colonize. It is worth noting that a fawn was observed dead on the sandscape during sandscape monitoring work in 2014, but it most likely washed ashore.

Photo 7. Very robust yew on Raspberry Island, including in gaps as shown to the right of the trail.

Sand Island

Fresh browse, scat, and tracks of deer were observed on Sand Island but these were uncommon along the transects that we surveyed. Not surprisingly, we did observe abundant relict signs of previous high deer densities (browsed stems, yew skeletons, old deer trails). Species that were freshly browsed included Canada yew, mountain maple, and even the less-palatable balsam fir. The hemlock and cedar component of the southern region of Sand Island had the most obvious deer activity including trails and bedding spots, suggesting that the sparser understory beneath the evergreen canopy has served as winter refuge for deer. The tallest yew skeletons were observed on the south end of the island near, but not directly beneath, large hemlocks.

York Island

Healthier stands of yew were observed on the east side of York Island and adjacent to dense balsam fir, but otherwise we observed intermittent yew skeletons (dead yew). The balsam fir may have been "camouflaging" the yew from the browsing deer. Healthy stems were noted on many of these skeletons, which may promote recovery of individuals. All signs of browse appear to be old, suggesting that deer presence is minimal to none and that deer management in the early 2000s was effective.

Photo series 8. *Clockwise from left:* Animal trail through short-statured yew; browsed and stunted yew; and a lack of yew beneath an evergreen canopy on the southern end of Sand island.

Zone 2 islands

<u>Basswood Island</u>

We observed a deer and fresh deer trails, scat piles, and deer rubs on Basswood. Fresh browse signs were observed on white pine regeneration, maples, juneberry (*Amelanchier* spp.), ironwood (*Ostrya virginiana*), honeysuckle (*Lonicera canadensis*), and even leatherwood (*Dirca palustris*), which is surprising because its chemical defenses generally ward off herbivory. Despite these apparent impacts, Basswood Island has a diverse shrub and herb understory and healthy hemlock regeneration, suggesting that deer densities and browsing pressure are relatively low compared to many mainland forests in the Great Lakes region. However, it is not clear if deer densities on Basswood are adequate for supporting the re-establishment of Canada yew.

Photo 9. Upland deciduous forest on Basswood Island with an open understory due to the lack of Canada yew.

<u>Bear Island</u>

There is a clear gradient in yew abundance on Bear Island, with the most robust patches occurring in the northern and lower/wetter half of the island. These northern stands are dominated by white cedar, balsam fir, yellow birch, and mountain maple. While the yew was common on this north end, it had a patchy distribution between thickets of balsam fir and healthy patches of regenerating white cedar. Running east to west in the center of the island is an approximately 1-km-wide strip of old growth yellow birch, hemlock, red oak, and white cedar with a sparse yew understory. Yew within this region is more common at the edges of the island. The southern portion of the island is steeper and contains an upland sugar maple, red oak, and birch canopy with dense maple regeneration. Yew at this south end is nearly absent.

There was little deer sign observed, but an old pellet group was noted near an underused animal path. Deer pellets decay quickly, usually not lasting longer than two years (S. Windels, personal communication), so the origin of the deer pellet was probably winter 2011–2012.

<u>Hermit Island</u>

Canada yew was present in 42% of our plots in 2013, but abundance was generally low (range = 0%–16%, average of 3% cover). Hermit's overstory is predominantly upland mesic woods, and in the understory, there is a strong presence of beaked hazelnut (*Corylus cornuta*), mountain maple, and sugar maple regeneration. We did observe some deer browse on yew here, but most recent browsing has occurred on the deciduous woody understory species.

Manitou Island

Yew was frequently observed on Manitou, but it is rather patchy and sparser in stature and density than islands that are managed in Zone 1. There was low-to-no deer sign observed except for light browsing noted on deciduous species, but it is not clear that this was definitively deer browse. Thick patches of mountain maple and regenerating sugar maple and hemlock suggest that the browse pressure on this island has been low in recent years. The canopy is mixed hemlock-hardwoods with lowland conifer. Hemlock and large white cedar cast deep shade, which likely precludes yew establishment (and perhaps recovery) in dense stands of these evergreen tree species. Relatively lower abundance of yew also seems to be related to dense patches of balsam fir here. We noted that yew was more robust in areas of small gaps in the canopy.

Photo 10. Yew is patchily distributed on Manitou, but robust where present.

Michigan Island

The dominance of yew varies across Michigan Island from being sparse and mixed with mountain maple, balsam fir, and cedar, to having medium abundance of 30%–50% cover, and to being the dominant understory species present at 60%–100% cover. Deer numbers have likely wavered between low and no deer on Michigan Island since the 1950s. The largest recorded harvest of deer on this island occurred in 1964 (13 deer) just prior to a lapse in harvest records for the islands (National Park Service 2014). Deer were thought to no longer be present by the mid-2000s (National Park Service 2014), but evidence that we observed in 2013 suggests that deer do currently occupy Michigan Island. Population numbers are likely low, but we did note signs of browsing on yew, white cedar, and deciduous species such as mountain maple in 42% of the plots. In addition to browsed branches, some yew branches were stripped of their leaves down to branch bases. We observed old hare browse, but no fresh signs of hare activity on yew in 2013. It should be

documented, however, that fresh but sparse hare browsing was observed by the lead author on common juniper (*Juniperus communis*) in 2014, so hare are present on the island.

Oak Island
Yew was not seen within plots, but it was observed persisting as sparse individuals on north-facing slopes of ravines on the north end of the island. These yew plants were short with only 1–5 branches each and none showed recent browse signs. Three deer were observed by our field crew, deer beds were seen, and deer trails and browse were noted. However, current deer browse pressure appears to be low based on healthy tree regeneration patterns throughout the island. North- and west-facing ravine slopes contain large and regenerating hemlock (field notes indicate "magnificent regeneration"). These ravines may serve as refuges for hemlocks from browsing deer, but hemlock's presence here may also reflect scarification of ravine slope soils by water running off upland portions of the island. The presence, however, of healthy hemlock regeneration in some areas of the uplands does support the idea that deer browse pressure has been low enough to support a broader establishment of this preferred browse species.

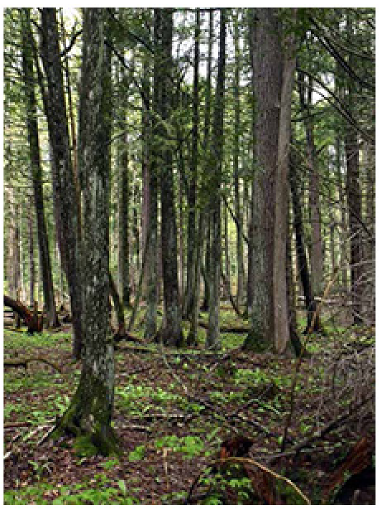



Photo series 11. Yew-free understory of second-growth upland forest on Oak, and evidence of recent and intensive land-use on Oak that may have influenced deer and fire impacts on Canada yew.

Rocky Island
We did not note any signs of recent browse or deer activity on Rocky Island. The booming deer population of the 1940s–1950s is an era gone by. Today's forests exhibit signs of recovery, albeit slow, of the lush and expansive yew understory that locals remember seeing prior to a swift and relatively short-lived occupation by deer (Judziewicz and Koch 1993). Yew distribution is relatively patchier on this island than what we have observed on islands that have never had deer, but many of these patches are very robust and healthy. The canopy reflects an aging mixed conifer-hardwood stand with large birches (paper and yellow), cedar, balsam fir, and red and sugar maples. Large and dense yew was noticeable in blow-down areas on the island, suggesting that growth rates of this species may increase as the canopy continues to break up in wind- and age-related tree falls. As is the pattern on other islands, yew density and stature decline in shady understories beneath cedar and

balsam fir canopies. Elsewhere on the island, low yew abundance was linked with better drained soils, higher levels of sugar maple regeneration, exceptionally dense mountain maple, beaked hazelnut, and in general a more highly diverse understory that likely presents a strong competitive influence on any yew establishment and growth.

Photo series 12. Yew in relatively denser patches (*left*), and yew scattered and sparse on Rocky Island.

<u>Stockton Island</u>

Yew is present intermittently throughout Stockton Island. It tends to occur in small patches of one or two healthy individuals spaced 1–100 m apart. We also observed it sparsely occupying microsites on ravine sides. Crew members indicated some deer browsing and stripping on Canada yew (12% of plots), but most of the browsing was on deciduous species such as mountain maple, sugar maple, beaked hazelnut, and occasionally hemlock (30% of plots show browsing on non-yew species). The crew did not record signs of deer scat, rubs, or informal trails. The lush regenerating layer of hemlock, cedar, red oak, and sugar maple indicate that the deer browsing pressure, and hence deer densities, have recently been kept at low and seemingly sustainable levels. This was not the case in the 1940s–1950s when deer were observed to be very abundant by a State wildlife biologist (National Park Service 2014).

<u>South Twin Island</u>

While there was no sign of deer activity on South Twin Island, snowshoe hare are quite common. The yew here is sparse in places but when present it is generally abundant and healthy, especially associated with canopy gaps. Its patchy distribution may reflect inclusions of thick balsam fir, maple, and white cedar regeneration that limit yew's establishment.

Photo series 13. Short-statured yew (*left*) and yew with stripped leaves on South Twin Island.

Discussion

Canada yew is still thriving throughout much of the archipelago and even appears to be increasing in some places. This could reflect maturing forests. Yet, Canada yew on the Apostle Islands maintains a precarious existence, both broadly and at the scale of individual islands. There is a wealth of data showing that white-tailed deer can rapidly and pervasively affect the abundance, growth, reproduction, and recovery of Canada yew (studies reviewed by Windels and Flaspohler 2011). Much of this research comes out of previous investigations on the Apostle Islands (Beals et al. 1960, Beals and Cottam 1960, Judziewicz and Koch 1993, Balgooyan and Waller 1995, Allison 2006, Maragi 2013, Mudrak et al. 2009, National Park Service 2014). Our observations and data provide further support for the imbalanced deer-yew relationship demonstrated by striking declines of yew on some islands since the early 1990s. The spatial and temporal extent of our research has provided an opportunity to confirm in several cases what resource managers already know, but it also illuminates patterns and events that may have otherwise gone undetected (*a la* "the vanishing present," as eluded to by Waller and Rooney [2008]).

Variation in Yew Abundance Over Space and Time in Relation to Human and Deer History

As Allison (2006) proclaims, the spatial extent of yew coverage—not the occurrence—"makes this resource special" for the Apostle Island National Lakeshore. This is indeed true. Yet, the islands are not covered by a homogenous blanket of yew. Patterns of yew vary, even on remote North Twin Island, where our crew was challenged by navigating through thick stands of yew and where they observed yew more than twice their head height. On this remote old-growth island, yew varied in both stature and abundance. On other islands, yew "blankets" were adjacent to yew-free understories, or Canada yew may exist as scattered individuals or short, few-stemmed sprigs in ravines. Microsite-level variations within and among landscapes (i.e., variation in soil, moisture, light, nutrients, and other factors) are inherent traits of natural ecosystems that can explain some of this variation that we see in yew's distribution within and among islands. Windels and Flaspohler (2011) provide a detailed review of the literature on what is known about preferred yew habitat, so we limit our discussion of it here.

In addition to natural variation, the spatial patterns of yew are reflective of the complex stories surrounding Euro-American settlement. Intensive logging in the late 1800s and early 1900s (and up until the 1970s) occurred in most forests on the islands. Fires were known to have followed logging in some areas among the islands (i.e., Oak, Hermit, Stockton, and the south tip of Outer Island). Some islands were active sites for homesteads and fishing camps. Post-logging early successional habitats became the new "normal" in the north woods and on the Apostle Islands, offering an abundance of suitable habitat for white-tailed deer. Historically low deer densities in northern Wisconsin ($<3.9/km^2$; Dahlberg and Guettinger 1956) quickly became forgotten as deer densities sky rocketed and record harvests were reached on the mainland and on some of the Apostle Islands (National Park Service 2014). These are the stories that are central to the narrative of Canada yew's distribution and abundance among the Apostle Islands. While the legacy of a vibrant and varied

human history is evident, single or concomitant influences of these multiple factors (i.e., fire, logging, and browsing) remains hazy.

On islands such as Oak and Basswood where yew is sparsely present, it is unclear what the relative impacts were of the intensive and repeated logging operations (Beals and Cottam 1960), fire (four-fifths of Oak Island burned in 1943) (Judziewicz and Koch 1993), and a fairly steady but mostly low deer presence (National Park Service 2014). We can, however, make inferences from overall patterns that we have observed in our assessment of the status and changes in yew among other islands, starting with Bear Island where we observed signs of yew recovery on the north end.

Similar to Oak and Basswood, Bear Island was intensively logged at the turn of the 20th century and logging operations extended into the 1950s (Judziewicz and Koch 1993). Peak deer harvests (5.4 deer/km^2) and higher average harvests during 1954–1971 (2.8/km^2) were higher than what was reported for Oak (0.82 deer/km^2 peak harvest, 0.39 deer/km^2 average harvest) or Basswood (3.6 deer/km^2 peak harvest, 2.0 deer/km^2 average harvest). Moderate deer populations have occupied Oak since the early 2000s, and Basswood has consistently had low numbers of deer since prior peaks (National Park Service 2014). We observed a single old deer scat pile on Bear Island but no evidence of deer browse on yew or non-yew species, suggesting that current deer numbers are zero or very low on Bear. Based on typical decomposition rates for deer scat (S. Windels, personal communication), deer were present as recently as winter 2011–2012. Yew was not common on Bear Island in the 1990s and it is not common today. Yet, we do show that yew is increasing in cover at the northern part of the island. Our field observations indicate that this area of the island is lower in elevation and wetter due to poorly drained clay soils. The southern end of the island is higher and has better drained soils, supporting more upland mesic tree species compared to the wet-mesic composition of the northern end of the island (Judziewicz and Koch 1993). Pole-sized trees recovering from post-logging disturbance were noted at the north end of the island by Judziewicz and Koch (1993). Recovering yew on this north end of Bear, but not elsewhere on Bear or on Oak or Basswood islands, brings up a few thoughts on recovery in this post-logging era: 1) recovery may be fastest in moister microsites than in better-drained uplands, 2) the relatively more upland part of Bear Island and relatively more upland Oak and Basswood islands may not have had much yew prior to Euro-American settlement, 3) recovery is likely contingent on not being exposed to frequent or even occasional deer browse that continues on Oak and Basswood islands, and 4) upland forests may have been logged more intensively than relatively wetter stands such as the north end of Bear Island, promoting more suitable habitat for Canada yew.

Turning to Outer Island, we found similar patterns in yew distribution in 2013 data as what Judziewicz and Koch (1993) noted in the early 1990s. Canada yew is more robust on the northern half than the southern half of Outer Island, likely due to the northern half experiencing less intensive logging (and in some places lack of logging) and a lack of intensive burning that occurred on the southern half of the island during the logging era. However, despite this intensive period of human disturbance on Outer Island, yew was present in the majority of our plots, and the abundance of yew on the southern end is on par with the abundance of yew on other islands managed as Zone1 islands. Thus, it appears that the lack of deer (at least, perhaps, up until very recently) is a key factor that has

promoted the persistence and post-fire recovery of Canada yew on Outer Island. Notable is yew's robust presence in upland, drier stands on Outer, while yew is less common in similar upland stands elsewhere in the park. Cooler temperatures of Outer Island than islands closer to the mainland may be an influential factor promoting recovery.

Similar to the southern tip of Outer Island, Hermit Island was intensively logged and burned (Judziewicz and Koch 1993), but yew presence and stature is much reduced on Hermit compared to Outer. Hermit's patchy yew population is likely a function of past high peak deer densities (7.3 deer/km^2 peak harvest). These patterns and others provide convincing evidence of the role of white-tailed deer as a primary driver of the spatial patterns we have observed in yew on the islands.

Yew Declines and Potential for Recovery

Windels and Flaspohler (2011) plotted Judziewicz's 1990s yew cover data against 1950s-era deer densities on the Apostle Islands and determined that islands with low yew densities had experienced deer densities over 7–12 deer/km^2 in the 1950s. They concluded that deer densities over this range tipped the balance away from a stable state for Canada yew. If park managers had not intervened to cull deer from Sand and York Islands in the early 2000s, the decline of yew cover would have rapidly approached levels observed on other islands that experienced high peak deer densities (and harvests) in the 1940s and 1950s (e.g., Rocky Island). Due to the quantitative changes that we documented in this report for Sand and York Islands, where the park has conducted extensive deer population surveys, we urge the park to follow up on declines that we have documented elsewhere on other islands such as Cat and Ironwood. Although yew has not declined on Outer Island, evidence suggests that deer may have accessed the island and additional monitoring could confirm to what extent. At a minimum, we recommend more formal deer browse assessments and annual (or biennial) monitoring of probable deer activity to ascertain if deer numbers are at the low levels desired by management.

Sand and York islands have experienced substantial recent losses in cover of Canada yew, but these islands currently still maintain frequent occurrences of yew that may ultimately promote recovery in dead zones. While some patches of dead yew do not show signs of resprouting, many of the yew "skeletons" are actively putting on new growth at plant bases (Bartnick and Duerkop 2011, Greiner 2012, our observations). During this time of renewed growth, these young, erect branches are at risk and sustained browsing could eliminate the potential for recovery at patch scales necessary for the yew to return to pre-2000 levels. As Holmes et al. (2009) conclude, recovery of yew may not be possible in areas with even low-to-moderate deer densities.

Resource managers at the Apostle Islands have been annually monitoring deer and yew populations on Sand and York islands since 2003 (National Park Service 2014) and they would be wise to continue to be vigilant. The risks at this early stage of recovery are at least four-fold. First, although nutrient chemistry of yew has not been well-studied (Windels and Flaspohler 2011), recently flushed leaves and twigs are likely more tender and contain higher concentrations of minerals and nutrients, making them more palatable to browsing deer (Chapin and Van Cleve 1989, Millard 1996). Second, older and longer branches lay prostrate and protected beneath winter snow cover, but younger branches stand more erect and can become more exposed to browsing deer in winter (Windels and Flaspohler 2011). Third, rates of spreading may increase with the formation of adventitious roots on

longer, prostrate branches (Windels and Flaspohler 2011), so browsing on shorter, erect branches may preclude the ability of these individuals to make horizontal advancements in clonal re-growth. And finally, patches of recovering yew may be more accessible to foraging deer than yew in dense and nearly impenetrable patches that deer may preferentially avoid from an energetic standpoint (Windels and Flaspohler 2013).

Biological Implications of Yew-Deer Interactions

Perennial photosynthetic structures lend themselves to a high risk of predation, which many plants compensate for by producing chemical or physical defenses. Many secondary chemical metabolites produced by plants for anti-herbivore defense can be energetically expensive to produce. Hence, photosynthetic gains must exceed losses for the evergreen habit to be advantageous over a deciduous life history (Coley et al. 1985, Givnish 2002). *Taxus canadensis* produces a suite of chemical compounds called taxanes found throughout the plant, but especially in the leaves. These are the source of the highly prized pharmaceutical cancer drug Taxol® (Cameron and Smith 2008). Higher concentrations of these compounds are found in the leaves during winter months (Cameron and Smith 2008), suggesting that these energetically "expensive" compounds likely confer some advantage in the winter months. It does not appear, however, that these chemical compounds serve as a defense against herbivory by white-tailed deer, supporting the idea that these chemicals evolved over a long time period in a landscape with no-to-low presence of white-tailed deer and even moose (Windels and Flaspohler 2011). Winter-browsing on yew on islands with deer is likely significant, but the rate of summer versus winter browsing on this species is not clear. Could deer on the Apostle Islands be browsing yew more readily during the growing season when taxane production is lower and preferentially be eating more deciduous species in the winter? This could potentially be better understood by dissecting gut samples that were collected (and frozen for later study) from deer harvested in fall and winter from Sand and York islands. Regardless, deer do eat yew.

Deer browsing of Canada yew foliage has implications for biogeochemical cycling in these relatively nutrient poor island ecosystems. High humidity and moist soils support frequent leaching of biologically available nutrients in northern forests. This, plus the accumulation of an acid rich organic layer containing evergreen detritus that accumulates when yew and other evergreen species replace their leaves, promotes a process of mineral and nutrient leaching called podzolization that is common in boreal regions (Givnish 2002). Many slow-growing evergreen species survive and even thrive in low nutrient habitats because of their dependence on internal recycling of nutrients more so than acquisition from the soil for support of growth and primary productivity (Millard 1996). Thus, evergreen needles often serve as nutrient storage vessels from which nutrients move in and out during internal retranslocation processes. When deer strip leaves off of Canada yew branches and then wander to other areas of the island, they are retranslocating these resources outside of individual yew patches. This may promote increased nutrient limitation in some patches, making recovery of yew difficult due to the high demands for biologic compounds for production of new plant tissues and costly production of taxanes. This raises several questions. How are deer directly and indirectly influencing nutrient and mineral content of soils across islands, and how might this influence recovery potential of Canada yew?

Finally, what important role is Canada yew serving for other flora and fauna in these island ecosystems? What is the impact on Canada yew by snowshoe hare, which are common on several islands? On island systems elsewhere in the Great Lakes region, hare have been observed eating yew, but no significant impacts were reported (King 1970). When yew declines, are small mammals such as the red-backed vole (*Myodes gapperi*) and woodland deer mice (*Peromyscus maniculatus*) that are common to the Apostle Islands affected? Are nesting birds negatively impacted? Do declines in yew promote invasion by non-native species? These are questions posed by Windels and Flaspohler (2011) that remain unanswered and ripe for study.

Other Potential Agents of Change

While past land-use and historic and current deer densities are highly influential to the spatial distribution and abundance of Canada yew in the Apostle Islands, other agents of current and future change should be considered. Ongoing shifts in climate parameters are a major concern for park managers and could hold major implications for the persistence and recovery of Canada yew. Annual mean temperature and mean summer temperatures have reached "extreme warm" levels relative to historic climate records for the Apostle Islands (Monahan and Fisichelli 2014). Although precipitation has not reached any extreme lows or highs since 1901 (Monahan and Fisichelli 2014), a long-term trend of lower precipitation levels over the past 15 years coupled with increased evaporative losses linked with warmer temperatures and higher off-shore wind-speeds (Austin and Colman 2007, Desai et al. 2009) can promote drought conditions. Lake Superior water levels reached record sustained low water levels between 1998 and 2013 (Gronewold and Stow 2014). Low lake levels and associated groundwater tables on the islands can exaggerate drought conditions.

Canada yew is a relatively shallow-rooted species that appears to prefer cool, poorly drained wet-mesic soils (Windels and Flaspohler 2011). The Apostle Island's maritime climate likely promotes yew's existence in relatively drier microsites in the park and region, but this could be changing as temperatures and evaporative demands increase. Yew's physiological response to repair injured tissues and to produce new foliage after being browsed may magnify the influence of drier soils on this species. Perhaps the best approach to managing yew in this era of a changing climate is to reduce stressors such as deer herbivory that can speed up and magnify impacts of climate change.

The impacts of climate change in Great Lakes region forests can also be accelerated by the invasion of non-native earthworms (Windels and Flaspohler 2014). No island has been observed to be substantially or heavily invaded by earthworms, but islands with evidence of minimal earthworm invasion include Basswood, Cat, Devils, Michigan, Outer, Raspberry, Sand, and Stockton (Sanders and Grochowski 2012). Earthworm invasions can speed up the rate of decomposition in forest soils, ultimately eliminating an organic layer from the soil surface. The loss of this important duff layer has multiple implications for Apostle Island forests. A major impact is that exposed soils experience greater temperature extremes. Many forest plant species require an organic layer to prevent seeds from desiccating and to provide protection and nourishment for emerging seedlings (Bohlen et al. 2004, Frelich et al. 2006). Canada yew is more often than not associated with organic soils and they are shallow rooted beneath this organic layer (Windels and Flaspohler 2011), so loss of organic soils could have devastating effects on Canada yew establishment and persistence. It will be important to

continue monitoring earthworm presence and advancement throughout the islands. This is currently a component of the Great Lakes Inventory and Monitoring Network's terrestrial vegetation monitoring protocol (Sanders and Grochowski 2002).

Conclusion

Canada yew on the Apostle Islands has suffered recent declines, especially on Sand and York islands where deer densities in the 2000s were on par with densities observed on other islands in the 1950s. On islands with a past history of high deer abundances (i.e., Rocky, Stockton, Hermit, Oak, and Manitou), yew has not recovered to abundances observed on islands with no or low historic deer numbers. Slight increases in yew on some of these islands from the 1990s to 2013 suggest recovery is occurring, but at strikingly slow rates. This pattern of slow recovery is due to low growth rates and occasional browsing by deer that reside on some of these islands even at recent low densities (Allison 2006). Recovery of yew has been the swiftest on deer-free islands such as Outer Island. Although we lack definitive data on the impact of past land-use on Canada yew among the islands, the status and history of deer appear to outweigh the influences of historical logging and burning. Declines in yew and indications of browse observed on Cat and Ironwood suggest that the influence of deer in the National Lakeshore may be more widespread than currently thought by park managers. We recommend that resource managers follow-up with frequent monitoring of deer activity on these and other islands. If resource managers at the Apostle Islands National Lakeshore had not instituted measures in recent years to reduce the deer herds on Sand and York islands, the declines in yew there would no doubt have been on par with declines observed on Rocky Island in the 1950s. Much of the yew on these islands has become "skeletonized" and is dead, but many of the plants are persisting with sparse branches or new growth from the bases. Survival of these individuals is not certain and we may continue to see declines in total yew abundance on Sand and York islands as the "deer browsing debt" is paid (cf. Tilman et al's 1994 "extinction debt"). Yew on these islands is at a tipping point. Sustained low deer numbers are necessary to avoid drastic losses of yew and concomitant shifts in other ecosystem elements that are unique to the islands. Yew has likely been an important component of these islands for hundreds and thousands of years since glaciation (Windels and Flaspohler 2011), yet the narrative is likely much more complex than meets the eye. Managers are urged to apply the precautionary principle when managing the Apostle Islands deer herds and assume that "deer and yew are not compatible" (Allison 2006).

Literature Cited

Allison, T. D. 2006. Canada yew and white-tailed deer at the Apostle Islands: Summary of research to-date with recommendations for continued monitoring and management. Great Lakes Inventory and Monitoring Network Report GLKN/2006/04. National Park Service, Ashland, Wisconsin.

Austin, J. A., and S. M. Colman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. Geophysical Research Letters 34: L06604.

Balgooyen, C. P., and D. M. Waller 1995. The use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin, USA. Natural Areas Journal 15:308–318.

Bartnick, T. D., and P.R. Duerkop. 2011 Deer pellet and browse report: Sand and York Islands, Apostle Islands National Lakeshore. Unpublished report.

Beals, E. W., and G. Cottam 1960. Forest vegetation of the Apostle Islands, Wisconsin. Ecology 41:743–751.

Beals, E. W., G. Cottam, and R. J. Vogl. 1960. Influence of deer on vegetation of the Apostle Islands, Wisconsin. Journal of Wildlife Management 24:68–80.

Bohlen, P. J., P. M. Groffman, T. J. Fahey, M. C. Fisk, E. Suarez, D. M. Pelletier, and R. T. Fahey. 2004. Ecosystem consequences of exotic earthworm invasion of north temperate forests. Ecosystems 7:1–12.

Cameron, S. I., and R. F. Smith. 2008. Seasonal changes in the concentration of major taxanes in the biomass of wild Canada yew (*Taxus canadensis* Marsh.). Pharmaceutical Biology 46:35–40.

Chapin, F. S. III, and K. Van Cleve. 1989. Approaches to studying nutrient uptake, use and loss in plants. Pages 185–207 *in* R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. Plant Physiological Ecology: Field Methods and Instrumentation. Chapman and Hall, London, England.

Coley, P. D., J. P. Bryant, and F. S. Chapin III. 1985. Resource availability and plant antiherbivore defense. Science 230:895–899.

Dahlberg, B. L., and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin. Wisconsin Conservation Department Technical Bulletin No. 14. Wisconsin Conservation Department, Madison, Wisconsin. Available at http://digital.library.wisc.edu/1711.dl/EcoNatRes.DNRBull14.

Desai, A. R., J. A. Austin, V. Bennington, and G. A. McKinley. 2009. Stronger winds over a large lake in response to weakening air-to-lake temperature gradient. Nature Geoscience 2:855–858.

Frelich, L. E., C. M. Hale, S. Scheu, A. R. Holdsworth, L. Heneghan, P. J. Bohlen, and P. B. Reich. 2006. Earthworm invasion into previously earthworm-free temperate and boreal forests. Biological Invasions 8:1235–1245.

Givnish, T. J. 2002. Adaptive significance of evergreen vs. deciduous leaves: Solving the triple paradox. Silva Fennica 36:703–743.

Greiner, A. 2012. 2012 Deer pellet and browse report: Sand and York Islands, Apostle Islands National Lakeshore. Unpublished Report.

Gronewold, A.D., and C. A. Stow. 2014. Water loss from the Great Lakes. Science 343:1084–1085.

Holmes, S. A., C. R. Webester, D. J. Flaspohler, and R. E. Froese. 2009. Death and *Taxus*: The high cost of palatability for a declining evergreen shrub, *Taxus canadensis*. Canadian Journal of Forest Research 39:1366–1374.

Judziewicz, E. J., and R. G. Koch 1993. Flora and vegetation of the Apostle Islands National Lakeshore and Madeline Island, Ashland and Bayfield Counties, Wisconsin. The Michigan Botanist 32:43–189.

King, D. R. 1970. Deer and hare population-range relationships on Garden and South Fox Islands, Michigan. Dissertation. University of Michigan, Ann Arbor, Michigan.

Maragi, F. 2013. Deer impacts on forested communities and Canada yew populations at Apostle Islands National Lakeshore, Wisconsin. Thesis. University of Minnesota, Duluth, Minnesota.

Millard, P. 1996. Ecophysiology of the internal cycling of nitrogen for tree growth. Journal of Plant Nutrition and Soil Science 159:1–10.

Monahan, W. B., and N. A. Fisichelli. 2014. Climate exposure of US national parks in a new era of change. PLoS ONE 9(7): e101302. Available at: http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0101302.

Mudrak, E. L., S. E. Johnson, and D. M. Waller. 2009. Forty-seven year changes in vegetation at the Apostle Islands: Effects of deer on forest understory. Natural Areas Journal 29:167–176.

National Park Service. 2014. Harvestable species plan and environmental assessment: Apostle Islands National Lakeshore. National Park Service, Bayfield, Wisconsin. Available at: www.nps.gov/apis/learn/management/upload/Harvestable-Species-Plan-and-EA-Apostle-Islands-NL-4-14-2.pdf.

Sanders, S., and J. Grochowski. 2012. Implementation of a long-term vegetation monitoring program at Apostle Islands National Lakeshore. Natural Resource Technical Report NPS/GLKN/NRTR—2012/613. National Park Service, Fort Collins, Colorado.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Van Deelen, T. R., K. S. Pregitzer, and J. B. Haufler. 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. American Midland Naturalist 135:181–194.

Waller, D. M., S. E. Johnson, R. J. Collins, and E. W. Williams. 2009. Threats posed by ungulate herbivory to forest structure and plant diversity in the Upper Great Lakes Region and a review of methods to assess those threats. Technical Report GLKN/2009/01. National Park Service, Great Lakes Inventory and Monitoring Network, Ashland, Wisconsin.

Waller, D. M., and T. P. Rooney (editors). 2008. The Vanishing Present: Wisconsin's Changing Lands, Waters, and Wildlife. University of Chicago Press, Chicago, Illinois.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: The analysis of proportions in ecology. Ecology 92:3–10.

Windels, S. K., and D. J. Flaspohler. 2011. The ecology of Canada yew (*Taxus canadensis* Marsh.): A review. Botany 89:1–17.

Windels, S. K., and D. J. Flaspohler. 2013. Scale-dependent browsing patterns on Canada yew (*Taxus canadensis*) by white-tailed deer (*Odocoileus virginianus*). International Journal of Forestry Research 2013: Article ID 276583. Available at: https://doi.org/10.1155/2013/276583.

Windels, S. K., and D. J. Flaspohler. 2014. Considerations for conservation and restoration of Canada yew in protected areas. Natural Areas Journal 34:249–253.

NPS 633/175245, April 2021

National Park Service
U.S. Department of the Interior

Natural Resource Stewardship and Science
1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525