



Forest Health Monitoring at Isle Royale National Park

2019 Field Season

Natural Resource Report NPS/GLKN/NRR—2022/2474



ON THE COVER

Balsam fir (*Abies balsamea*) heavily browsed by moose.

NPS / A. WAKEEN

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Executive Summary

Isle Royale National Park (ISRO), situated in western Lake Superior, supports 53,823 ha of forested land, most of which is designated wilderness. In 2019, the Great Lakes Inventory and Monitoring Network (GLKN) resampled permanent forest monitoring sites in the park, marking the second assessment of these sites. The goal of this long-term monitoring project is to provide managers with routine updates on the state of island forest communities; these data can also be used to tease apart changes in forest communities and elucidate causal agents when novel problems or situations arise.

We initiated a comprehensive forest monitoring program at Isle Royale in 2010, establishing 52 sites at that time. We resampled those sites in 2019 and established an additional eight plots. Sampled and derived metrics included trees (density and basal area of live trees, seedlings, and snags), understory (herb and shrub frequency), browse (bite marks on woody species and presence and height of herbaceous species), richness, and earthworm impacts. We first classified sites into five broad forest types using the initial (2010) dataset (Sugar Maple-Yellow Birch, Cedar-mixed, Paper Birch-mixed, Mixed Conifer-Hardwood, and Balsam Fir), then examined changes since that time.

Analysis of 2019 data shows regeneration of several overstory species remains impaired, particularly in forest types common on the western end of the island, where high moose browse pressure has resulted in neither balsam fir nor trembling aspen being common. While sugar maple was still abundant, density of small saplings fell 33% between the two sampling events. In paper birch forests, we saw little regeneration of hardwoods. Senescing paper birch dominates the forest, while, in some areas, few other individuals of paper birch or other species are present, either in the subcanopy or understory. In Mixed Conifer-Hardwood and Balsam Fir sites, concentrated on the central and eastern parts of the island, trembling aspen has increased in the smallest size classes. This is likely a release from browsing pressure from the period of 2006–2011 when moose density was lower.

Higher recent moose density was reflected in seedling data in forest types common on the west side. Pooling species together, seedling density fell 26.2% at Sugar Maple-Yellow Birch sites and 25.8% at Cedar-Mixed sites. Browse on woody species was markedly higher in 2019. Mean site-level proportion browse (i.e., frequency of the 30 direct-browse circles in each site showing bite marks on woody individuals regardless of species) was highest in Sugar Maple-Yellow Birch sites, where 24.5% of direct browse circles had bite marks in 2019 (compared with 2.1% in 2010). At the species level, among trees, parkwide proportion browse was greatest on red maple (0.40) and sugar maple (0.35), with six species having a proportion browse value greater than 0.2. For shrubs, parkwide proportion browse was greatest on four species of the genus *Cornus* (dogwood), ranging from 0.41–0.80. In total, seven shrub species had proportion browse values greater than 0.2.

Changes in the herbaceous layer between the two sampling events were notable. Site-level species richness fell 20% in Sugar Maple-Yellow Birch sites and 6.6% in Paper Birch-mixed sites. Species known to be preferred by moose also experienced declines, both in terms of site-level richness and site-level abundance. Declines in abundance were most notable in the forest types common on the west side of the island, where abundance of preferred herbs declined 38% in Sugar Maple-Yellow Birch sites and 22% in Cedar-Mixed sites.

We attribute the marked changes we observed to increased herbivores on the island. While moose abundance was slightly greater than 500 individuals at the time of our initial sampling, the population had been low for approximately four years prior to the 2010 sampling event. However, as wolf density declined, moose irrupted, reaching an estimated 2,000 individuals at the time of our 2019 sampling. In addition to moose, snowshoe hare density also reached high levels, with a spike in abundance in 2012 and 2013. Hares browse many of the same species as moose at the same time period, so definitively teasing out impacts attributable to one or the other is not possible with our data. Higher density of hare on the island is believed to be an indirect result of low wolf abundance.

Isle Royale forests also face threats from climate change and invasive species. As air and water temperatures rise, the moderating effect of Lake Superior will attenuate, possibly allowing habitat for boreal species to shift outside of the park. This will create uncertain conditions for forest overstories, particularly within the boreal forest on the island's east side, and in a band around the perimeter.

The greatest invasive plant threat may come from bird-dispersed species, including *Rhamnus* spp. L. (buckthorns) and *Lonicera* spp. L. (honeysuckles). These are aggressive shrubs with native distributions in Europe that are now located on the mainland in Minnesota and Michigan. Due to the size of the island, any seeds deposited on the island will likely not be near a trail or populated area; thus, a population could become well-established over the course of a few years, before becoming known to managers.

Isle Royale forests are also facing the imminent threat of emerald ash borer (*Agrilus planipennis* Fairmaire), a non-native insect now present in Thunder Bay, Ontario, and Houghton, Michigan. While not abundant on the island, black ash is widespread, often growing in very wet areas with no other overstory species. Where this occurs, loss of black ash could result in complete loss of the overstory.

If park management goals are to maintain the character of park forests, herbivore density must be kept low. A wolf reintroduction program began in late 2018. To date, 19 wolves captured from multiple mainland locations in Michigan, Minnesota, and Ontario, Canada, have been released on the island. This program is a multi-year effort, and assessment of its success by managers is ongoing.

Park managers may also wish to study the four moose exclosures on the island to gauge differences in browse preferences and impacts between moose and hare. This could help explain long-term vegetation changes.

The park should continue monitoring for invasive plants, especially those on the island's perimeter, where park visitors may be most likely to introduce non-native material. Currently, forests of Isle Royale are generally in good health, though facing numerous threats. If degraded, the resources needed for restoration will likely be prohibitive. Managers, therefore, should work toward maintaining ecological diversity and function as a way to promote overall ecosystem resistance and resilience.

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Introduction

In 2019, the Great Lakes Inventory and Monitoring Network (GLKN) resampled permanent forest monitoring sites at Isle Royale National Park (ISRO). This marked the second assessment of these sites, which were established and initially sampled in 2010 (Sanders and Grochowski 2011). Sites were sampled in accordance with the network-wide protocol (Sanders and Grochowski 2014b), allowing consistent monitoring methods and comparisons across nine Great Lakes national park units.

Long-term monitoring of forest health provides managers with routine updates on which to base management decisions (Blossey 1999). It can also provide an early warning of potential issues (Pierce et al. 2006, Morrissey et al. 2012). Perhaps more importantly, monitoring can be used to elucidate causal agents and assess changes in dynamic environments (Woods 2000, Pureswaran et al. 2015). This is especially true in areas experiencing both new and fluctuating stressors. One such area is Isle Royale.

Isle Royale National Park is an archipelago in Lake Superior composed of one large island (72 km long, 14 km wide at largest dimensions) and more than 400 smaller barrier islands (Figure 1). Forests dominate the terrestrial component of this park, with a gradient of types across the island. To the southwest, northern hardwood forests of sugar maple (*Acer saccharum* Marsh.) with a yellow birch (*Betula alleghaniensis* Britton) component are typically found in upland areas, with cedar (*Thuja occidentalis* L.) forests dominating in low lying pockets (The Nature Conservancy 1999). The central third of the island experienced a large burn in 1936 (McInnes et al. 1992) and forests here are composed largely of senescing paper birch (*Betula papyrifera* Marshall) with a notable young spruce (*Picea* A. Dietr.) and balsam fir (*Abies balsamea* (L.) Mill.) component. To the east, boreal forests predominate and white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), and balsam fir are abundant. This boreal component is also present around the periphery of the island where Lake Superior moderates temperatures (Slavick and Janke 1987).

The remoteness of the island has allowed it to largely escape pressures common on the mainland, such as invasive plant species (Sanders and Grochowski 2013). Logging and other resource extraction has not occurred since 1940, when the archipelago was designated a national park. One of the largest stressors to the flora is climate change. The park, which sits at the southern boundary of the boreal biome (Fisichelli et al. 2012), has largely been buffered against high temperatures due to the moderating effects of Lake Superior (Austin and Colman 2007, 2008). This is particularly relevant on the east end of the island where low elevations and numerous bays and inlets ensure the land masses have a closer proximity to the moderating effects of the lake. However, as water and air temperatures continue to rise, the climatic conditions facilitating boreal habitat on the east end may cease to exist (Monahan and Fisichelli 2014).

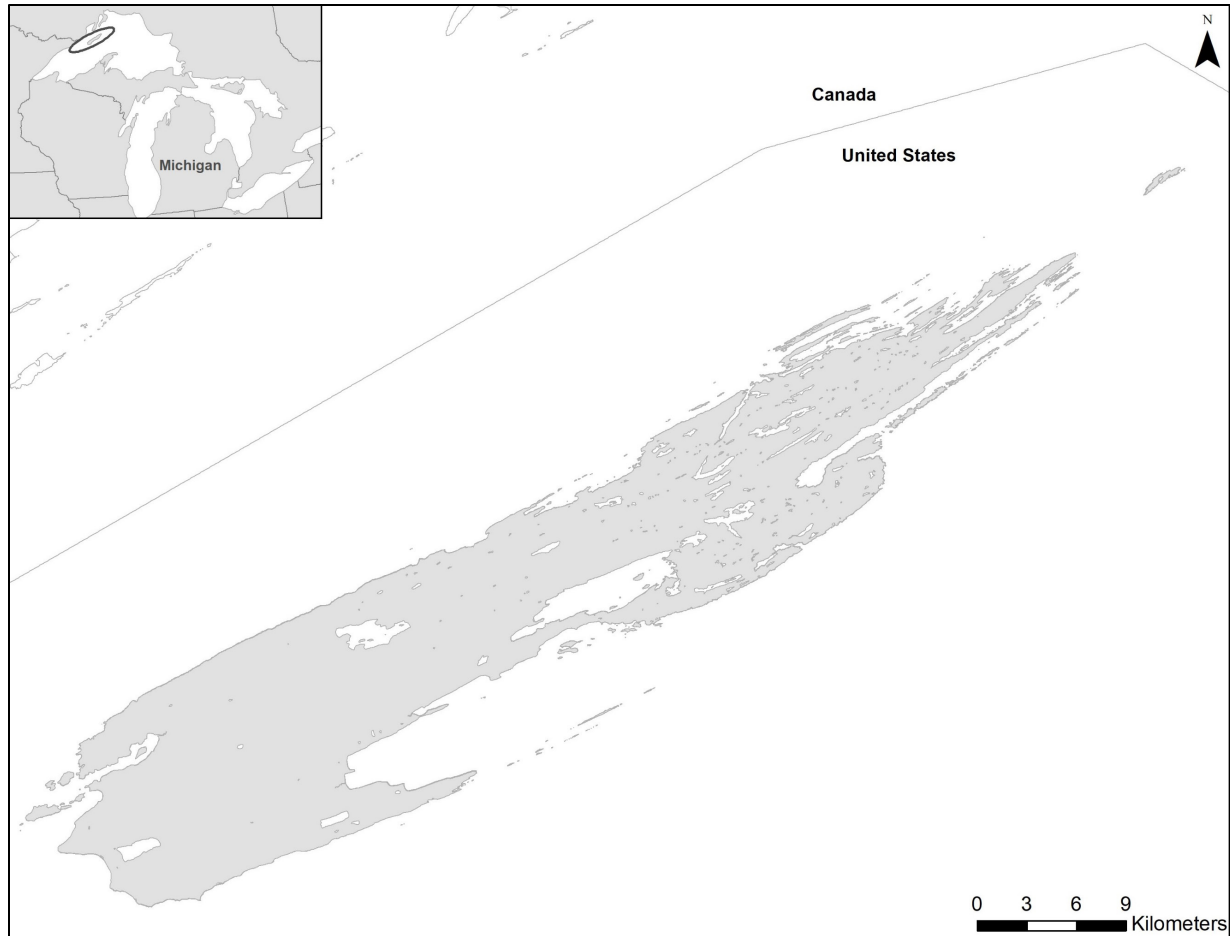


Figure 1. Great Lakes region (*inset*) and Isle Royale National Park (*main map*).

While climate change represents a major stressor on the island's flora, which will likely increase in the coming decades, the greatest current impacts to the flora are from the resident moose (*Alces alces* Linnaeus) population. The park supports populations of both wolf (*Canis lupus* Linnaeus) and moose and is the site of a renowned long-term study of their population dynamics (Robinson et al. 2019, Hoy et al. 2020). From the study's onset in 1958 through 2010, wolf abundance on the island has typically ranged between 12 and 30 individuals, while moose abundance has ranged between approximately 385 and 1,500 individuals. Our initial sampling period in 2010 followed a six-year low in moose abundance, with estimates of 385–650 individuals between 2006 and 2010. Coincidentally, wolf abundance was undergoing a long-term decline, eventually reaching two individuals between 2016 and 2018. Moose abundance consequently irrupted, reaching more than 2,000 individuals at the time of our 2019 sampling.

Here we report on the current (2019) status of ISRO forests, noting changes in metrics between 2010 and 2019. We discuss our findings in light of recent moose densities and provide context with respect to other drivers and stressors.

Methods

Sampling Design and Field Methods

Sampling Design

Sampling was conducted at ISRO from 12 June through 24 August 2019. Site selection was made in 2010 prior to the initial sampling event using a generalized random-tessellation stratified design (Stevens and Olsen 2000). This design ensured that our sites were both randomly located and spatially balanced throughout the park.

Basic Measurements: Trees, Groundlayer, and Coarse Woody Material

We sampled trees, seedlings, coarse woody material, herbs, and browse at each site using the Hybrid plot (Johnson et al. 2006, 2008) (Figure 2). Three 50-m parallel transects comprise the plot, with each in an east-west orientation and permanently marked with rebar sunk into the ground. We recorded the species, diameter at breast height (DBH), live/dead status, and damage or disease (see below) for all trees with a DBH ≥ 2.5 cm and standing within 3 meters of the central transect line (Sanders and Grochowski 2014b). The total area sampled for trees was 300 m² for each transect, or 900 m² for the entire plot.

We assessed the groundlayer in 1-m² quadrats placed every 5 m along each transect ($n = 30$ per plot). Within each quadrat, we recorded all herbaceous, vine, and shrub species present, allowing us to determine frequency for all species-plot combinations. We also counted seedlings, defined as tree species < 2.5 cm DBH, but at least 15 cm in height and showing evidence of growth from the previous year (thus, we did not assess the current year's seedlings). Some species we commonly encountered reproduce vegetatively (e.g., trembling aspen [*Populus tremuloides* Michx.] and red maple). Individual sprouts (i.e., both ramets and genets) were deemed "seedlings" if no aboveground connections between them and a parent tree were visible.

We assessed coarse woody material (CWM) using the planar intercept method (Brown 1974, Woodall and Monleon 2008). For pieces with decay class 1–4 (Woodall and Monleon 2008), we tallied pieces with a diameter at transect intersect ≥ 7.5 cm and length ≥ 0.9 m; for decay class 5, minimum size of inclusion was 7.5 cm at transect and 1.5 m in length. For all pieces, we recorded the decay class, and measured the large end diameter, small end diameter, and length. The latter was recorded only along the piece where the minimum diameter criterion was met.

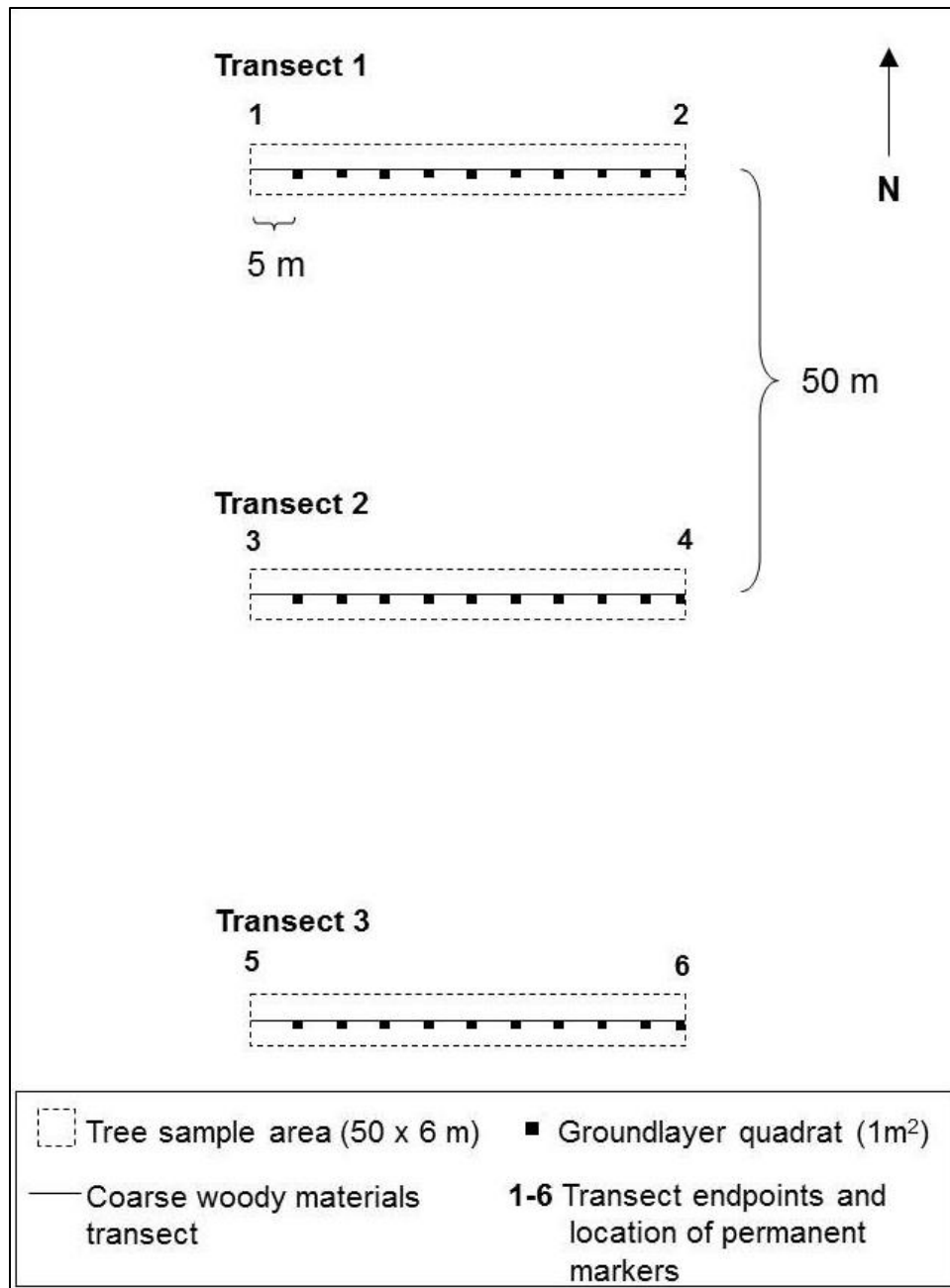


Figure 2. Great Lakes Network Hybrid plot showing three parallel transects (*solid lines*), tree sampling areas (*bounding dashed rectangles*), and quadrat locations (*solid squares*).

Browse

We examined browse pressure using two distinct measures. *Direct browse* is an assessment of moose browse visible on *woody* species. This includes bite marks and leaf stripping *directly evident and observable* on individual plants, appearing to occur on the current year's growth. Our methods did not include an assessment of bark stripping, nor did we include browse attributable to snowshoe hare (*Lepus americanus* Erxleben). Our sampling period extended over the course of the growing season. We acknowledge that this limitation introduces bias into our sampling, whereby those sites sampled

later in the season would be expected to show more browse than sites sampled earlier. Nonetheless, we feel that our assessments of woody browse are valuable in that they provide insight on general levels of pressure and on species preferences, but they should be interpreted with these qualifiers in mind.

Indirect browse measures were used to assess the impacts of herbivory on *herbaceous* species. This type of assessment measures changes in herbaceous demography, which are often only *indirectly observed over time* (Webster et al. 2001, Kirschbaum and Anacker 2005). In the case of white-tailed deer (*Odocoileus virginianus* Zimmermann) browse, these changes are typically manifested as fewer and smaller individuals of preferred herbaceous browse species (Anderson 1994, Webster et al. 2001, Knight et al. 2009) and are well-documented in the literature (Williams et al. 2000, Knight 2003). Although moose browse on forbs is also detailed in the literature (Belovsky and Jordan 1978, Edwards 1983, Rotter and Rebertus 2015), little detail is available regarding the long-term demographic impact on these species.

We assessed direct browse in 2-m² (0.8-m radius) circles centered every five meters along each of the three 50-m transects, for a total of 30 direct browse circles per plot, equal to a total sampling area of 60 m² per plot. Within each direct browse sampling circle, we recorded all woody species present within the browse zone—defined as the space between ground level and 3 m in height—and noted those circles where we observed any evidence of moose browse, and on which species in the circle this occurred.

We used direct browse data to calculate the Proportion of Browse (Frerker and Waller 2013) at two levels. At the site level, pooling across species, the numerator is the total of the 30 circles in which any browse was observed, regardless of species, while the denominator is the number of circles where any woody species were present. Here, we present mean site-level browse by forest type. At the species level, for each species, we divided the total number of circles in which we observed browse by the total number of circles where it was present. We present this data park-wide.

We assessed the indirect impacts (typically evidenced by fewer and smaller plants) of summer browse on herbs by several means. We used existing literature (Belovsky and Jordan 1978, Edwards 1983, Jordan and Moen 2014) and our personal knowledge to identify preferred browse species as those that are both relatively common in the park and favored by moose (Table 1). We identified the number of preferred herbaceous species at each site, as well as the abundance of preferred herbs, determined by the total number of preferred species-quadrat combinations at each site. For example, a site where *Aralia nudicaulis* L. (wild sarsaparilla) was present in 22 quadrats, *Clintonia borealis* Aiton (Raf) (bluebead lily) in 11 quadrats, and *Cornus canadensis* L. (bunchberry) in three quadrats would have three preferred browse species present at an abundance of 36 preferred species. To examine browse impacts on herb demographics (Koh et al. 2010, U.S. Department of Agriculture 2010, Wilbur et al. 2017), we selected two target taxa on which to collect additional data: *Aralia nudicaulis* and *Streptopus* Michx. spp. (twistedstalk)—both *S. lanceolatus* var. *roseus* (Michx.) Reveal (rosy twistedstalk) and *S. amplexifolius* (L.) DC. (clasping twistedstalk). For these taxa, in quadrats where they were present, we measured maximum height and noted whether the tallest individual was reproductive. For each target species, where present, at the site level, we calculated

the target herb frequency, based on the frequency of presence in the 30 quadrats; we then determined target herb maximum height, by calculating the site-level mean of the tallest individual (if present) in each quadrat.

Table 1. Preferred browse species at ISRO for calculating number of preferred herbs and abundance of preferred herbs.

Species	Common name
<i>Aralia nudicaulis</i> L. ^{a,b,c,d}	wild sarsaparilla
<i>Athyrium felix-fimina</i> ^b	ladyfern
<i>Chamerion angustifolium</i> ^{a,b}	fireweed
<i>Clintonia borealis</i> (Aiton) Raf. ^a	bluebead lily
<i>Cornus canadensis</i> L. ^{a,d}	bunchberry
<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs ^{b,d}	spinulose woodfern
<i>Dryopteris cristata</i> (L.) A. Gray ^b	crested woodfern
<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray ^b	intermediate woodfern
<i>Eurybia macrophylla</i> (L.) Cass. ^{a,b}	bigleaf aster
<i>Gymnocarpium dryopteris</i> (L.) Newman ^a	oakfern
<i>Heracleum sphondylium</i> ssp. <i>montanum</i> (Schleich. ex Gaudin) Brig. ^{a,b}	cowparsnip
<i>Impatiens capensis</i> Meerb. B	spotted touch-me-not
<i>Maianthemum canadense</i> Desf. ^a	Canada mayflower
<i>Maianthemum racemosum</i> (L.) Link ^e	false Solomon's seal
<i>Polygonatum pubescens</i> (Willd.) Pursh ^e	hairy Solomon's seal
<i>Prenanthes alba</i> L. ^b	rattlesnakeroot
<i>Streptopus amplexifolius</i> (L.) DC. ^{c,e}	clasping twistedstalk
<i>Streptopus lanceolatus</i> var. <i>roseus</i> (Michx.) Reveal ^{a,b,c,d}	rosy twistedstalk
<i>Thalictrum dasycarpum</i> Fisch. & Avé-Lall. ^b	purple meadowrue
<i>Trientalis borealis</i> Raf. ^{a,c}	starflower
<i>Trillium cernuum</i> L. ^b	Whip-poor-will flower
<i>Uvularia grandiflora</i> Sm. ^e	largeflower bellwort

^a Edwards (1983)

^b Jordan and Moen (2014)

^c GLKN, personal knowledge

^d Focal taxa for additional data collection

^e Belovsky and Jordan (1978)

Tree Health

We used an evidence-based approach to assess tree health, whereby we examined each tree for the presence of broad classes of disease, damage, or injury (U.S. Department of Agriculture 2010). These classes included dieback, epicormic sprouting, wilted foliage, defoliation, discolored foliage, insect sign, and human induced stress. If a tree exhibited symptoms of one of these primary classes, a further classification of the damage or disease was made based on predefined characteristics within each of the primary classes. For example, if a tree was classified as having discolored foliage, we would note whether this damage was in the form of (among other choices) marginal browning of the leaves, interveinal browning of the leaves, the leaves possessing a white coating, or a general yellowing of the leaves. This symptom-based assessment of damage and disease allows us to easily classify tree health issues, from which a diagnosis of the root cause can possibly be assigned upon further investigation. We feel that this symptom-based approach is more accurate than directly assigning a root cause to problems observed when at the field site. For some symptoms, there are dozens of possible causes and a pathologist or entomologist with specialization in the region would be needed to accurately assess the problem. Large-scale or persistent symptoms noted with this method can alert the park staff to potential disease or insect outbreaks, which would require further investigation by the park to identify the exact disease or pest.

Earthworm Impacts

We conducted earthworm assessments at vegetation monitoring sites to determine the extent of invasive earthworm presence at ISRO. We used a simple visual evaluation of the forest floor that followed methods developed for the Invasive Earthworm Rapid Assessment Tool (IERAT) (Loss et al. 2013). For this evaluation, we determined whether the forest floor was intact and layered, partially intact, or only present as the previous year's leaves. We noted and quantified the presence of earthworm casts, or excretions, as well as that of middens, or piles of cast material, created by the nightcrawler (*Lumbricus terrestris* L.) (Hale and Host 2005). At each site, we performed four assessments at separate locations we judged to be representative. From these evaluations, we ranked sites as earthworm-free, minimally invaded, moderately invaded, substantially invaded, or heavily invaded. For example, an earthworm-free sample has fresh litter, duff, and organic matter present, and no evidence of earthworm casts or middens. A moderately invaded sample has both fresh and decayed litter but no organic matter present, earthworm casts are present but not abundant, and earthworm middens may be present or absent. A heavily invaded sample would have fresh litter but no decayed litter and no organic matter, and earthworm casts and middens would be abundant (Loss et al. 2013). No earthworm assessments were carried out in 2010, so comparisons of earthworm impacts between the two time periods will not be made.

Plant Identification

We attempted to identify all plants to the species level while in the field. When this was not possible, we typically collected specimens for later identification. In some instances, it was not possible to distinguish between multiple species present in a park unless they were flowering or fruiting, which often was not the case. In these instances, we identified only to the genus or family level. Examples include *Carex* sp. L. (sedge) and Asteraceae (daisy family). For *Amelanchier* sp. Medik. (serviceberry), another genus that presented identification challenges, we assigned individual plants

to one of three groups of species complexes, with Group 1 containing *A. bartramiana* (Tausch) M. Roem.; Group 2 containing *A. arborea* (F. Michx.) Fernald, *A. laevis* Wiegand, and *A. interior* E.L. Nielsen; and Group 3 containing an uncertain number of species (Smith 2008). Finally, if a grass was not in flower or fruit, it was typically only possible to identify to the family (Poaceae) level. All nomenclature follows that of the Integrated Taxonomic Information System (2020).

Classifications and Summaries

Forest Type Classification

We classified all sites in the field using both the Kotar classification system (Burger and Kotar 2003) and the National Vegetation Classification System (NVCS) (The Nature Conservancy 1999). While both of these classification systems are in widespread use, they also both have notable drawbacks. For example, the Kotar system was developed for the Upper Peninsula of Michigan. While there are many similarities between that region and the park, there are also nuanced differences, which lead to poor fit for some sites. Further, this system focuses on mesic and dry-mesic sites and does not include wetter sites, such as cedar forests. The NVCS system was developed for the park based on field work in the early 2000s. As such, the forest has changed, in some places substantially, and numerous sites did not fit clearly into one of the preexisting categories. A further drawback of both systems is that their use resulted in our sites falling into a large number of types with only a small number of sites in each type.

We wanted to explore and summarize data in an efficient and practical manner, so after the field season, we grouped sites into similar, broad forest types using cluster analysis. We assigned sites to one of five broad forest types based on overstory composition using hierarchical cluster analysis (Maechler et al. 2019), followed by ancillary tests (indicator species analysis [De Cáceres and Legendre 2009] and silhouette width [Maechler et al. 2019]) to confirm group placement. We prepared our initial (2010) site $\times$ species matrix by including only those tree species present in at least 12% ($n = 6$) of sampling sites (McCune and Grace 2002). This community matrix consisted of importance values for each tree species at each site, defined as the mean of the relative frequency and relative basal area (Dyer 2006, Elliott and Swank 2008). We used the R statistical environment, version 3.5.2 (R Core Team 2020) for all analyses. We assigned forest type names based on the dominant tree species in these groups and confirmed group placement using non-metric multidimensional scaling to verify the legitimacy of these groups, again using R (Okasanen et al. 2020).

Coefficients of Conservatism and the Modified Floristic Quality Index

We identified the coefficient of conservatism (CoC) values for all species located during the sampling at ISRO (Voss and Reznicek 2012). These values range from 0–10 and reflect the likelihood a species will be present in habitats with alterations from pre-settlement conditions (Swink and Wilhelm 1994). Zero (0) reflects either non-native species or generalists with no faithfulness to any particular habitat, and 10 denotes conservative species found only in high-quality, non-degraded habitats. We then used CoC values to calculate the modified floristic quality index (mFQI) (Rooney and Rogers 2002, Sanders and Grochowski 2014a), where mFQI is simply the mean of the CoC values for all species present within that site. We then summarized mFQI by year and forest type.

Representation of Change

We present tree densities by diameter class and species to inform about successional projections. We also present the current status of select indices where data are not available or comparable between the two sampling periods.

For most indices, we calculated means and standard errors and show short-term change between the sampling periods via graphs and tables. Generally, we are interested in how these change between years, but also how they vary within forest types. These metrics include sapling density and site-level proportion browse. For other metrics (e.g., species-level data) we are mainly interested in the differences between years. Thus, for these metrics, we do not summarize by forest type.

We forgo statistical tests of change for this report. Specific tests of change with direct management relevance will be analyzed separately and presented elsewhere.

Results

All 52 sites originally sampled in 2010 were resampled in 2019, and an additional eight sites were added in 2019 (Figure 3). The taxa sampled included 22 trees species, 31 species of shrubs, 150 forb taxa, 46 graminoids, and 27 fern species (Appendix A). The sites were classified into five broad forest types (Figure 3). All reporting detailed here reflects only the 52 sites sampled in both years.

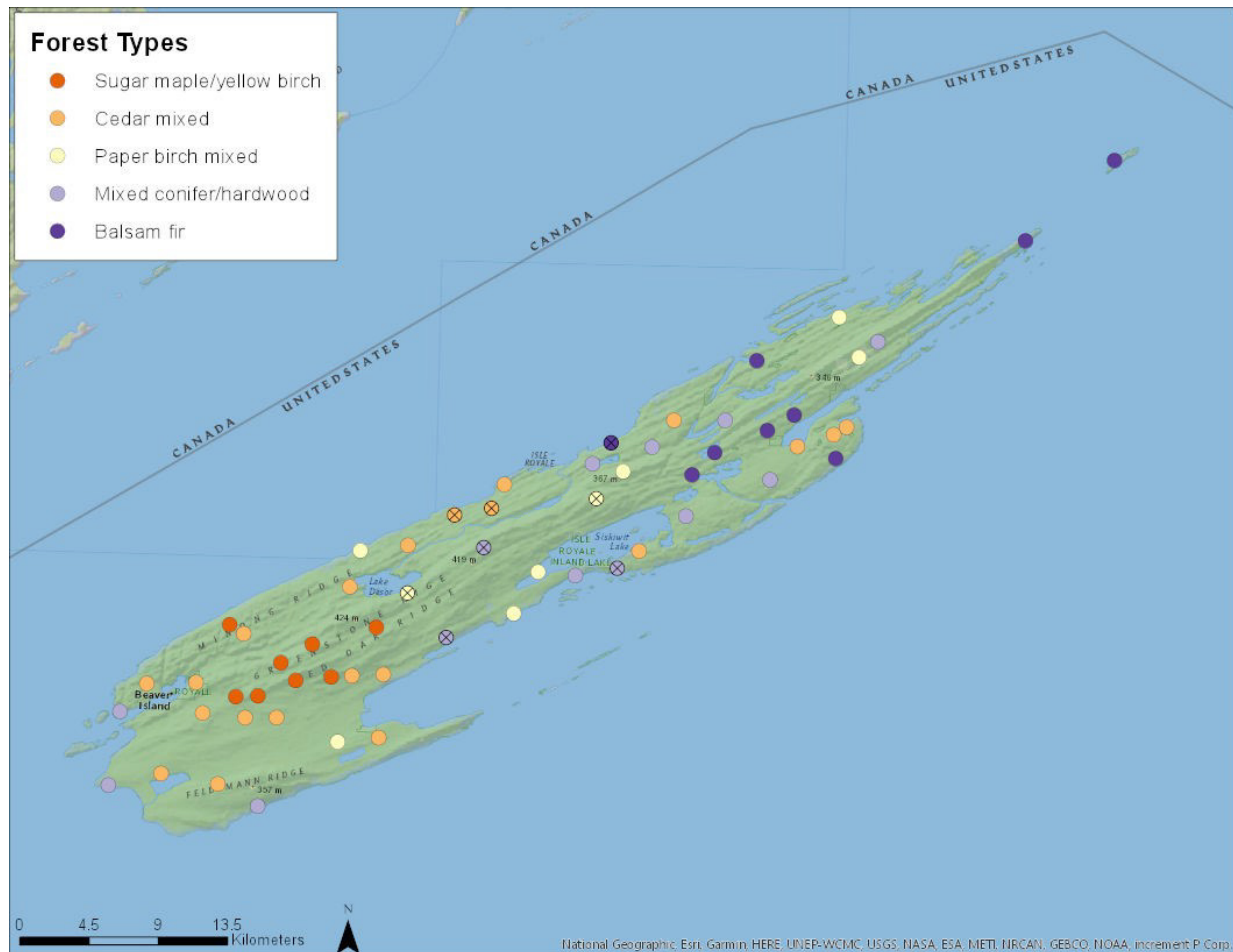


Figure 3. Locations and forest types of the 60 permanent forest monitoring sites at Isle Royale National Park. The 52 solid circles represent sites sampled both years. The eight circles designated with an X were sampled only in 2019. Circle color indicates forest type.

Successional Projections

Among conifers (Figure 4, left), cedar dominated the Sugar Maple-Yellow Birch and Cedar-Mixed forests on the western end of the island, with few other species present. In both Paper Birch Mixed forests and Mixed Conifer-Hardwood forests, white spruce was present in all size classes, though not abundant in small size classes. In both of these forest types, balsam fir was most common in smaller size classes. In Balsam Fir forests, balsam fir dominated all size classes with few other species present.

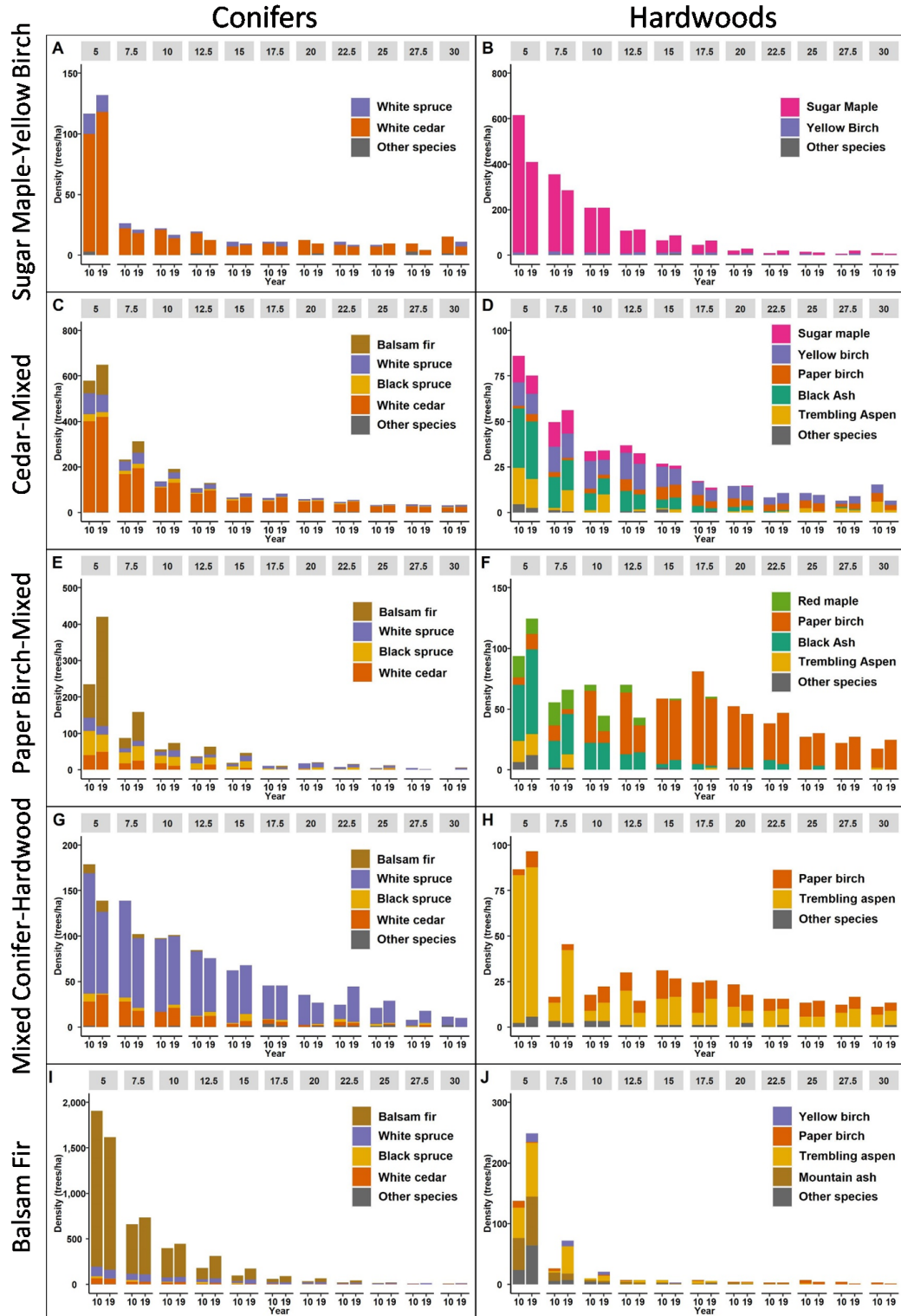


Figure 4. Diameter by size classes (in cm) for sites in five forest types, with conifers on left and hardwoods on the right. Note the difference in scales on the y-axes. Diameter at breast height classes across the top of each graph represent the maximum value in 2.5 cm classes.

Among hardwoods (Figure 4, right), sugar maple dominated all size classes shown in Sugar Maple-Yellow Birch forests. In this forest type, yellow birch was not abundant in small size classes, but was the most common species in classes >30 cm diameter at breast height (DBH). Density of hardwood species was low in Cedar-Mixed forests; both yellow and paper birch were common in all size classes. Black ash (*Fraxinus nigra* Marsh.) was the only species exhibiting higher densities in small size classes. In Paper Birch Mixed forests, paper birch was dominant only in mid-size and large size classes. Here, red maple (*Acer rubrum* L.) was present generally only in the small size classes. In both Mixed Conifer-Hardwood and Balsam Fir forests, stand types were composed primarily of conifers, while trembling aspen dominated the hardwood component across most size classes.

Short-Term Change

Live tree density (Figure 5, left) was generally higher in Balsam Fir forests, where it increased from $3,681 \pm 882$ trees/ha to $3,956 \pm 571$ trees/ha between the sampling periods. Density generally was also higher by the second sampling event for other forest types except Sugar Maple-Yellow Birch, where it dropped from $1,879 \pm 192$ trees/ha in 2010 to $1,631 \pm 157$ trees/ha in 2019. This pattern was also reflected in live tree basal area (Figure 5, right), which increased between the two sampling events in Balsam Fir forests (from 25.57 ± 3.4 to 28.39 ± 2.3 m²/ha) but declined in Sugar Maple-Yellow Birch forests (37.02 ± 4.0 to 32.92 ± 3.3 m²/ha).

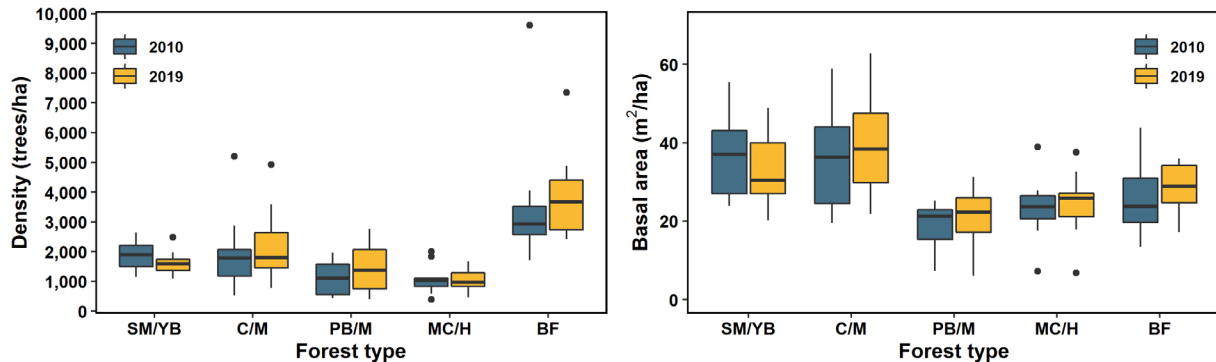


Figure 5. Live tree density (*left*) and basal area (*right*) by forest type. This figure incorporates individuals ≥ 2.5 cm DBH of all tree species. Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

For comparisons of seedling density, we excluded one site in Sugar Maple-Yellow Birch forest that had 198,000 seedlings/ha in 2010, or three times greater than the next most abundant site. Since we do not tally the current year's flush of seedlings, this was likely a reflection of a large flush the prior year that has persisted. Seedling density was generally lower in 2019. Most notably, at Sugar Maple-Yellow Birch sites, seedling density fell 26.2%; at Cedar-Mixed sites, it declined 25.8% (Figure 6, left). Density of small saplings (≥ 2.5 cm, < 5.0 cm DBH) was greatest in Balsam Fir forests both years. This was generally similar between years for all forest types except Sugar Maple-Yellow Birch, where it decreased from 731.9 ± 133.3 to 541.6 ± 118.4 saplings/ha (Figure 6, right).

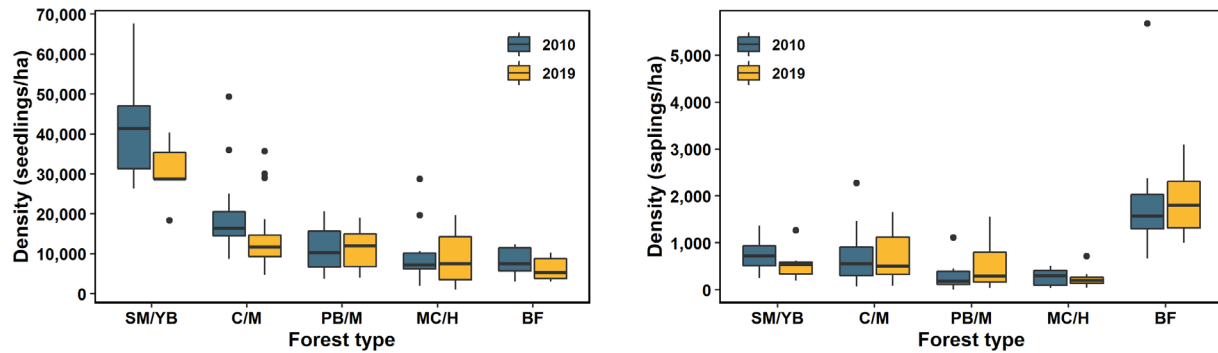


Figure 6. Seedling density by forest type (excluding site 4052) (*left*) and small sapling (≥ 2.5 cm DBH, < 5.0 cm DBH) density by forest type (*right*). Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Species-specific summaries parkwide across all forest types generally showed declines in seedling density between sampling events (Table 2). Most notably, sugar maple seedling density declined 51% to 13,460 seedlings/ha, while balsam fir seedling density declined nearly 15% to 2,793 seedlings/ha. Density of small saplings (from 2.5 cm DBH up to, but not including, 5.0 cm DBH) did not follow the same pattern. Of the eight species present at greater than 10 small saplings/ha in either year, five increased and three decreased. Specifically, sugar maple, white spruce, and black spruce declined 30.9, 22.4, and 41.8 saplings/ha, respectively.

Table 2. Seedling and small sapling density (m^2/ha) by species for both sampling years.

Species ^a		Seedlings		Small saplings	
Common Name	Latin Name	2010	2019	2010	2019
Balsam fir	<i>Abies balsamea</i>	3,282.05	2,792.88	291.45	307.91
Cedar	<i>Thuja occidentalis</i>	3,083.33	2,970.25	176.15	189.26
Sugar maple	<i>Acer saccharum</i>	27,352.94	13,459.77	92.31	63.79
White spruce	<i>Picea glauca</i>	630.95	577.90	80.26	62.31
Trembling aspen	<i>Populus tremuloides</i>	3,731.18	2,441.48	32.48	36.54
Black spruce	<i>Picea mariana</i>	809.52	800.00	24.79	14.53
Black ash	<i>Fraxinus nigra</i>	1,181.82	1,238.10	19.23	20.51
Showy mountain ash	<i>Sorbus decora</i>	2,525.64	1,933.33	8.37	13.28
Yellow birch	<i>Betula alleghaniensis</i>	1,633.33	1,407.41	5.98	6.62
Paper birch	<i>Betula papyrifera</i>	962.96	538.46	3.48	4.49
Red maple	<i>Acer rubrum</i>	2,200.00	3,700.00	2.99	1.71
Pin cherry	<i>Prunus pensylvanica</i>	1,583.33	1,444.44	2.14	9.84

^a Species for which no seedlings for small saplings were located either year are *Larix laricina*, *Pinus banksiana*, and *P. resinosa*.

Table 2 (continued). Seedling and small sapling density (m2/ha) by species for both sampling years.

Species ^a		Seedlings		Small saplings	
Common Name	Latin Name	2010	2019	2010	2019
Mountain maple	<i>Acer spicatum</i>	2,483.87	2,267.43	1.41	1.10
White pine	<i>Pinus strobus</i>	0.00	0.00	0.85	0.21
Chokecherry	<i>Prunus virginiana</i>	1,000.00	1,466.67	0.00	0.00
Red oak	<i>Quercus rubra</i>	333.33	333.33	0.00	0.00

^a Species for which no seedlings for small saplings were located either year are *Larix laricina*, *Pinus banksiana*, and *P. resinosa*.

Coarse Woody Material and Standing Dead Trees

In general, measures of coarse woody material varied somewhat between forest types but changed little between sampling periods. Density of pieces was low in Sugar Maple-Yellow Birch forests but increased between years from 490.1 ± 98.1 to 591.7 ± 123.3 pieces/ha. Likewise, in Paper Birch Mixed forests, density increased from 705.8 ± 141.0 to 976.1 ± 119.0 pieces/ha (Figure 7). The increase here is also reflected in the volume estimation, which increased 16% between the sampling events. Within forest types, biomass changed little between the sampling events. Large, advanced-decay pieces were high in forest types common in the west and west-central parts of the island (Sugar Maple-Yellow Birch and Cedar-Mixed) but changed little between the two sample years (Figure 7).

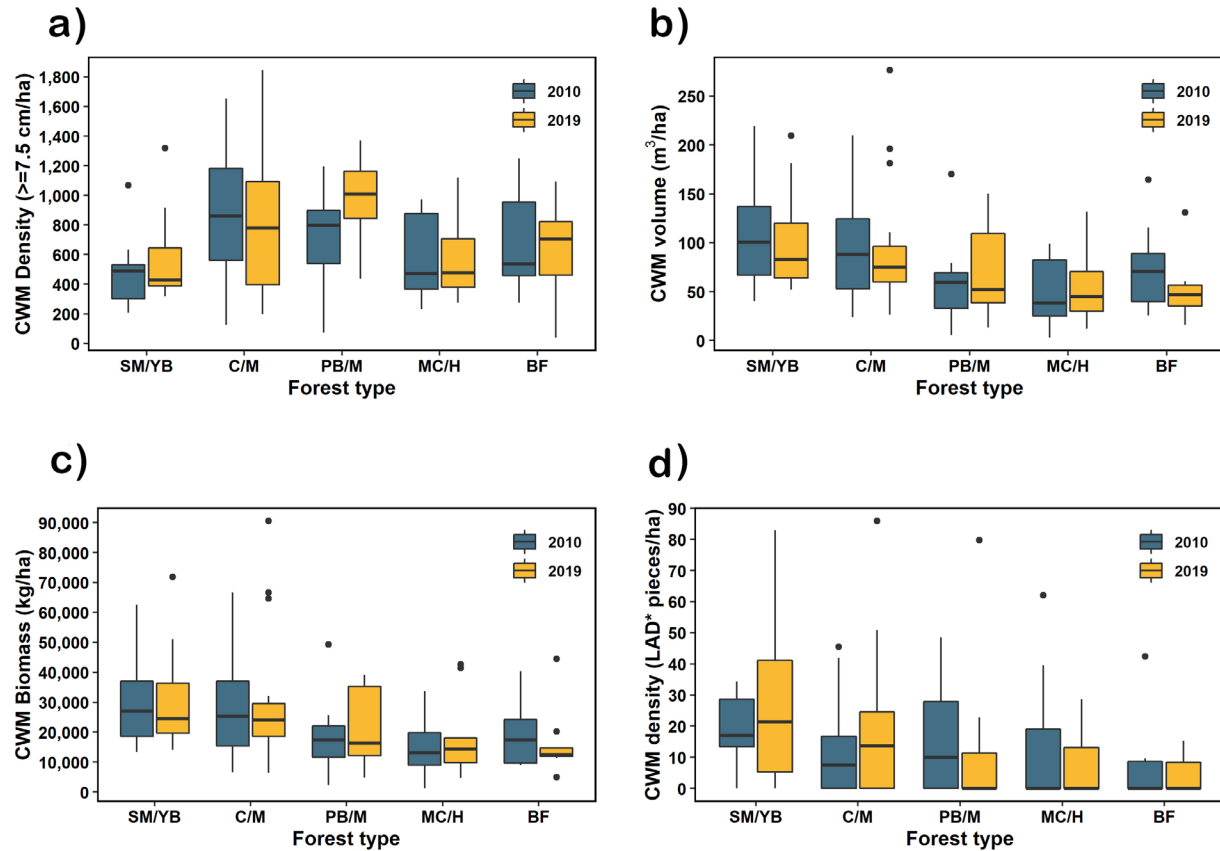


Figure 7. Coarse woody material by forest type and year: density (a), volume (b), biomass (c), and large, advanced decay(*), piece density (d). Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Density of large snags (standing dead trees) ≥ 30 cm DBH was generally similar between the sampling years in forest types, except for Paper Birch-Mixed forests, where it declined from 28.6 ± 14.3 to 19.04 ± 11.0 snags/ha (Figure 8, left). Basal area declined here as well, from 3.56 ± 2.1 to 2.59 ± 1.7 m^2/ha (Figure 8, right).

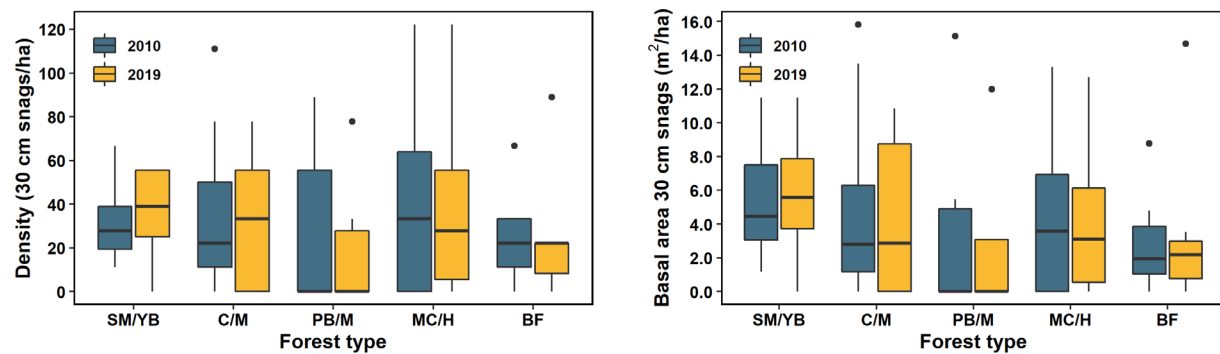


Figure 8. Density (left) and basal area (right) of snags ≥ 30 cm DBH for all forest types in both years. Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Browse and Disease

Site-level proportion browse (i.e., frequency of the 30 direct-browse circles in each site showing bite marks on woody individuals regardless of species) varied across forest types but was universally higher in 2019 compared with 2010 (Figure 9). Mean site-level proportion browse was highest in Sugar Maple-Yellow Birch sites, where 24.5% of direct browse circles had bite marks in 2019 (compared with 2.1% in 2010).

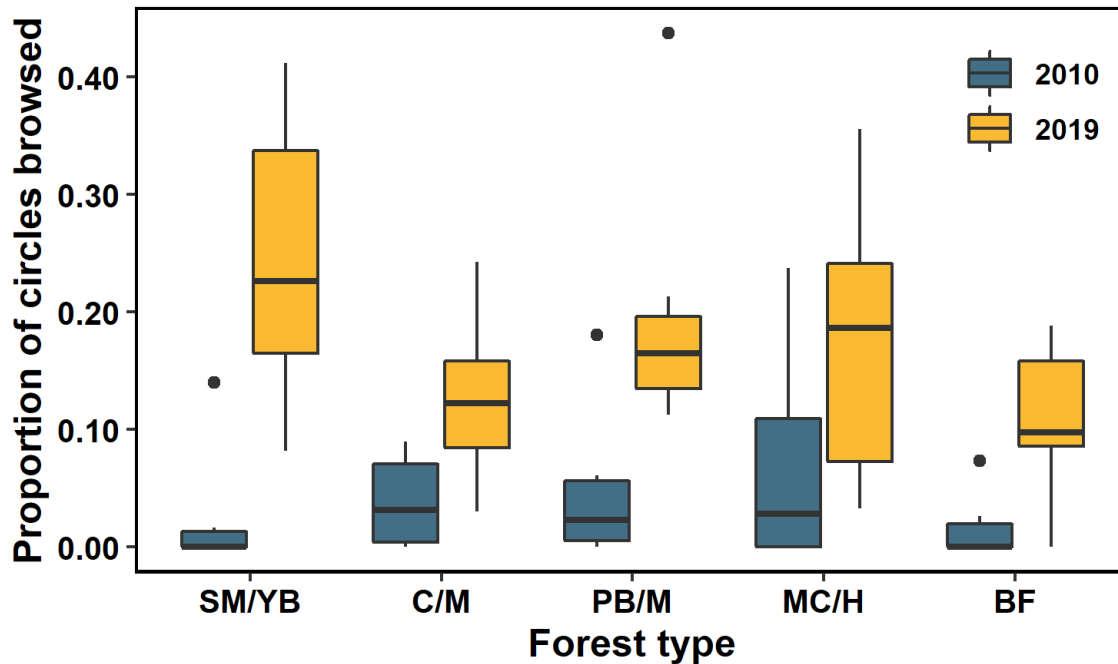


Figure 9. Proportion of browse in thirty 2-m² browse circles in each site. Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Parkwide, species-level assessments of browse on woody species were much higher in 2019 (Table 3). For the 2019 assessment, the greatest browse pressure was seen on three species of *Cornus* L. (dogwood), where the frequency of circles browsed at sites for *C. alternifolia* L. f. (alternate-leaf dogwood), *C. rugosa* L. (round-leaf dogwood), and *C. sericea* L. (redosier dogwood) were 0.80, 0.52, and 0.45, respectively. Eleven shrub species had browse in at least 10% of circles (Table 3). For tree species, red maple and sugar maple experienced the greatest browse pressure. As with shrubs, 11 species of trees experienced browse in at least 10% of circles in 2019 (Tables 3 & 4).

Table 3. Park-wide species-level proportion browse in 2010 and 2019 on shrubs. Taxa are sorted based on 2019 browse frequency. This table reflects all sites, both years, including those sites sampled only in 2019.

Species ^a	2010	2019
<i>Cornus alternifolia</i>	0.00	0.80
<i>Cornus rugosa</i>	0.00	0.52
<i>Cornus sericea</i>	0.15	0.45
<i>Corylus cornuta</i>	0.12	0.41
<i>Amelanchier</i> sp. (Grp. 3)	0.23	0.32
<i>Viburnum edule</i>	0.06	0.25
<i>Amelanchier</i> sp.	0.00	0.20
<i>Diervilla lonicera</i>	0.04	0.18
<i>Amelanchier</i> sp. (Grp. 2)	0.06	0.16
<i>Alnus viridis</i> ssp. <i>crispa</i>	0.00	0.11
<i>Taxus canadensis</i>	0.00	0.10
<i>Lonicera canadensis</i>	0.01	0.09
<i>Alnus incana</i> ssp. <i>rugosa</i>	0.02	0.07
<i>Lonicera hirsuta</i>	0.00	0.06
<i>Ribes triste</i>	0.00	0.06
<i>Rosa acicularis</i>	0.00	0.04
<i>Rubus parviflorus</i>	0.01	0.04
<i>Lonicera dioica</i>	0.00	0.04
<i>Rubus sachalinensis</i> var. <i>sachalinensis</i>	0.00	0.01
<i>Rhus typhina</i>	1.00	0.00

^a There was no recorded browse on 20 shrub taxa in either year: *Arctostaphylos uva-ursi*, *Juniperus communis* var. *depressa*, *Lonicera involucrata*, *Oplopanax horridus*, *Rhamnus alnifolia*, *Rhododendron groenlandicum*, *Ribes glandulosum*, *Ribes hirtellum*, *Ribes hudsonianum*, *Rosa blanda*, *Rubus flagellaris*, *Rubus hispidus*, *Rubus pubescens*, *Salix* sp., *Sambucus racemosa*, *Shepherdia canadensis*, *Vaccinium angustifolium*, *Vaccinium macrocarpon*, *Vaccinium myrtilloides*, *Viburnum opulus* var. *americanum*.

Table 4. Park-wide species-level proportion browse in 2010 and 2019 on trees. Taxa are sorted based on 2019 browse frequency. This table reflects all sites, both years, including those sites sampled only in 2019.

Species ^a	2010	2019
<i>Acer rubrum</i>	0.05	0.40
<i>Acer saccharum</i>	0.01	0.35
<i>Abies balsamea</i>	0.01	0.28
<i>Prunus virginiana</i>	0.02	0.24
<i>Betula alleghaniensis</i>	0.10	0.23
<i>Sorbus decora</i>	0.08	0.22
<i>Acer spicatum</i>	0.02	0.19
<i>Betula papyrifera</i>	0.19	0.18
<i>Populus tremuloides</i>	0.05	0.15
<i>Prunus pensylvanica</i>	0.00	0.11
<i>Fraxinus nigra</i>	0.00	0.10
<i>Picea mariana</i>	0.00	0.05
<i>Thuja occidentalis</i>	0.00	0.02
<i>Picea glauca</i>	0.00	0.00
<i>Larix laricina</i>	0.00	0.00
<i>Pinus banksiana</i>	0.00	0.00
<i>Pinus strobus</i>	0.00	0.00
<i>Populus grandidentata</i>	0.00	0.00
<i>Quercus rubra</i>	0.00	0.00

^a There was no recorded browse on six tree species in either year: *Larix laricina*, *Picea glauca*, *Pinus banksiana*, *Pinus strobus*, *Populus grandidentata*, *Populus balsamifera*, *Quercus rubra*.

Of the 19 herbaceous species identified as preferred by moose, the mean number present in sites was generally similar across forest types, except Sugar Maple-Yellow Birch, where it was low and further declined from 7.0 ± 0.85 to 5.87 ± 0.90 preferred species/site (Figure 10, left). The abundance of preferred herbaceous species, measured as the number of preferred species-quadrat combinations, was universally lower across all forest types (Figure 10, right). This was most notable in the forest types common on the west side of the island, where abundance declined from 49.2 ± 11.3 to 30.5 ± 7.6 preferred species (38% decline), and in Cedar-Mixed forests, where the number of preferred species was reduced from 104.6 ± 5.5 to 81.3 ± 4.8 per site (22% decline).

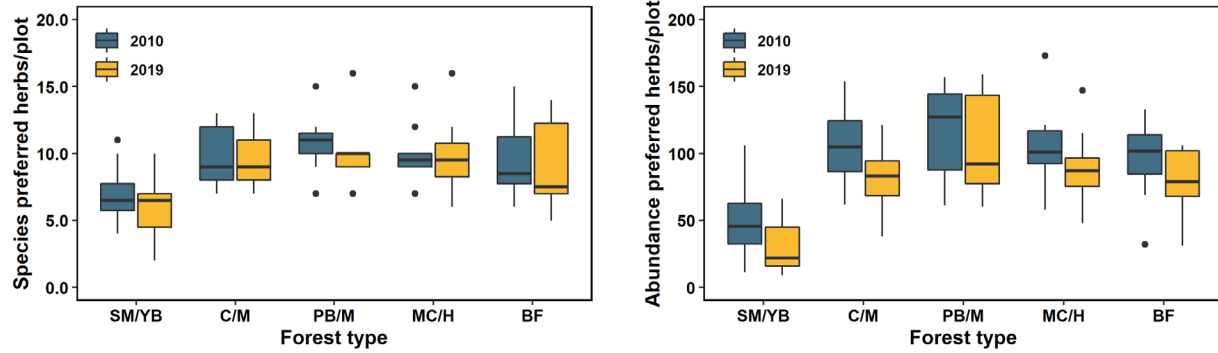


Figure 10. Number of preferred browse species (*left*) and abundance of preferred browse species (*right*) in sites for all forest types in both years. Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Our two target understory taxa for additional measurements were *Aralia nudicaulis* and *Streptopus* spp. In 2010, *Aralia nudicaulis* was present in groundlayer quadrats at all 52 sites, but only at 50 of those in 2019. Where present, frequency of *A. nudicaulis* was lower in all forest types but particularly in Balsam Fir forest sites, where its frequency in quadrats declined 47% from 0.60 ± 0.1 to 0.34 ± 0.1 (Figure 11, left). The maximum height of *A. nudicaulis* in quadrats where present did not change appreciably between the two sampling events (Figure 11, right).

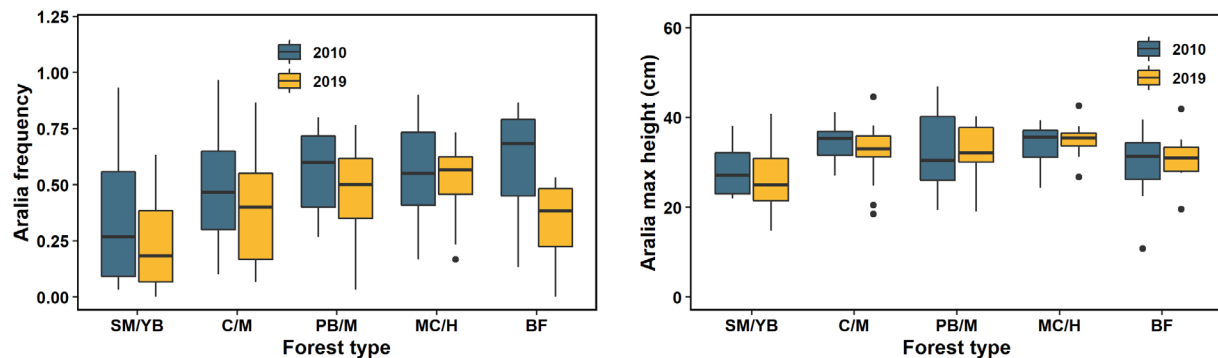


Figure 11. Frequency of *Aralia nudicaulis* within the 30 groundlayer quadrats in each site (*left*), and maximum height of *A. nudicaulis* where present (*right*). Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Streptopus spp. were present in groundlayer quadrats in only 47 of the 52 sites in 2010 and in 44 sites in 2019. Frequency of *Streptopus* spp. was lower across all forest types, most notably in the forest types dominant on the west side of the island. In Sugar Maple-Yellow Birch forest sites, this declined from 0.22 ± 0.9 to 0.04 ± 0.03 , while in Cedar-Mixed forests it decreased from 0.23 ± 0.05 to 0.10 ± 0.30 (Figure 12, left). In those sites where present, maximum height declined in all forest types (Figure 12, right), but was most prominent in forest types that dominate the west side. In Sugar Maple-Yellow Birch forests, this declined from 18.11 ± 2.2 cm to 12.8 ± 2.1 , while in Cedar-Mixed

forests it decreased from 19.12 ± 8.1 to 15.17 ± 2.0 (Figure 12, right). No consistent damage or disease was noted in any one forest type or tree species.

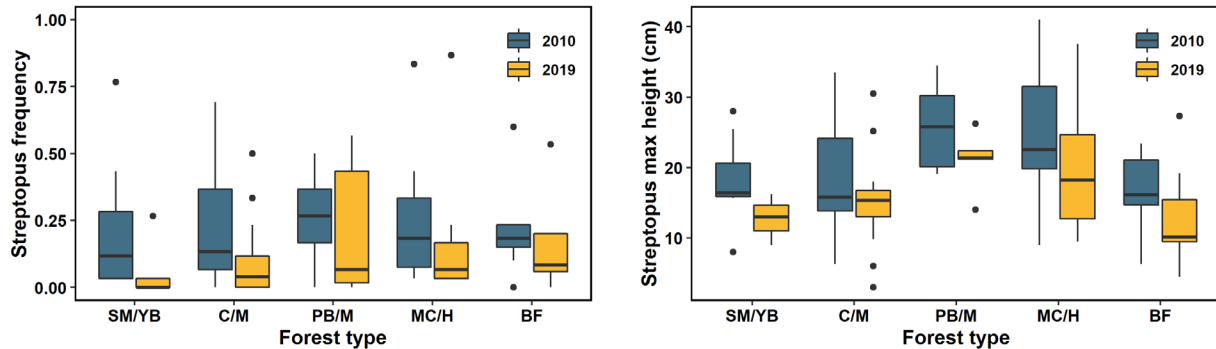


Figure 12. Frequency of *Streptopus* spp. within the 30 groundlayer quadrats in each site (*left*), and maximum height of *Streptopus* spp. where present (*right*). Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Community Indices

Species richness was universally lower in 2019, most notably in Sugar Maple-Yellow Birch sites where richness fell 20% from 49.3 ± 4.6 to 39.3 ± 3.3 taxa/site and in Paper Birch-Mixed sites where it dropped 6.6% from 69.4 ± 2.7 to $67.9.6 \pm 3.1$ taxa/site (Figure 13, left). With the exception of Balsam Fir forests, the site-level mean coefficient of conservatism was also generally the same between sampling years (Figure 13, right).

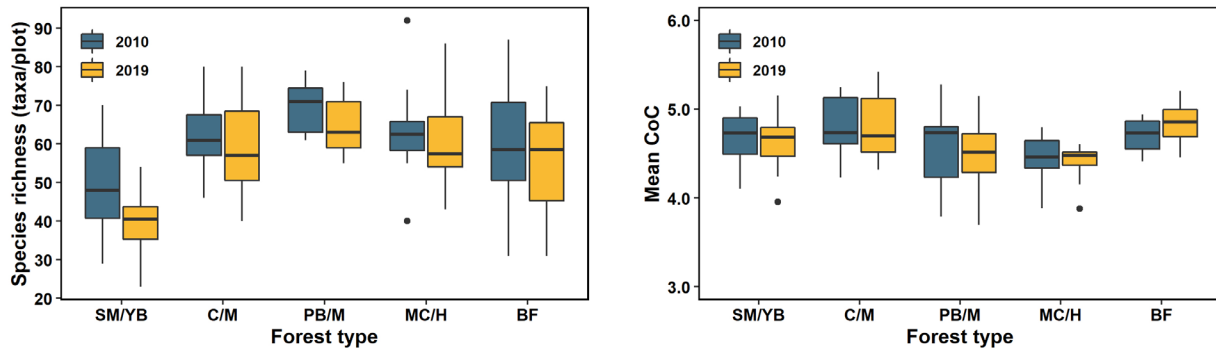


Figure 13. Taxa richness (*left*) and Mean CoC (*right*) for all forest types in both years. Data does not include *Carex* spp. or Poaceae. Mean CoC value for species present in sites (*right*). Forest type abbreviations are: SM/YB: Sugar Maple-Yellow Birch; C/M: Cedar-Mixed; PB/M: Paper Birch-Mixed; MC/H: Mixed Conifer-Hardwood; BF: Balsam Fir.

Earthworm Impacts

Impacts of earthworms varied greatly throughout the park with no evident pattern. Eleven sites were earthworm-free, while six were heavily invaded (Figure 14, Table 5).

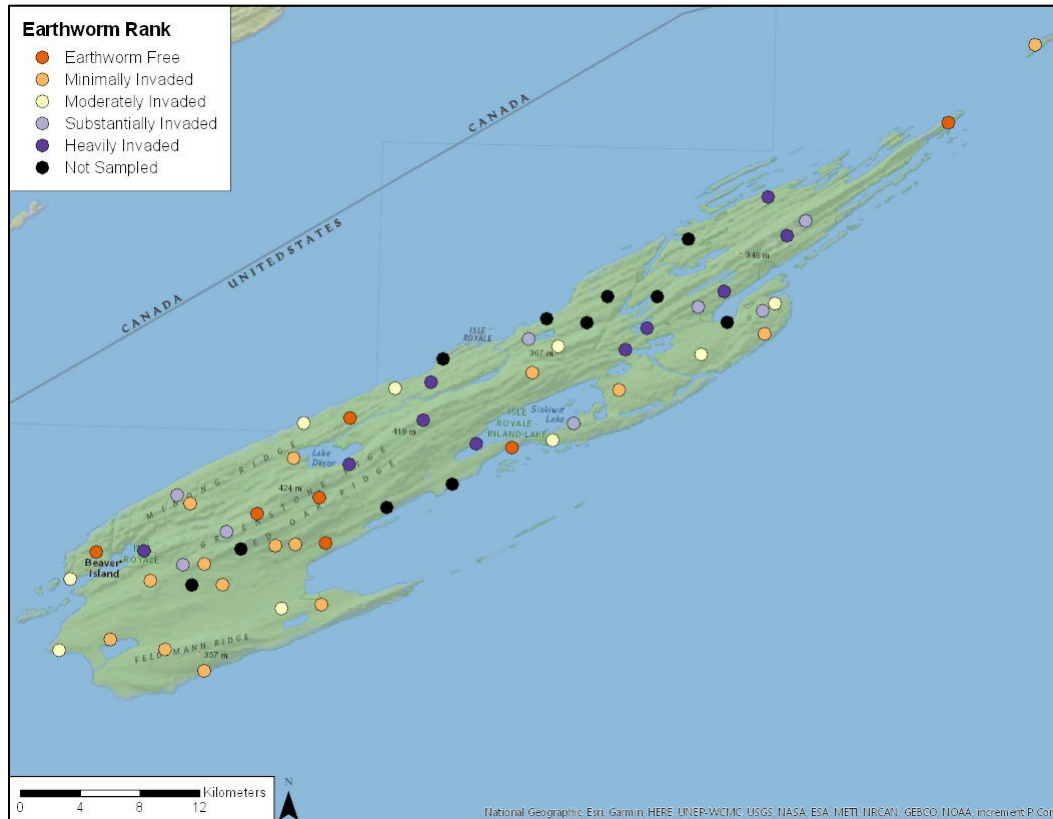


Figure 14. Earthworm invasion ranks at each site in 2019. These designations show the highest level of impairment of the four assessments completed at each site.

Table 5. Classification of sites into categories denoting severity of earthworm invasion. For severity, we used the most severe (i.e., “worst”) classification of the four samples collected at each site. Eleven sites were not assessed due to time constraints.

Habitat	Severity of Invasion				
	Earthworm-free	Minimally invaded	Moderately invaded	Substantially invaded	Heavily invaded
Sugar maple-yellow birch	2	2	0	3	0
Cedar-mixed	2	8	1	1	2
Paper birch mixed	1	2	5	0	3
Mixed conifer-hardwood	1	1	3	3	3
Balsam fir	1	2	0	1	2

Discussion

Changes and patterns in tree density largely reflect recent (previous 15 years) moose density. Low moose density on the island from 2006 through 2011 has allowed a modest recovery of trembling aspen. While park-wide trembling aspen density increased 29% (data not shown), most of this is in size classes 5–7.5 cm DBH (a 7.7-fold increase, from 2.7 to 20.9 trees/ha) and 7.5–10 cm DBH (3.7-fold increase from 1.9 to 7.1 trees/ha). Low browse pressure during the earlier six-year period has allowed saplings to grow beyond the browse zone. In the smallest size class (2.5–5.0 DBH), aspen density increased only 12.3% between sampling events, from 32.5 to 36.5 trees/ha, reflecting the recent irruption in moose abundance. This pattern was most notable in Cedar-Mixed sites (see Figure 4, panel D) and in Mixed Conifer-Hardwood sites (see Figure 4, panel H).

Proportion browse recorded in 2019 was highest in Sugar Maple forests (see Figure 9), which are limited to the island's west side. Here, density of small saplings (2.5–5.0 cm DBH) of sugar maple fell 33.2% from 2010 to 2019 (see Figure 4, panel B), while smaller size class balsam fir remained, in effect, absent from the landscape (see Figure 4, panel A).

Moose browse preferences vary by tree species (see Table 3), and our results suggest relatively low regeneration of key tree species such as trembling aspen, balsam fir, and yellow birch. Inhibition of overstory regeneration can have cascading ecosystem effects including impacts to nutrient cycling (McInnes et al. 1992, Pastor and Naiman 1992, Christenson et al. 2014), loss of wildlife habitat (Rae et al. 2014), and altered forest structure (Connor et al. 2000). Indeed, “spruce savannas” have been identified (Rotter and Rebertus 2015) as a consequence of long-term moose browsing pressure. In addition, we noted several areas in the vicinity of Lake Desor with senescing paper birch and few other overstory trees, while dense bracken fern blanketed the understory. Once this birch falls, the successional trajectory (for both the overstory and understory) remains unclear.

The changes to the herbaceous layer between 2010 and 2019 were striking. The declines in species richness, particularly in Sugar Maple-Yellow Birch forests, further attest to moose impacts, although the herbivory by snowshoe hare may be as great, or greater. For moose, the extent to which they impact the herbaceous layer, and the mechanisms by which this occurs, are unclear. Gilliam and Roberts (2003) noted that under high moose browse pressure, the impacts to the herbaceous layer are largely indirect and not attributable to feeding. This supports McInnes et al. (1992) who found greater herbaceous biomass and species richness outside of exclosures on Isle Royale than within them, citing the removal of competing shrub and tree biomass as the reason. This study was conducted in boreal stands, while the changes we observed were greatest in broadleaf-dominated sites. Rotter and Rebertus (2015) found species richness at ISRO was greater in highly-browsed “spruce savannas,” than in reference stands with closed canopies. In the savannas, 40% of cover was by old-field species.

Although moose browse on terrestrial herbs has not been widely reported in the literature, exceptions do exist. McMillan (1953) examined feeding preferences of moose in Yellowstone National Park. He found 7.8% of observations of moose food utilization occurred on terrestrial herbs, with the remaining percentages on shrubs and aquatic herbs. Belovsky and Jordan (1978) developed a time-

energy budget for moose on Isle Royale; they quantified browse on terrestrial herbs (176.3 kg/km²) as representing 7.3% of their diet. Edwards (1978) noted moose browse on ISRO for several terrestrial herbaceous species including *Aralia nudicaulis*, *Clintonia borealis*, *Streptopus roseus* [recognized here as *Streptopus lanceolatus* var. *roseus*], *S. amplexifolius*, *Heracleum lanatum* [recognized here as *Heracleum sphondylium* ssp. *montanum* (Schleich. Ex Gaudin) Briq (cow parsnip)], *Maianthemum canadense*, *Gymnocarpium dryopteris*, *Geocaulon lividum* (Richardson) Fernald (false toadflax), *Fragaria virginiana* Duchesne (wild strawberry), and *Actaea rubra* (Aiton) Willd. (red baneberry). These species leaf out early and are primarily browsed in May and early June before woody browse material is readily available. She noted that most understory herbs were rarely eaten following shrub and tree leafout, although two exceptions are *Aster macrophyllus* L. [here recognized as *Eurybia macrophylla* (L.) Cass. (bigleaf aster)] and *Epilobium angustifolium* L. [here recognized as *Chamerion angustifolium* (L.) Holub (fireweed)], which are consumed by moose throughout the growing season. Herbaceous feeding preferences are likely influenced by multiple factors. Edwards (1978) reported that the likelihood of an individual plant being eaten depended on its nearest neighboring plant. She further noted that prior to woody species leafout, she observed moose preferentially feeding on *Eurybia macrophylla*, while large numbers of other herbs were incidentally consumed (Joan Edwards, personal communication, 1 March 2021).

Teasing apart the impacts to terrestrial herbs from moose with those of snowshoe hare are difficult. It may not be possible from our work because they feed on many of the same species during the same time period. Wolff (1978) identified annual patterns of hare browse in central Alaska and found that herbs composed 49.4% of their diet in May, but less than 10% during the rest of the year. Taxa identified as eaten included *Equisetum* spp. L. (horsetail) (31% of May diet) and *Chamerion angustifolium* 11% of May diet). Belovsky (1984) examined snowshoe hare feeding and nutrition requirements on Isle Royale and noted the herbs consumed to include *Dryopteris spinulosa* [here recognized as *Dryopteris* sp. Adans. (woodfern)], *Streptopus lanceolatus* var. *roseus*, *A. nudicaulis*, *Clintonia borealis*, and *Equisetum* spp.

We distinguished between moose and hare browse on woody browse assessments and did not record the latter. Typically, hare browse is evidenced as a clean cut across the stem at a 45° angle to its long axis. While Belovsky and Jordan (1978) noted this is also possible on herbaceous material, including leaf petioles and herb stalks, we did not find this to be realistic or even possible on non-woody material. The best way to distinguish herbaceous species use between moose and hare is via exclosures, where moose do not have access. Indeed, four exclosures (232.3 m² each) are present on the island, with one each near Daisy Farm, Windigo, Siskiwit Lake, and Siskiwit Camp. Risenhoover and Maass (1987) assessed differences between woody vegetation within and outside of the exclosures, but we are unaware of any current assessment of these differences, nor are we aware of attempts to distinguish browse on herbaceous species by these two herbivores.

Snowshoe hare abundance generally follows 9- to 11-year cycles in boreal forests (Krebs et al. 1986, Keith 1990), with this cycle largely regulated by predators (Krebs et al. 1986, Krebs et al. 1995, Boonstra et al. 1998). On Isle Royale, the main predator of hare is the red fox (*Vulpes vulpes* Linnaeus). Estimates of fox abundance have been made on the island since 1972, while indices of

hare abundance have been compiled since 1974. From the study onset through 2008, this index, determined by the number of hares seen per 100 km of summer hiking, has typically remained below five. A spike in abundance began in 2009, with the index peaking in 2012 and 2013 at slightly more than 30 in both years. From 2016 through 2018, this index remained near five (Hoy et al. 2020). The abundance of snowshoe hares is believed to be an indirect result of low wolf density. Fewer wolves meant fewer moose kills to scavenge on, so the red fox population declined (Vucetich and Peterson 2013). High hare abundance could explain the decline of spruce in small size classes (see Table 2 and Figure 4), as hare browse of spruce is well-documented (Cater and Chapin III 2000, Olnes and Kielland 2017, Olnes et al. 2019).

The forests on Isle Royale face other threats besides browse, foremost among them being climate change and invasive species. Boreal forests occupy the island's east side, as well as around the perimeter, dominated by balsam fir and white spruce, with a lesser amount of black spruce. This is maintained largely by the moderating effect of Lake Superior. As the lake continues to warm (Austin and Colman 2007, 2008), habitat for boreal species may shift outside of the park (Monahan and Fisichelli 2014). As both air and water temperatures rise, boreal cover could decrease.

The greatest invasive plant threat may come from bird-dispersed species. *Rhamnus cathartica* L. (European buckthorn), and *R. frangula* L. (glossy buckthorn) are both aggressive shrubs with native distributions in Europe. *Rhamnus cathartica* is now established in Minnesota on the Superior National Forest near Babbitt, as well as in Silver Bay and near Little Marais (EDDMapS 2021). *Rhamnus frangula* now grows in several localities around Lake Superior including near Silver Bay, Minnesota, in Tettegouche State Park and on the Keweenaw Peninsula, including in Houghton, Michigan. Non-native honeysuckles (*Lonicera* sp. L.) also pose a serious threat. Notably, *Lonicera tatarica* L., native to Siberia and eastern Asia, has established populations in both St. Louis County, Minnesota, and Houghton County, Michigan. Any seeds deposited on the island will likely not be near a trail or populated area; thus, a population could become well-established over the course of a few years before it becomes known to managers.

Isle Royale forests are also facing the imminent threat of emerald ash borer (*Agrilus planipennis* Fairmaire). This insect, which is largely dispersed by humans via movement of firewood, is now present in Thunder Bay, Ontario, and Houghton, Michigan. While not abundant on the island, black ash is widespread, often co-occurring with cedar in wet pockets on the west side, and in low-lying swales between ridges in the east. Black ash also often grows in very wet areas with no other overstory species. Where it occurs, loss of black ash could result in complete loss of the overstory.

Management Recommendations

If park management goals are to maintain the character of park forests, herbivore density must be kept low. A wolf reintroduction program began in late 2018; to date, 19 wolves have been captured from multiple mainland locations in Michigan, Minnesota, and Ontario, Canada, and released on the island. This program is a multi-year effort and assessment of its success by managers is ongoing.

Park managers may also wish to study the four moose exclosures on the island to determine which herbaceous species are present and at what densities. This would help tease apart differences in species preferences between moose and hare and provide estimates of browse pressure from hare.

The island supports numerous rare, herbaceous species, including both western and Arctic disjuncts (Slavick and Janke 1987, Sanders et al. 2020) and rare orchids and sedges (MNFI 2021). The park also supports the western disjunct shrub *Lonicera involucrata* (Richardson) Banks ex Spreng. (involucre honeysuckle), for which Isle Royale and Bayfield County, Wisconsin, are the only two locations in the United States, east of the Rocky Mountains. Managers may wish to conduct searches in the Daisy Farm and Three Mile area and, if found, fence in and monitor individuals.

The park should continue monitoring for invasive plants. Currently, the park regularly checks campsites, focusing most on those on the island's perimeter, where recreational boaters may be most likely to introduce non-native material. As noted earlier, bird-dispersed species are a particular threat. It would be beneficial for park managers to develop a plan for removal and/or control of these species. Also posing a risk to park ecosystems is *Valeriana officinalis* L. (garden valerian). This species is known to have a large population on Belle Isle and is also known to grow on Mott Island. Removal of this species could allow the park to avoid long-term problems.

Currently, forests of Isle Royale are generally in good health, though facing numerous threats. If degraded, the resources needed for restoration will likely be prohibitive. Therefore, it behooves managers to work toward maintaining ecological diversity and function (Hisano et al. 2018) as a way to promote overall ecosystem resistance and resilience.

Literature Cited

- Anderson, R. C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* 4:104–109.
- Austin, J. A., and S. M. Coleman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. *Geophysical Research Letters* 34:L06604. Available at: [doi:10.1029/2006GL029021](https://doi.org/10.1029/2006GL029021).
- Austin, J. A., and S. M. Colman. 2008. A century of temperature variability in Lake Superior. *Limnology and Oceanography* 53:2724–2730.
- Belovsky, G. E. 1984. Showshee hare optimal foraging and its implications for population dynamics. *Theoretical Population Biology* 25:235–264.
- Belovsky, G. E., and P. A. Jordan. 1978. The time-energy budget of a moose. *Theoretical Population Biology* 14:76–104.
- Blossey, B. 1999. Before, during and after: The need for a long-term monitoring in invasive plant species management. *Biological Invasions* 1:301–311.
- Boonstra, R., C. J. Krebs, and N. C. Stenseth. 1998. Population cycles in small mammals: The problem of explaining the low phase. *Ecology* 79:1479–1488.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16. Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Burger, T. L., and J. Kotar. 2003. A guide to forest communities and habitat types of Michigan. The Department of Forest Ecology and Management, University of Wisconsin-Madison, Madison, Wisconsin.
- Cater, T. C., and F. S. Chapin III. 2000. Differential effects of competition or microenvironment on boreal tree seedling establishment after fire. *Ecology* 81:1086–1099.
- Christenson, L. M., M. J. Mitchell, P. M. Groffman, and G. M. Lovett. 2014. Cascading effects of climate change on forest ecosystems: Biogeochemical links between trees and moose in the northeast USA. *Ecosystems* 17:442–457.
- Connor, K. J., W. B. Ballard, T. Dilworth, S. Mahoney, and D. Anions. 2000. Changes in structure of a boreal forest community following intense herbivory by moose. *Alces* 36:111–132.
- De Cáceres, M., and P. Legendre. 2009. Associations between species and groups of sites: Indices and statistical inference. *Ecology* 90:3566–3574.
- Dyer, J. M. 2006. Revisiting the deciduous forests of eastern North America. *Bioscience* 56:341–352.

- EDDMapS. 2021. Early Detection and Distribution Mapping System. The University of Georgia, Center for Invasive Species and Ecosystem Health. Available online at www.eddmaps.org/ (accessed 23 March 2021).
- Edwards, J. 1978. Moose-vegetation interactions at the northeastern end of Isle Royale National Park, Michigan. Dissertation. University of Michigan, Ann Arbor, Michigan.
- Edwards, J. 1983. Diet shifts in moose due to predator avoidance. *Oecologia* 60:185–189.
- Elliott, K. J., and W. T. Swank. 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecology* 197:155–172.
- Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2012. Climate and interrelated tree regeneration drivers in mixed temperate–boreal forests. *Landscape Ecology* 28:149–159.
- Frerker, K., and D. W. Waller. 2013. Comparing and evaluating methods used to assess the impacts of ungulate browsing in the Great Lakes Network national parks. Natural Resource Technical Report NPS/GLKN/NRTR—2013/680. National Park Service, Fort Collins, Colorado.
- Gilliam, F. S., and M. R. Roberts. 2003. *The Herbaceous Layer in Forests of Eastern North America*. Oxford University Press, New York, New York.
- Hale, C. M., and G. E. Host. 2005. Assessing the impacts of European earthworm invasions in beech-maple hardwood and aspen-fir boreal forests of the western Great Lakes region. Great Lakes Network Report GLKN/2005/11. National Park Service, Ashland, Wisconsin.
- Hisano, M., E. B. Searle, and H. Y. H. Chen. 2018. Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews* 93:439–456.
- Hoy, S. R., R. O. Peterson, and J. A. Vucetich. 2020. Ecological studies of wolves on Isle Royale: Annual report 2019–2020. Michigan Technological University, School of Forest Resources and Environmental Science, Houghton, Michigan.
- Integrated Taxonomic Information System (ITIS). 2020. ITIS online database. Available at: www.itis.gov (accessed 2 February 2020).
- Johnson, S. E., E. L. Mudrak, and D. M. Waller. 2006. A comparison of sampling methodologies for long-term monitoring of forest vegetation in the Great Lakes Network national parks. Great Lakes Network Report GLKN/2006/03. National Park Service, Ashland, Wisconsin.
- Johnson, S. E., E. L. Mudrak, E. A. Beever, S. Sanders, and D. M. Waller. 2008. Comparing power among three sampling methods for monitoring forest vegetation. *Canadian Journal of Forest Research* 38:143–156.

- Jordan, P. A., and R. A. Moen. 2014. A data collection protocol to analyze the impacts of moose and snowshoe hares on the woody vegetation of Isle Royale National Park. The University of Minnesota. NRRI Technical Report No. NRRI/TR-2013-44 Release 1.0. University of Minnesota, Duluth, Minnesota.
- Keith, L. B. 1990. Dynamics of snowshoe populations. *In* H. H. Genoways, editor. Current Mammalogy. Plenum Press, New York.
- Kirschbaum, C. D., and B. L. Anacker. 2005. The utility of *Trillium* and *Maianthemum* as phyto-indicators of deer impact in northwestern Pennsylvania, USA. *Forest Ecology and Management* 217:54–66.
- Knight, T. M. 2003. Floral density, pollen limitation, and reproductive success in *Trillium grandiflorum*. *Oecologia* 442:557–563.
- Knight, T. M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal* 29:110–116.
- Koh, S., D. R. Brazely, A. J. Tanentzap, D. R. Voigt, and E. Da Silva. 2010. *Trillium grandiflorum* height is an indicator of white-tailed deer density at local regional scales. *Forest Ecology and Management* 259:1472–1479.
- Krebs, C., B. Gilbert, S. Boutin, A. Sinclair, and J. Smith. 1986. Population biology of snowshoe hares. I: Demography of food-supplemented populations in the southern Yukon, 1976–1984. *Journal of Animal Ecology* 55:963–982.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. Sinclair, J. N. Smith, M. R. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- Loss, S. R., R. M. Hueffmeier, C. M. Hale, G. E. Host, G. Sjerven, and L. E. Frelich. 2013. Earthworm invasions in northern hardwood forests: A rapid assessment method. *Natural Areas Journal* 33:21–30.
- Maechler, M., A. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2019. Cluster: Cluster analysis basics and extensions. R package version 2.1.0.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM software, PO Box 129, Gleneden Beach, Oregon.
- McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73:2059–2075.
- McMillan, J. F. 1953. Some feeding habits of moose in Yellowstone Park. *Ecology* 34:102–110.
- MNFI (Michigan Natural Features Inventory). 2021. Michigan’s rare plants. Available at: mnfi.anr.msu.edu/species/plants (accessed 3 March 2021).

- Monahan, W. B., and N. A. Fisichelli. 2014. Climate exposure of U.S. national parks in a new era of change. *PLoS ONE* 9:e101302.
- Morrissey, R. C., N. T. King, J. R. Seifert, and D. F. Jacobs. 2012. Structural and compositional dynamics of a near-natural temperate deciduous forest in the central United States. *Journal of the Torrey Botanical Society* 139:379–390.
- Okasanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, H. H. Stevens, E. Szoecs, and H. Wagner. 2020. *Vegan: Community Ecology Package*. R package version 2.5-7. Available at: <https://CRAN.R-project.org/package=vegan>.
- Olnes, J., and K. Kielland. 2017. Asynchronous recruitment dynamics of snowshoe hares and white spruce in a boreal forest. *Forest Ecology and Management* 384:83–91.
- Olnes, J., K. Kielland, H. Genet, and R. Ruess. 2019. Postfire deciduous canopies drive patterns in snowshoe hare herbivory of regenerating black spruce. *Canadian Journal of Forest Research* 49:1392–1399.
- Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *The American Naturalist* 139:690–705.
- Pierce, A. R., G. Parker, and K. Rebenold. 2006. Forest succession in an oak-hickory dominated stand during a 40-year period at the Ross Biological Reserve, Indiana. *Natural Areas Journal* 26:351–359.
- Pureswaran, D. S., L. De Grandpré, D. Paré, A. Taylor, M. Barrette, H. Morin, J. Régnière, and D. D. Kneeshaw. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. *Ecology* 96:1480–1491.
- R Core Team. 2020. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: www.R-project.org.
- Rae, L. F., D. M. Whitaker, and I. G. Warkentin. 2014. Multiscale impacts of forest degradation through browsing by hyperabundant moose (*Alces alces*) on songbird assemblages. *Diversity and Distributions* 20:382–395.
- Risenhoover, K. L., and S. A. Maass. 1987. The influence of moose on the composition and structure of Isle Royale forests. *Canadian Journal of Forest Research* 17:357–364.
- Robinson, J. A., J. Räikkönen, L. M. Vucetich, J. A. Vucetich, R. O. Peterson, K. E. Lohmueller, and R. K. Wayne. 2019. Genomic signatures of extensive inbreeding in Isle Royale wolves, a population on the threshold of extinction. *Science Advances* 5:eaau0757.
- Rooney, T. P., and D. Rogers, A. 2002. The modified floristic quality index. *Natural Areas Journal* 22:340–344.

- Rotter, M. C., and A. J. Rebertus. 2015. Plant community development of Isle Royale's moose-spruce savannas. *Botany* 93:75–90.
- Sanders, S., and J. Grochowski. 2011. Implementation of a long-term vegetation monitoring program at Isle Royale National Park. Natural Resource Technical Report NPS/GLKN/NRTR—2011/387. National Park Service, Fort Collins, Colorado.
- Sanders, S., and J. Grochowski. 2013. The forests of Isle Royale National Park: Can we preserve this pristine wilderness in the face of climate change? *Natural Areas Journal* 33:66–77.
- Sanders, S., and J. Grochowski. 2014a. Alternative metrics for evaluating forest integrity and assessing change at four northern-tier U.S. national parks. *American Midland Naturalist* 171:185–203.
- Sanders, S., and J. Grochowski. 2014b. Forest vegetation monitoring protocol version 2.0: Great Lakes Inventory and Monitoring Network. Natural Resource Report NPS/GLKN/NRR—2014/799. National Park Service, Fort Collins, Colorado.
- Sanders, S., J. Kirschbaum, and S. E. Johnson. 2020. Response of 25 rare plant species on rocky shorelines of Isle Royale National Park in the face of extreme water levels in Lake Superior. *The Great Lakes Botanist* 59:159–177.
- Slavick, A. D., and R. A. Janke. 1987. The vascular flora of Isle Royale National Park. *The Michigan Botanist* 26:91–134.
- Smith, W. R. 2008. *Trees and Shrubs of Minnesota*. University of Minnesota Press, Minneapolis, Minnesota.
- Stevens, D. L., Jr., and A. R. Olsen. 2000. Spatially-restricted random sampling designs for design-based and model-based estimation. Pages 609–616 in G. B. M Heuvelink and M. J. P. M. Lemmens, editors. *Proceedings of the 4th International Symposium on Spatial Accuracy Assessment in Natural Resources and Environmental Sciences*, Amsterdam. Delft University Press.
- Swink, F., and G. Wilhelm. 1994. *Plants of the Chicago Region*, Fourth Edition. The Indiana Academy of Science, Lisle, Illinois.
- The Nature Conservancy. 1999. USGS-NPS Vegetation Mapping Program: Classification of the vegetation of Isle Royale National Park. Unpublished report submitted to the National Park Service. Available at: <https://irma.nps.gov/DataStore/Reference/Profile/2168776>.
- U.S. Department of Agriculture. 2010. IPED field guide pest evaluation and detection. Northeastern Areas State and Private Forestry, Newtown Square, Pennsylvania.
- Voss, E. G., and A. A. Reznicek. 2012. *Field Manual of Michigan Flora*. The University of Michigan Press, Ann Arbor, Michigan.

- Vucetich, J. A., and R. O. Peterson. 2013. Ecological studies of wolves on Isle Royale: Annual report 2012–2013. Michigan Technological University School of Forest Resources and Environmental Science, Houghton, Michigan.
- Webster, C. R., M. A. Jenkins, and G. R. Parker. 2001. A field test of herbaceous plant indicators of deer browsing intensity in mesic hardwood forests of Indiana, USA. *Natural Areas Journal* 21:149–158.
- Wilbur, H. M., K. L. Burke, R. B. Wilbur, and A. Rosenbauer. 2017. Recovery of the herb layer in a southern Appalachian forest following chronic herbivory by deer *Odocoileus virginianus*. *Castanea* 82:98–113, 116.
- Williams, C. E., E. V. Mosbacher, and W. J. Moriarity. 2000. Use of turtlehead (*Chelone glabra* L.) and other herbaceous plants to assess intensity of white-tailed deer browsing on Allegheny Plateau riparian forests, USA. *Biological Conservation* 92:207–205.
- Wolff, J. O. 1978. Food habits of snowshoe hares in interior Alaska. *The Journal of Wildlife Management* 42:148–153.
- Woodall, C. W., and V. J. Monleon. 2008. Sampling protocol, estimation, and analysis procedures for the down woody materials indicator of the FIA program. General Technical Report NRS-22. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania
- Woods, K. D. 2000. Dynamics in late-successional hemlock-hardwood forests over three decades. *Ecology* 81:110–126.

Appendix A. All species located during 2019 sampling.

Table A-1. Ferns and fern allies located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Dennstaedtiaceae	<i>Pteridium aquilinum</i>	western brackenfern
Dryopteridaceae	<i>Dryopteris carthusiana</i>	spinulose woodfern
Dryopteridaceae	<i>Dryopteris cristata</i>	crested woodfern
Dryopteridaceae	<i>Dryopteris intermedia</i>	intermediate woodfern
Equisetaceae	<i>Equisetum arvense</i>	western horsetail
Equisetaceae	<i>Equisetum palustre</i>	marsh horsetail
Equisetaceae	<i>Equisetum pratense</i>	meadow horsetail
Equisetaceae	<i>Equisetum scirpoides</i>	dwarf scouring-rush
Equisetaceae	<i>Equisetum sylvaticum</i>	woodland horsetail
Lycopodiaceae	<i>Huperzia lucidula</i>	shining clubmoss
Lycopodiaceae	<i>Lycopodium annotinum</i>	stiff clubmoss
Lycopodiaceae	<i>Lycopodium clavatum</i>	running clubmoss
Lycopodiaceae	<i>Lycopodium complanatum</i>	groundcedar
Lycopodiaceae	<i>Lycopodium dendroideum</i>	tree groundpine
Onocleaceae	<i>Matteuccia struthiopteris</i>	ostrich fern
Onocleaceae	<i>Onoclea sensibilis</i>	sensitive fern
Ophioglossaceae	<i>Botrychium virginianum</i>	rattlesnake fern
Osmundaceae	<i>Osmunda claytoniana</i>	interrupted fern
Osmundaceae	<i>Osmunda regalis</i>	royal fern
Osmundaceae	<i>Osmundastrum cinnamomeum</i>	cinnamon fern
Polypodiaceae	<i>Polypodium virginianum</i>	rock polypody
Pteridaceae	<i>Cryptogramma acrostichoides</i>	American rockbrake
Thelypteridaceae	<i>Phegopteris connectilis</i>	long beechfern
Woodsiaceae	<i>Athyrium filix-femina</i>	subarctic lady fern
Woodsiaceae	<i>Cystopteris fragilis</i>	fragile fern
Woodsiaceae	<i>Gymnocarpium dryopteris</i>	western oakfern
Woodsiaceae	<i>Woodsia ilvensis</i>	rusty woodsia
Apiaceae	<i>Heracleum sphondylium</i> ssp. <i>montanum</i>	common cowparsnip

Table A-2. Herbaceous (forb) species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Apiaceae	<i>Osmorhiza</i> sp.	sweetroot
Apiaceae	<i>Sanicula marilandica</i>	Maryland sanicle
Apocynaceae	<i>Apocynum androsaemifolium</i>	spreading dogbane
Araceae	<i>Arisaema triphyllum</i>	Jack-in-the-pulpit
Araceae	<i>Calla palustris</i>	water arum
Araceae	<i>Symplocarpus foetidus</i>	skunk cabbage
Araliaceae	<i>Aralia nudicaulis</i>	wild sarsaparilla
Asparagaceae	<i>Maianthemum canadense</i>	Canada mayflower
Asparagaceae	<i>Maianthemum racemosum</i>	feathery false Solomon's-seal
Asparagaceae	<i>Maianthemum trifolium</i>	threeleaf false lily of the valley
Asparagaceae	<i>Polygonatum pubescens</i>	hairy Solomon's seal
Asteraceae	<i>Achillea millefolium</i>	common yarrow
Asteraceae	<i>Anaphalis margaritacea</i>	western pearly everlasting
Asteraceae	<i>Antennaria neglecta</i>	field pussytoes
Asteraceae	<i>Antennaria</i> sp.	pussytoes
Asteraceae	<i>Asteraceae</i>	sunflowers
Asteraceae	<i>Bidens cernua</i>	sticktight
Asteraceae	<i>Cirsium</i> sp.	thistle
Asteraceae	<i>Doellingeria umbellata</i>	parasol whitetop
Asteraceae	<i>Eurybia macrophylla</i>	bigleaf aster
Asteraceae	<i>Eutrochium maculatum</i>	spotted joeypyeweed
Asteraceae	<i>Hieracium aurantiacum</i>	orange hawkweed
Asteraceae	<i>Hieracium caespitosum</i>	yellow hawkweed
Asteraceae	<i>Hieracium</i> sp.	hawkweed
Asteraceae	<i>Hieracium umbellatum</i>	narrow-leaf hawkweed
Asteraceae	<i>Lactuca canadensis</i>	wild lettuce
Asteraceae	<i>Lactuca</i> sp.	lettuce
Asteraceae	<i>Leucanthemum vulgare</i>	oxeye-daisy
Asteraceae	<i>Petasites frigidus</i> var. <i>palmatius</i>	arctic sweet coltsfoot
Asteraceae	<i>Prenanthes alba</i>	white rattlesnake-root

Table A-2 (continued). Herbaceous (forb) species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Asteraceae	<i>Solidago canadensis</i>	common goldenrod
Asteraceae	<i>Solidago gigantea</i>	giant goldenrod
Asteraceae	<i>Solidago nemoralis</i>	gray goldenrod
Asteraceae	<i>Solidago</i> sp.	goldenrod
Asteraceae	<i>Solidago uliginosa</i>	bog goldenrod
Asteraceae	<i>Symphyotrichum ciliolatum</i>	Lindley's aster
Asteraceae	<i>Symphyotrichum lateriflorum</i> var. <i>lateriflorum</i>	calico aster
Asteraceae	<i>Symphyotrichum puniceum</i> var. <i>puniceum</i>	purplestem aster
Asteraceae	<i>Symphyotrichum</i> sp.	aster
Asteraceae	<i>Taraxacum officinale</i>	common dandelion
Asteraceae	<i>Tragopogon</i> sp.	salsify
Balsaminaceae	<i>Impatiens capensis</i>	spotted touch-me-not
Boraginaceae	<i>Cynoglossum virginianum</i> var. <i>boreale</i>	wild comfrey
Brassicaceae	<i>Cardamine pensylvanica</i>	Quaker bittercress
Brassicaceae	<i>Cardamine</i> sp.	bittercress
Brassicaceae	<i>Turritis glabra</i>	tower rockcress
Campanulaceae	<i>Campanula aparinoides</i>	marsh bellflower
Campanulaceae	<i>Campanula rotundifolia</i>	bluebell bellflower
Caryophyllaceae	<i>Cerastium fontanum</i>	mouse-ear chickweed
Caryophyllaceae	<i>Stellaria</i> sp.	starwort
Colchicaceae	<i>Uvularia grandiflora</i>	large-flower bellwort
Cornaceae	<i>Cornus canadensis</i>	Canadian bunchberry
Ericaceae	<i>Chimaphila umbellata</i>	pipsissewa
Ericaceae	<i>Gaultheria hispidula</i>	creeping snowberry
Ericaceae	<i>Moneses uniflora</i>	one-flowered pyrola
Ericaceae	<i>Monotropa uniflora</i>	one-flower Indian-pipe
Ericaceae	<i>Orthilia secunda</i>	one-sided pyrola
Ericaceae	<i>Pyrola asarifolia</i>	pink shinleaf
Ericaceae	<i>Pyrola elliptica</i>	large-leaved shinleaf
Ericaceae	<i>Pyrola minor</i>	lesser shinleaf

Table A-2 (continued). Herbaceous (forb) species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Ericaceae	<i>Pyrola sp.</i>	shinleaf
Fabaceae	<i>Lathyrus ochroleucus</i>	pale vetchling peavine
Fabaceae	<i>Trifolium pratense</i>	red clover
Fabaceae	<i>Trifolium repens</i>	white clover
Fabaceae	<i>Vicia americana</i>	American vetch
Geraniaceae	<i>Geranium bicknellii</i>	northern crane's-bill
Iridaceae	<i>Iris versicolor</i>	harlequin blueflag
Lamiaceae	<i>Clinopodium vulgare</i>	wild basil
Lamiaceae	<i>Lycopus americanus</i>	waterhorehound
Lamiaceae	<i>Lycopus uniflorus</i>	oneflower bugleweed
Lamiaceae	<i>Mentha arvensis</i>	wild mint
Lamiaceae	<i>Scutellaria lateriflora</i>	mad dog skullcap
Liliaceae	<i>Clintonia borealis</i>	bluebead lily
Liliaceae	<i>Lilium philadelphicum</i>	wood lily
Liliaceae	<i>Streptopus amplexifolius</i>	clasping twistedstalk
Liliaceae	<i>Streptopus lanceolatus</i> var. <i>roseus</i>	twistedstalk
Linnaeaceae	<i>Linnaea borealis</i>	twinflower
Melanthiaceae	<i>Trillium cernuum</i>	whip-poor-will-flower
Menyanthaceae	<i>Menyanthes trifoliata</i>	common bogbean
Onagraceae	<i>Chamerion angustifolium</i> ssp. <i>angustifolium</i>	fireweed
Onagraceae	<i>Circaea alpina</i>	small enchanter's nightshade
Onagraceae	<i>Epilobium ciliatum</i>	hairy willowweed
Onagraceae	<i>Epilobium coloratum</i>	willowweed
Onagraceae	<i>Epilobium palustre</i>	marsh willowweed
Orchidaceae	<i>Corallorhiza maculata</i>	spotted coralroot
Orchidaceae	<i>Corallorhiza</i> sp.	coralroot
Orchidaceae	<i>Corallorhiza striata</i>	striped coralroot
Orchidaceae	<i>Corallorhiza trifida</i>	yellow coralroot
Orchidaceae	<i>Cypripedium arietinum</i>	ram's-head lady's-slipper
Orchidaceae	<i>Cypripedium parviflorum</i> var. <i>makasin</i>	greater yellow lady's slipper

Table A-2 (continued). Herbaceous (forb) species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Orchidaceae	<i>Cypripedium sp.</i>	lady's slipper
Orchidaceae	<i>Dactylorhiza viridis</i>	longbract frog orchid
Orchidaceae	<i>Galearis rotundifolia</i>	roundleaf orchid
Orchidaceae	<i>Goodyera oblongifolia</i>	western rattlesnake plantain
Orchidaceae	<i>Goodyera repens</i>	lesser rattlesnake plantain
Orchidaceae	<i>Goodyera sp.</i>	rattlesnake plantain
Orchidaceae	<i>Goodyera tessellata</i>	checkered rattlesnake plantain
Orchidaceae	<i>Neottia convallarioides</i>	broadleaf twayblade
Orchidaceae	<i>Neottia cordata</i>	heartleaf twayblade
Orchidaceae	<i>Orchidaceae</i>	orchids
Orchidaceae	<i>Platanthera hookeri</i>	Hooker's orchid
Orchidaceae	<i>Platanthera hyperborea</i>	northern green orchid
Orchidaceae	<i>Platanthera obtusata</i>	northern small bogorchid
Orchidaceae	<i>Platanthera orbiculata</i>	lesser roundleaved orchid
Orchidaceae	<i>Platanthera psycodes</i>	lesser purple fringed orchid
Orchidaceae	<i>Platanthera sp.</i>	fringed orchid
Orobanchaceae	<i>Castilleja septentrionalis</i>	Labrador Indian paintbrush
Orobanchaceae	<i>Melampyrum lineare</i>	narrowleaf cowweed
Oxalidaceae	<i>Oxalis montana</i>	mountain woodsorrel
Papaveraceae	<i>Corydalis sempervirens</i>	rock harlequin
Plantaginaceae	<i>Chelone glabra</i>	white turtlehead
Plantaginaceae	<i>Collinsia parviflora</i>	small-flower blue-eyed Mary
Plantaginaceae	<i>Plantago sp.</i>	plantain
Plantaginaceae	<i>Veronica americana</i>	brooklime
Plantaginaceae	<i>Veronica officinalis</i>	common gypsyweed
Polygalaceae	<i>Polygala paucifolia</i>	gaywings
Polygonaceae	<i>Fallopia cilinodis</i>	fringed black bindweed
Primulaceae	<i>Trientalis borealis</i>	starflower
Ranunculaceae	<i>Actaea pachypoda</i>	white baneberry
Ranunculaceae	<i>Actaea rubra</i>	red baneberry

Table A-2 (continued). Herbaceous (forb) species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Ranunculaceae	<i>Anemone americana</i>	roundlobe hepatica
Ranunculaceae	<i>Anemone virginiana</i>	Virginia anemone
Ranunculaceae	<i>Aquilegia canadensis</i>	red columbine
Ranunculaceae	<i>Caltha palustris</i>	yellow marsh-marigold
Ranunculaceae	<i>Clematis virginiana</i>	virgin's bower
Ranunculaceae	<i>Coptis trifolia</i>	threeleaf goldthread
Ranunculaceae	<i>Ranunculus abortivus</i>	smallflower crowfoot
Ranunculaceae	<i>Ranunculus acris</i>	tall buttercup
Ranunculaceae	<i>Ranunculus hispidus</i>	bristly buttercup
Ranunculaceae	<i>Ranunculus recurvatus</i>	littleleaf buttercup
Ranunculaceae	<i>Ranunculus rhomboideus</i>	Labrador buttercup
Ranunculaceae	<i>Ranunculus</i> sp.	buttercup
Ranunculaceae	<i>Thalictrum dasycarpum</i>	purple meadow-rue
Rosaceae	<i>Agrimonia gryposepala</i>	tall hairy agrimony
Rosaceae	<i>Comarum palustre</i>	purple marshlocks
Rosaceae	<i>Fragaria virginiana</i>	wild strawberry
Rosaceae	<i>Geum aleppicum</i>	yellow avens
Rosaceae	<i>Potentilla</i> sp.	cinquefoil
Rubiaceae	<i>Galium asprellum</i>	rough bedstraw
Rubiaceae	<i>Galium boreale</i>	northern bedstraw
Rubiaceae	<i>Galium trifidum</i>	three-petal bedstraw
Rubiaceae	<i>Galium triflorum</i>	sweetscented bedstraw
Santalaceae	<i>Comandra umbellata</i>	bastard toadflax
Santalaceae	<i>Geocaulon lividum</i>	false toadflax
Saxifragaceae	<i>Micranthes virginensis</i>	early saxifrage
Saxifragaceae	<i>Mitella nuda</i>	naked miterwort
Scrophulariaceae	<i>Verbascum thapsus</i>	common mullein
Verbenaceae	<i>Verbena hastata</i>	swamp verbena
Violaceae	<i>Viola</i> sp.	violet

Table A-3. Graminoid species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Cyperaceae	<i>Carex arctata</i>	drooping woodland sedge
Cyperaceae	<i>Carex aurea</i>	golden-fruit sedge
Cyperaceae	<i>Carex brunnescens</i>	brownish sedge
Cyperaceae	<i>Carex canescens</i>	silvery sedge
Cyperaceae	<i>Carex communis</i>	fibrousroot sedge
Cyperaceae	<i>Carex cristatella</i>	crested sedge
Cyperaceae	<i>Carex deweyana</i>	round-fruit short-scale sedge
Cyperaceae	<i>Carex disperma</i>	softleaved sedge
Cyperaceae	<i>Carex flava</i>	yellow sedge
Cyperaceae	<i>Carex gracillima</i>	graceful sedge
Cyperaceae	<i>Carex interior</i>	inland sedge
Cyperaceae	<i>Carex intumescens</i>	greater bladder sedge
Cyperaceae	<i>Carex leptalea</i>	bristlystalked sedge
Cyperaceae	<i>Carex leptoneuria</i>	nerveless woodland sedge
Cyperaceae	<i>Carex magellanica</i>	boreal bog sedge
Cyperaceae	<i>Carex pedunculata</i>	long-stalk sedge
Cyperaceae	<i>Carex projecta</i>	necklace sedge
Cyperaceae	<i>Carex retrorsa</i>	retorse sedge
Cyperaceae	<i>Carex stipata</i>	stalk-grain sedge
Cyperaceae	<i>Carex stricta</i>	uptight sedge
Cyperaceae	<i>Carex trisperma</i>	threeseeded sedge
Cyperaceae	<i>Carex utriculata</i>	Northwest Territory sedge
Cyperaceae	<i>Carex vaginata</i>	sheathed sedge
Cyperaceae	<i>Eriophorum viridicarinatum</i>	thinleaf cottonsedge
Cyperaceae	<i>Scirpus cyperinus</i>	woolgrass
Cyperaceae	<i>Scirpus</i> sp.	bulrush
Juncaceae	<i>Juncus effusus</i>	lamp rush
Juncaceae	<i>Luzula parviflora</i>	smallflowered woodrush
Poaceae	<i>Avenella flexuosa</i>	wavy hairgrass
Poaceae	<i>Bromus ciliatus</i>	fringed brome

Table A-3 (continued). Graminoid species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Poaceae	<i>Calamagrostis canadensis</i>	bluejoint reedgrass
Poaceae	<i>Cinna latifolia</i>	slender wood-reed
Poaceae	<i>Danthonia spicata</i>	poverty wild oat grass
Poaceae	<i>Dichanthelium</i> sp.	rosette grass
Poaceae	<i>Elymus repens</i>	quackgrass
Poaceae	<i>Elymus trachycaulus</i>	slender wild rye
Poaceae	<i>Glyceria canadensis</i>	rattlesnake mannagrass
Poaceae	<i>Glyceria</i> sp.	mannagrass
Poaceae	<i>Glyceria striata</i>	fowl mannagrass
Poaceae	<i>Milium effusum</i>	American milletgrass
Poaceae	<i>Oryzopsis asperifolia</i>	white-grain mountain-rice grass
Poaceae	<i>Phleum pratense</i>	timothy
Poaceae	<i>Poa compressa</i>	flat-stem blue grass
Poaceae	<i>Poa pratensis</i>	Kentucky bluegrass
Poaceae	<i>Poa</i> sp.	bluegrass
Poaceae	<i>Schizachne purpurascens</i>	false melic grass

Table A-4. Shrub species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Adoxaceae	<i>Sambucus racemosa</i>	red elderberry
Adoxaceae	<i>Viburnum edule</i>	squashberry
Adoxaceae	<i>Viburnum opulus</i> var. <i>americanum</i>	American cranberrybush
Anacardiaceae	<i>Rhus typhina</i>	staghorn sumac
Araliaceae	<i>Oplopanax horridus</i>	devil's club
Betulaceae	<i>Alnus incana</i> ssp. <i>rugosa</i>	speckled alder
Betulaceae	<i>Alnus viridis</i> ssp. <i>crispa</i>	green alder
Betulaceae	<i>Corylus cornuta</i>	beaked hazelnut
Rosaceae	<i>Crataegus</i> sp.	hawthorn
Caprifoliaceae	<i>Lonicera canadensis</i>	American fly honeysuckle
Caprifoliaceae	<i>Lonicera dioica</i>	glaucous honeysuckle
Caprifoliaceae	<i>Lonicera hirsuta</i>	hairy honeysuckle
Caprifoliaceae	<i>Lonicera involucrata</i>	twinberry honeysuckle
Caprifoliaceae	<i>Lonicera villosa</i>	mountain fly honeysuckle
Caprifoliaceae	<i>Symphoricarpos albus</i>	snowberry
Cornaceae	<i>Cornus alternifolia</i>	alternate-leaf dogwood
Cornaceae	<i>Cornus rugosa</i>	round-leaf dogwood
Cornaceae	<i>Cornus sericea</i>	red-osier dogwood
Cupressaceae	<i>Juniperus communis</i> var. <i>depressa</i>	common juniper
Diervillaceae	<i>Diervilla lonicera</i>	northern bush-honeysuckle
Elaeagnaceae	<i>Shepherdia canadensis</i>	russet buffalo-berry
Ericaceae	<i>Arctostaphylos uva-ursi</i>	bearberry
Ericaceae	<i>Rhododendron groenlandicum</i>	bog Labrador tea
Ericaceae	<i>Vaccinium angustifolium</i>	lowbush blueberry
Ericaceae	<i>Vaccinium macrocarpon</i>	cranberry
Ericaceae	<i>Vaccinium myrtilloides</i>	velvetleaf huckleberry
Grossulariaceae	<i>Ribes glandulosum</i>	skunk currant
Grossulariaceae	<i>Ribes hudsonianum</i>	northern black currant
Grossulariaceae	<i>Ribes lacustre</i>	prickly currant
Grossulariaceae	<i>Ribes triste</i>	swamp red currant

Table A-4 (continued). Shrub species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Rhamnaceae	<i>Rhamnus alnifolia</i>	alder-leaf buckthorn
Rosaceae	<i>Amelanchier</i> sp.	serviceberry
Rosaceae	<i>Crataegus</i> sp.	hawthorn
Rosaceae	<i>Rosa acicularis</i>	prickly rose
Rosaceae	<i>Rosa blanda</i>	smooth rose
Rosaceae	<i>Rubus flagellaris</i>	whiplash dewberry
Rosaceae	<i>Rubus hispidus</i>	bristly dewberry
Rosaceae	<i>Rubus parviflorus</i>	western thimbleberry
Rosaceae	<i>Rubus pubescens</i>	dwarf red raspberry
Rosaceae	<i>Rubus sachalinensis</i> var. <i>sachalinensis</i>	red raspberry
Taxaceae	<i>Taxus canadensis</i>	Canada yew

Table A-5. Tree species located in GLKN sampling sites at Isle Royale NP, 2019.

Family	Species	Common name
Betulaceae	<i>Betula alleghaniensis</i>	yellow birch
Betulaceae	<i>Betula papyrifera</i>	paper birch
Cupressaceae	<i>Thuja occidentalis</i>	northern white cedar
Fagaceae	<i>Quercus rubra</i>	northern red oak
Oleaceae	<i>Fraxinus nigra</i>	black ash
Pinaceae	<i>Abies balsamea</i>	balsam fir
Pinaceae	<i>Larix laricina</i>	tamarack
Pinaceae	<i>Picea glauca</i>	white spruce
Pinaceae	<i>Picea mariana</i>	black spruce
Pinaceae	<i>Pinus banksiana</i>	jack pine
Pinaceae	<i>Pinus resinosa</i>	red pine
Pinaceae	<i>Pinus strobus</i>	white pine
Rosaceae	<i>Prunus pensylvanica</i>	pin cherry
Rosaceae	<i>Prunus virginiana</i>	chokecherry
Rosaceae	<i>Sorbus americana</i>	American mountain ash
Rosaceae	<i>Sorbus decora</i>	northern mountain ash
Salicaceae	<i>Populus balsamifera</i>	balsam poplar
Salicaceae	<i>Populus grandidentata</i>	bigtooth aspen
Salicaceae	<i>Populus tremuloides</i>	quaking aspen
Sapindaceae	<i>Acer rubrum</i>	red maple
Sapindaceae	<i>Acer saccharum</i>	sugar maple
Sapindaceae	<i>Acer spicatum</i>	mountain maple

The Department of the Interior protects and manages the nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

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