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Research Article

Comprehensive Assessment of White-tailed Deer Browse in the Presence of Beech Bark Disease at a Great Lakes National Park

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ABSTRACT

In northern hardwood forests, white-tailed deer (*Odocoileus virginianus*) impact both tree regeneration and groundlayer composition, leading to a dominance of American beech (*Fagus grandifolia*), an unpalatable species, as well as a reduction of preferred groundlayer species. Deer become especially problematic in areas with beech bark disease, such as at Sleeping Bear Dunes National Lakeshore. We analyzed datasets from Sleeping Bear Dunes, collected in 2009 and 2018, to assess vegetation change in three management units: a mainland unit with a long history of deer occupancy, and two islands, one with high deer pressure and one with no known history of permanent deer presence. For each unit, we tested for change in species richness and mean coefficient of conservatism. We also examined the groundlayer, testing for change in indices of abundance and size of preferred and avoided species. Finally, we compared regeneration of palatable and unpalatable tree species. We found increased nonnative species richness, decreased number and abundance of preferred herbaceous species, as well as decreased height of a preferred species. We also detected increased sapling density of beech while that of palatable species declined. Our data provide further evidence of the impacts of white-tailed deer on the forest understory. Management goals should focus on maintaining deer densities at or below 5 deer km^{-2} in order to promote growth of the full suite of herbaceous species typical of the region and habitat and to allow adequate regeneration of the overstory.

Index terms: American beech; browse; Sleeping Bear Dunes National Lakeshore; *Trillium grandiflorum*; white-tailed deer management

INTRODUCTION

Overstory regeneration is impaired in northern hardwood forests with high white-tailed deer (*Odocoileus virginianus* Zimmerman) occupation (Tilghman 1989; Krueger and Peterson 2006; Casabon and Pothier 2007). Within the range of American beech (*Fagus grandifolia* Ehrh., or simply "beech"), a species generally unpalatable to deer (Sage et al. 2003; Kain et al. 2011), high browse pressure imposes a strong selection gradient allowing beech to become the dominant and, at times, the only woody species remaining, particularly in smaller size classes that represent more recent (e.g., previous 20 y) establishment (Kain et al. 2011). This situation is further complicated by the arrival of beech bark disease (BBD), an insect–fungal complex, involving a nonnative beech scale insect (*Cryptococcus fagisuga* Lindinger) and two native canker fungi (*Neonectria ditissitima* and *N. faginata*) (Roy and Nolet 2018). Beech mortality is typically 50–85% (Houston et al. 1979; Houston 1994), with the majority of tree death occurring within 10 y of arrival of the scale to an area (Miller-Weeks 1983). In aftermath forests of BBD (Shigo 1972), beech stump sprouts can form dense thickets, indirectly limiting light and nutrients available to other tree species, which are not directly affected by the disease organisms (Forrester et al. 2003). One such area where this scenario is occurring is Sleeping Bear Dunes National Lakeshore.

Sleeping Bear Dunes National Lakeshore (SLBE) is a unit of the U.S. National Park Service (NPS) located in northern lower Michigan and composed of three management zones: a mainland unit (ML) located directly on the Lake Michigan shore; North Manitou Island (NMI), 10.1 km from the mainland; and South Manitou Island (SMI), 10.8 km offshore (Figure 1). BBD was first detected in the park in 2008 (J. Christian, SLBE Chief of Natural Resources, pers. comm.). As of 2020, all park forests with beech as a primary component were classified either as within the BBD killing front or as aftermath forests (Shigo 1972). The impacts of BBD to the park flora, both directly and indirectly, interface with those caused by white-tailed deer (Runkle 2007; Nuttle et al. 2013).

Deer occupation has shaped SLBE forests, via a long and varied history. Most recently, on the mainland, consistent and relatively high (7.7–11.2 deer km^{-2}) deer pressure has led to a depauperate understory and limited regeneration of overstory species (Sanders and Grochowski 2010; Sanders and Kirschbaum 2019). On NMI, legacy effects of four decades of artificially high deer densities, maintained as part of a private game reserve, are evident. Here, dense stands of Canada yew (*Taxus canadensis* Marsh.), formerly exceeding 2 m in height, were largely eliminated by 1939 (SLBE 1985). In contrast, SMI has no known history of permanent white-tailed deer occupancy, although deer have been documented on SMI on two occasions. The first was in the early 2000s when three females were removed from the island by the Animal and Plant Health Inspection Service and, more recently, in spring 2020 when tracks were observed in wet sand by a park employee. Since that time, however, no other visual signs or indications have been noted. On SMI, dense thickets of Canada yew are common, as are regenerating cedar (*Thuja occidentalis* L.) and hemlock (*Tsuga canadensis* (L.) Carrière). The herbaceous layer supports a number of species

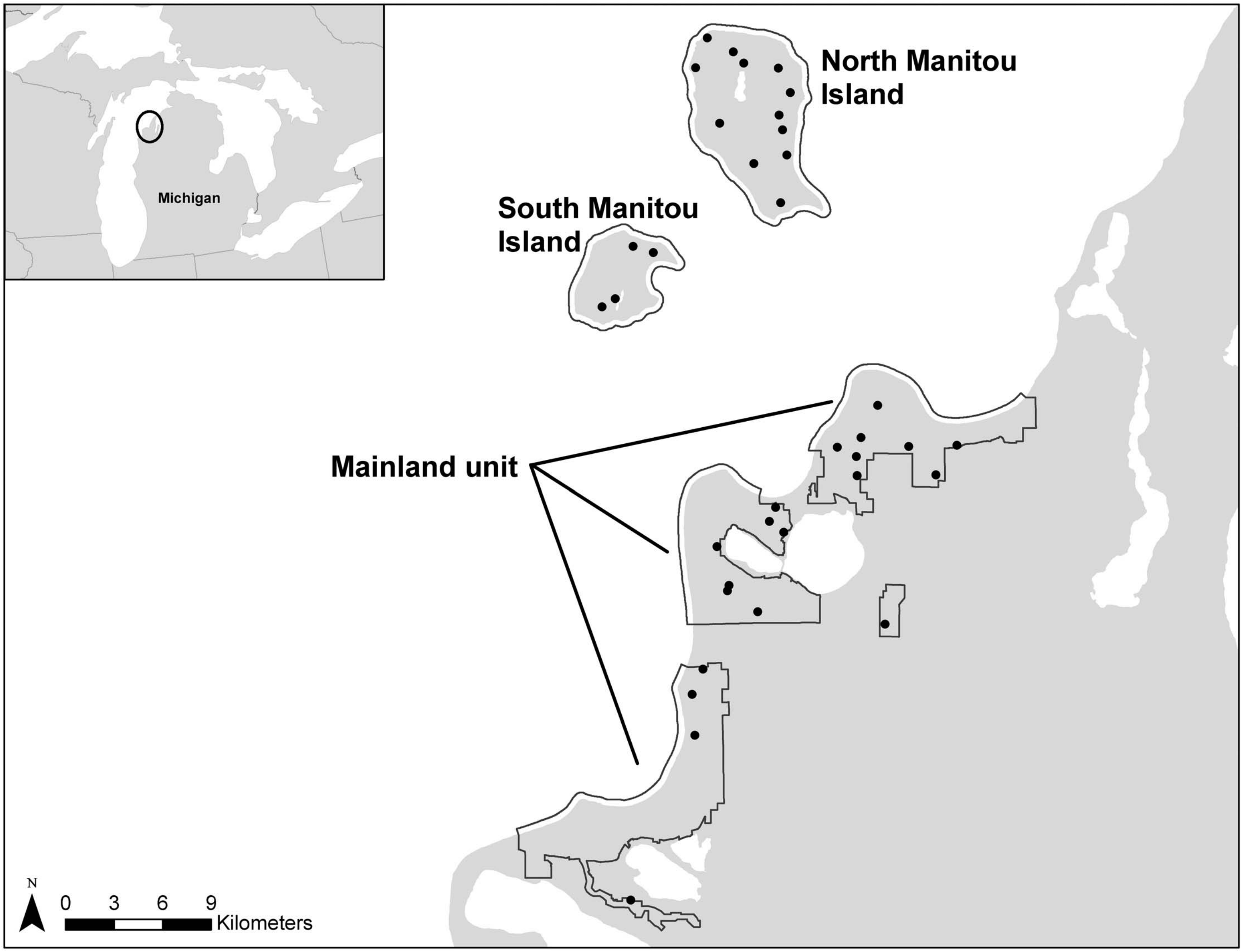

Figure 1.—Location of Sleeping Bear Dunes National Lakeshore in northern Michigan. The black line outlines park lands and includes a 0.40 km-wide swath of Lake Michigan.

preferred by deer. Because of this history, SMI serves as a reference point, and allows one to gauge ecosystem impacts on the forest, attributable to deer.

Datasets of herbivore impacts on vegetation, where available, often focus on direct measures of browse, such as bite marks which are *directly visible* on a plant (Mysterud et al. 2010). While informative, direct measures fail to fully assess the extent of the problem when a community has been so highly impacted that certain taxa are no longer common and available to be browsed. In contrast, indirect measures of browse assess long-term impacts by quantifying changes in abundance or height (Kalisz et al. 2014; Frerker et al. 2017). Such measures are only *indirectly observed* over a long period of time, for instance, several years. Detailed data of this type are available for lands within the Great Lakes region administered by the NPS, including SLBE.

Here, we capitalize on an existing dataset to assess vegetation change and gauge the impacts of deer at Sleeping Bear Dunes National Lakeshore in each of the three management units. Our first objective is to examine measures of site quality that incorporate both herbaceous and woody species. Incorporating the entire suite of species is especially relevant on islands where species richness is generally lower and the presence of one or a few species can sway values (Sanders and Grochowski 2014). For our second objective, we focus on the herbaceous layer and examine measures of abundance and size, and include species preferred by deer, as well as those generally avoided. Our third objective addresses woody species; we look at regeneration of palatable and unpalatable tree species and compare the distributions across size classes. This comprehensive approach allows us to paint a detailed picture of how the combined impacts of deer and BBD are impacting the flora of Sleeping Bear Dunes National Lakeshore and will be used to inform the park's management decisions.

METHODS

Study Location

Sleeping Bear Dunes National Lakeshore sits in the north central hardwood forest ecoregion (USEPA 2013). Sand dunes, steep bluffs, and gently rolling topography predominate, shaped largely by glacial moraines and outwash plains (Weber 1973; Drexler 1975). The islands formed ~12,000 y ago, over limestone bedrock, and rise to elevations of 129 m (NMI) and 130 m (SMI) above Lake Michigan. Soils are generally well-drained with loamy sands and sandy loams common (Weber 1973; USDA 2013). Forests dominate the vegetation at the Lakeshore, with upland sites typically supporting American beech, sugar maple (*Acer saccharum* Marsh.), white pine (*Pinus strobus* L.), and basswood (*Tilia americana* L.), with a lesser component of red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), aspen (*Populus* spp. L.), and birch (*Betula* spp. L.) (Hop et al. 2011). Remnant stands of jack pine (*Pinus banksiana* Lamb.) are found in well-drained soils, while white cedar and black ash (*Fraxinus nigra* Marsh.) are present in wetter sites (Sanders and Kirschbaum 2019).

White-tailed deer are not known to have inhabited either island prior to 1925, when five does and four bucks were introduced on NMI for a private hunting preserve (SLBE 1985). Here, artificially high density (>30 deer km^{-2}) was maintained for four decades, sustained by a supplemental feeding program initiated in 1937 and continued until 1977 (Hurley and Flaspohler 2005). During this time, the herd experienced high winter mortality, largely resulting from starvation among fawns (SLBE 1985). Erratic deer density, including two population crashes, ensued in the five years following the cessation of feeding. The initial NMI deer management plan (SLBE 1985) established 300 deer as a management goal for the island, a value corresponding to 5.18 individuals km^{-2}. Efforts to reach this goal commenced in the mid-1980s with the establishment of an annual hunting season on NMI. In 1985, 825 deer were taken, followed by a mean of 237 taken annually from 1986 through 1995 (SLBE 1996). While former park natural resource staff noted deer density on NMI has stabilized to ~3 km^{-2} by 2005 (Hurley and Flaspohler 2005), more recent visual assessments of the island by park staff suggest density is now considerably higher.

In contrast to NMI, documentation supports SMI as being deer free as far back as 1853 (SLBE 1985), although this island is generally believed by biologists to have never supported a resident deer population. While the islands do have a number of similarities vegetatively (both are dominated by northern hardwood forests, both support conifer-dominated coastal forests on the islands' east sides, and they are both circled by coastal dunes), there are notable differences between them. Hazlett and VandeKopple (1985) surveyed both islands in 1982 and 1983, documenting 33 plant species common on SMI but rare on NMI. These include not only species widely acknowledged to be preferable to deer (e.g., large-flowered trillium [*Trillium grandifolium* (Michx.) Salisb.] and rosy twistedstalk [*Streptopus lanceolatus* var. *roseus* (Aiton) Reveal]), but less palatable species as well, including ferns and *Juniperus* spp. L. The extent to which these differences are due to non-browse deer impacts (e.g., trampling, altered nutrient cycling) vs. direct, human impacts, which include homesteading and logging, is unclear. NMI has a longer and more intensive logging history with operations ceasing in 1978; this contrasts with SMI where logging has not occurred since 1964 (Hazlett and VandeKopple 1985). Nonetheless, the second NMI deer management plan (SLBE 1996) notes *Juniperus* spp. at that time as being "robust" throughout the island.

We are unaware of long-term records documenting historical deer density on the mainland unit of SLBE, although abundance has generally been high in recent years. Michigan Department of Natural Resources target management goals in 2009 were 7.7–9.7 deer km^{-2} in Leelanau County and 9.3–10.8 deer km^{-2} in Benzie County, although actual densities were believed to be closer to 8.5 and 11.2 deer km^{-2} in the two counties, respectively (Sanders and Grochowski 2010).

Field Methods

Sampling was conducted at SLBE 27 May–30 June 2009 and 15 June–26 August 2018. Site selection was made in 2009 prior to the initial sampling event using a generalized random-tessellation stratified design (Stevens and Olsen 2004), ensuring that our sites were both randomly located and spatially balanced throughout the park. We limit our analyses here to those 36 sites in beech-maple forests (Sanders and Kirschbaum 2019). Of these, 25 were dominated by sugar maple and beech; the remaining 11 sites also supported red maple, particularly in smaller size classes, with red oak typically present as larger individuals (Sanders and Kirschbaum 2019).

We sampled trees and the groundlayer using a plot composed of three parallel 50 m transects, each in an east–west orientation and permanently monumented with below-ground rebar (Johnson et al. 2008; Sanders and Kirschbaum 2019; Figure 2). We recorded the species, diameter at breast height (dbh), and live/dead status for all trees with a dbh $\geq$ 2.5 cm and rooted within 3 m of the central transect line. For species that reproduce vegetatively (e.g., beech, red maple), we counted stems as unique saplings if no aboveground connection with the parent plant was readily seen. The total area sampled for trees was 300 m^2 for each transect, or 900 m^2 for the entire plot. We assessed the groundlayer in 1 m^2 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 a frequency determination for all species–site combinations. Since deer browse is known to decrease not only frequency, but also height of preferred species, we measured the height of the tallest individual of large-flowered trillium (*Trillium grandiflorum* (Michx.) Salixb.). We selected this species prior to sampling because it is relatively widespread and abundant at SLBE (Sanders and Kirschbaum 2010), is documented to be a preferred browse species by white-tailed deer (Frerker et al. 2017), and because of its broad use as a phytoindicator of browse impacts (Anderson 1994; Kirschbaum and Anacker 2005).

Statistical Analyses

The three management units differ considerably from one another and our interests lie in whether changes have occurred over time, within units, rather than between them. Thus, we examined NMI (12 sites), SMI (4 sites), and the ML (20 sites)

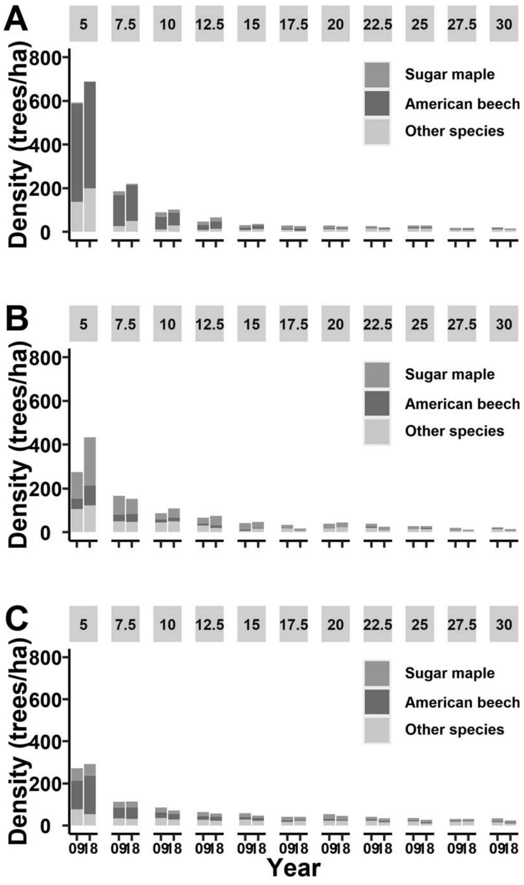

Figure 2.—Tree density by diameter size classes for sites on (A) North Manitou Island, (B) South Manitou Island, and (C) the mainland. Diameter classes, in cm, are shown across the top of each panel and represent the 2.5 cm range immediately lower (e.g., 5 cm is trees $\geq$ 2.5 and $<$ 5.0 cm). "Other species" represents the combined density of all tree species besides sugar maple and beech. On the *x*-axis, "09" and "18" are the sampling years (2009, 2018) truncated to two digits.

separately. While we did not make comparisons between them, we did apply Benjamini-Hochberg corrections (R Core Team 2021) to *P* values to decrease the likelihood of false discovery. For each metric (e.g., species richness), we grouped all three locations together and performed the test, correcting all three *P* values. For objectives 1 and 2 (see below), we used the nonparametric Wilcoxon signed-rank tests to determine whether the distributions of indices sampled in 2009 and 2018 were similar. We chose a nonparametric approach since, for all metrics, data from two of the three management units did not meet the assumptions for parametric analyses.

Our first objective addresses measures of quality that incorporate both woody and herbaceous species. We determined site-level *species richness* (α diversity; Mauer and McGill 2011), although we did not include graminoids (grasses [Poaceae], sedges [*Carex* sp. L.], etc.) in our analyses here, since not all individuals could be identified to the species level at all points during the sampling window. Likewise, we did not include ephemeral species since they were only found at sites sampled early in the season. From the species richness data, we determined the site-level *mean coefficient of conservatism* (mean CoC; Rooney and Rogers 2002; Sanders and Grochowski 2014). The CoC values are assigned to individual species within an area, such as at the state level. They range from 0 to 10 and reflect a species' likelihood that it will be present in habitats with alterations from presettlement conditions (Herman et al. 2001). Species with a value of 10 are those whose locations are limited to high-quality communities where conditions have changed little since presettlement time. In contrast, CoC values of zero are assigned to nonnative species and those with little fidelity to conditions found in remnant communities. For these analyses, we used the most current coefficient of conservatism values for the state of Michigan (Herman et al. 2001). As with species richness, we excluded all graminoids and ephemerals from this analysis; we then tested for change in both species richness and mean CoC between the time periods.

To address our second objective, examining measures of herbaceous abundance and size, we identified both preferred and avoided herbaceous species. Preferred species (Table 1) were selected based on reported palatability preferences of deer from the literature (Waller and Alverson 1997; Kirschbaum and Anacker 2005) and on personal knowledge. Decreased abundance of palatable herbaceous species is well documented in the literature (Williams et al. 2000; Webster et al. 2001; Knight 2003). 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. To examine browse impacts on herb height (Koh et al. 2010; Wilbur et al. 2017), we selected large-flowered trillium for additional information and analyses. For the sites where it was present, we calculated the *trillium frequency*, based on the frequency of presence in the 30 quadrats; we then determined *trillium maximum height*, by calculating the site mean of the tallest individual (if present) in each quadrat.

We considered all graminoids and ferns to be avoided species. We recognize that deer are known to browse these on occasion (McCaffery et al. 1974; Mosbacher and Williams 2009), but this is uncommon and it is well-documented that ferns, grasses, and other graminoids become more dominant as browsing pressure increases (Horsley et al. 2003; Rooney and Waller 2003; Averill et al. 2016). We are aware that deer avoid other species, as well. However, since avoided species vary, depending on the entire suite of species present (Augustine and McNaughton1998; Dumont et al. 2005), we felt that a simple grouping of graminoids and ferns was both concise and unbiased. As with preferred species, we assessed both the *number of avoided herbaceous species* at each site as well as the *abundance of avoided herbs*, determined by the total number of avoided species–quadrat combinations at each site. For analyses of change of avoided, as well as preferred species, with the exception of those for trillium, we used the Wilcoxon signed-rank test as described above. Small sample sizes and inconsistent site-occupancy precluded analyses on trillium indices; we present means and standard errors only.

Our third objective focused on woody species regeneration. For each management unit, we tested for change in small saplings ($\geq$2.5 cm dbh but $<$5.0 cm dbh) between time periods comparing the collective *sapling density of palatable species* (all species other than beech) and, in separate analyses, *sapling*

Table 1.—Preferred browse species at SLBE.

Species	Common name
Aralia nudicaulis L.[a]	wild sarsaparilla
Clintonia borealis (Aiton) Raf.[a]	bluebead lily
Maianthemum canadense Desf. [a]	Canada mayflower
Maianthemum racemosum (L.) Link[b]	false Solomon's seal
Maianthemum stellatum (L.) Link[c]	starry false lily of the valley
Medeola virginiana L.[d]	Indian cucumber
Panax quinquefolius L.[e]	American ginseng
Polygonatum biflorum (Walter) Elliott[f]	Solomon's seal
Polygonatum pubescens (Willd.) Pursh[g]	hairy Solomon's seal
Sanguinaria canadensis L.[h]	bloodroot
Streptopus lanceolatus var. *roseus* (Michx.) Reveal[i]	rosy twistedstalk
Trillium grandiflorum (Michx.) Salisb.[j]	large-flowered trillium
Uvularia grandiflora Sm.[h]	large-flowered bellwort

[a] Waller and Alverson (1997)
[b] Nuzzo et al. (2017)
[c] Augspurger and Buck (2017)
[d] Royo et al. (2010)
[e] McGraw et al. (2013)
[f] Webster (2016)
[g] Kraft et al. (2004)
[h] Augustine and DeCalesta (2003)
[i] Wiegmann and Waller (2006)
[j] Knight et al. (2009)

density of unpalatable species, i.e., beech, between sampling events. We used the Wilcoxon signed-rank test, as described above. We also constructed density vs. diameter graphs to view regeneration of common species across a range of size classes. Finally, for each year–management unit combination, we graphed the empirical cumulative distribution functions (ECDF) of both beech and non-beech species. These graphs are generated using a point for each sample unit (i.e., tree) and show the proportion of values of a distribution below a given value on the *x*-axis; in our case, this is diameter at breast height (Fan et al. 2005). We then compared the diameter distributions of beech with that of non-beech species using the Kolmogorov-Smirnov test (Arnold and Emerson 2011).

All analyses were carried out using R Studio (R Core Team 2021). All nomenclature follows that of the Integrated Taxonomic Information System (ITIS 2020).

RESULTS

Assessments of change collectively on both herbaceous and woody species, our first objective, showed change only on the ML where mean CoC declined from 4.13 to 3.71 ($P = 0.0009$) (Table 2).

Impacts on herbaceous species, our second objective, were also evident. The *number of preferred herbaceous species* per site dropped from 3.08 to 2.41 on NMI ($P = 0.0305$) and from 3.05 to 2.45 on the mainland ($P = 0.0853$; Table 2). *Abundance of preferred species* did not differ between years on NMI or SMI but decreased on the ML from 15.55 to 12.25 ($P = 0.0478$) species–quadrat combinations from 2009 to 2018. Overall low frequencies of trillium precluded statistical analyses; however, we present means and standard error for both metrics in all three management units in Table 2. At sites where it was present, *trillium frequency* was notably lower on SMI where it decreased from 0.27 (27% of quadrats at sites where it was present) in 2009 to 0.05 in 2018. On NMI, *trillium maximum height* dropped from 34.06 cm in 2009 to 25.09 cm in 2018. The only change detected in avoided herbs was on the mainland where the *number of avoided species* increased between the time periods from 2.70 to 4.15 species per site ($P = 0.0164$).

Our third objective focused on woody species regeneration. Change in *sapling density of unpalatable species* was detected on the ML where it rose from 136.1 to 181.1 saplings ha^{-1} (Table 2; $P = 0.0060$). Density–diameter graphs (Figure 2) showed notably

Table 2.—Means and standard errors for browse metrics. Significance ($\alpha = 0.10$) after applying Benjamini-Hochberg correction indicated by *. We did not test for differences between years for trillium indices due to the small sample size.

Metric	Mean ± SE 2009	Mean ± SE 2018
All species		
Species richness		
NMI	27.3 ± 4.3	27.1 ± 4.2
SMI	38.0 ± 4.0	36.0 ± 2.7
ML	28.5 ± 1.8	31.1 ± 2.0
Mean CoC		
NMI	4.15 ± 0.09	4.00 ± 0.13
SMI	4.03 ± 0.13	4.33 ± 0.12
ML*	4.13 ± 0.08	3.71 ± 0.13
Preferred herbaceous species		
Number of preferred herb species		
NMI*	3.08 ± 0.65	2.41 ± 0.62
SMI	4.25 ± 0.48	4.75 ± 0.48
ML*	3.05 ± 0.45	2.45 ± 0.32
Abundance of preferred herbs		
NMI	14.83 ± 4.92	15.25 ± 5.74
SMI	26.75 ± 2.83	27.25 ± 4.85
ML*	15.55 ± 3.15	12.25 ± 2.47
Trillium frequency		
NMI	0.13 ± 0.04	0.11 ± 0.04
SMI	0.27 ± 0.17	0.05 ± 0.02
ML	0.20 ± 0.07	0.15 ± 0.05
Trillium maximum height		
NMI	34.06 ± 3.60	25.09 ± 6.31
SMI	33.42 ± 0.15	35.00 ± 5.00
ML	13.59 ± 1.58	14.76 ± 2.32
Avoided herbaceous species		
Number of avoided species		
NMI	3.67 ± 0.70	3.50 ± 0.74
SMI	3.75 ± 0.85	2.50 ± 0.65
ML*	2.70 ± 0.38	4.15 ± 0.63
Abundance of avoided species		
NMI	11.33 ± 3.56	11.50 ± 3.58
SMI	9.00 ± 3.24	9.25 ± 3.97
ML	9.50 ± 2.66	12.35 ± 2.61
Palatable woody species		
Sapling density of palatable species		
NMI	158.3 ± 66.6	212.0 ± 105.8
SMI	236.1 ± 61.3	352.8 ± 128.7
ML	146.1 ± 29.7	120.6 ± 22.7
Unpalatable woody species		
Sapling density of unpalatable species		
NMI	449.1 ± 118.1	487.0 ± 85.8
SMI	47.2 ± 17.8	91.7 ± 45.5
ML*	136.1 ± 29.5	181.1 ± 36.0

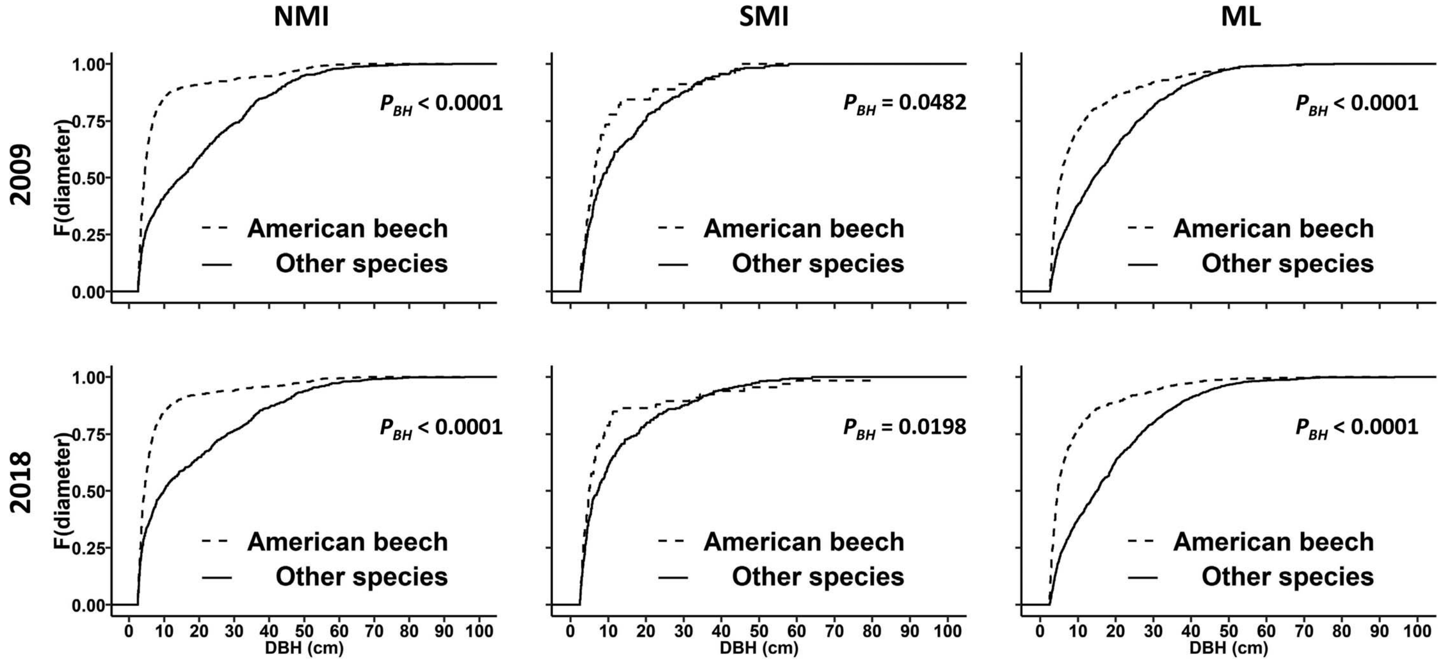

Figure 3.—ECDF graphs for each year–management zone combination, comparing beech diameter distribution with that of all palatable species. P_{BH} is the *P* value after applying the Benjamini-Hochberg correction.

different regeneration states between the management units. On NMI in 2009, beech comprised 75.8% and 76.1% of the individuals in 5 cm and 7.5 cm size classes, respectively, with sugar maple comprising only 1.1% and 9.4% of individuals in these classes. Here, the percentage of sugar maple dropped to 0.4% and 2.5% in 2018. In size classes greater than 17.5 cm dbh (2009) and 20 cm dbh (2018), sugar maple comprised a greater percentage of the total trees than beech. On SMI, sugar maple represents no less than 30% of individuals in size classes ≤10 cm dbh at either time period with beech never representing more than 24% of individuals in the same criteria. Like NMI, at mainland sites, beech dominates the small size classes comprising 31–50% of individuals in size classes ≤10 cm dbh in 2018 but comprising only about 10–15% of individuals in size classes ≥20 cm dbh the same year.

Tests comparing diameter distributions of beech with those of palatable species showed differences for all combinations of year and management unit (Figure 3).

DISCUSSION

High browse pressure at SLBE has led to lowered coefficient of conservatism (ML), decreased number (NMI, ML) and abundance (ML) of preferred herbaceous species, decreased height of a preferred species (NMI), and increased number of avoided species (ML). Further, we found differences in the successional trajectories of beech compared with the 24 other species, collectively. These other species (largely *Acer saccharum*, *A. rubrum*, *Ostrya virginiana* (Mill.) K. Koch [hophornbeam], *Tsuga canadensis*, and *Quercus rubra*) have proportionally fewer small individuals, which are important for regeneration. By and large, these results are in line with those of others documenting browse impacts by white-tailed deer in the Upper Midwest (Rooney and Gross 2003; Rooney and Waller 2003; Frerker et al. 2017). Nonetheless, several aspects of this work were surprising.

The ECDF graphs along with the Kolmogorov-Smirnov tests of regeneration on SMI (Figure 3) show beech had proportionally more stems in small diameter size classes than did other species, despite the absence of deer on the island. Beech reproduces both by seed and vegetatively, via root sprouts (Ward 1961), with proportionally greater vegetative reproduction where environmental conditions are harsher, including near the northern range boundary (Held 1983), where SLBE is located. It remains unclear from our current work if this difference in diameter distributions between beech and other species on SMI is due to an intrinsic ability of beech, or some other cause such as environmental factors, hare browse on other species, or seed deposition by birds such as blue jays (*Cyanocitta cristata* L.) (Johnson and Adkisson 1985; Tatina 2021). While stress from BBD infestation could trigger root sprouting (Jones and Raynal 1986), the timing of our sampling suggests otherwise. We observed high stem density even during our initial sampling event, just 1 y following the discovery of the disease in the park. We suspect the high density of small beech stems is likely a combination of multiple factors.

Perhaps the most surprising finding here is the decline in frequency of trillium on SMI. Two factors may be contributing to this. First, the tracks observed on a beach in wet sand support the presence of at least one white-tailed deer on the island in 2020. It is unknown how long this individual was on the island although no further sign has been reported or detected, despite multiple years of follow-up with a camara trap array. Deer are strong swimmers and it would not be inconceivable for them to swim from NMI, a distance of 5.4 km between the closest points, during the rutting season, or in response to a lack of food (Reimchen et al. 2008; Quigley and Moffatt 2014). Distance from

Table 3.—Means and standard errors of the number of nonnative species at sampling sites.

Zone	Mean ± SE 2009	Mean ± SE 2018	P_{BH}
NMI	0.92 ± 0.29	1.75 ± 0.37	0.0288
SMI	0.50 ± 0.50	1.00 ± 0.41	0.3458
ML	0.55 ± 0.15	2.95 ± 0.65	0.0012

the mainland is nearly twice that at 10.1 km. It would also not be inconceivable that there have been multiple unsuccessful colonization events over the years. Nonetheless, we believe colonization via an ice-bridge crossing would be very unlikely. Full ice coverage between islands themselves and between the islands and the mainland is an extremely rare event due to strong lake currents (V. Acharya, Plant Biologist, Sleeping Bear Dunes National Lakeshore). If, in the unlikely event that deer are reproducing on SMI, our work there is timely and will serve as a constructive reference point on which to base future comparisons. The second potential cause of trillium decline at SLBE is the phytoplasma *Candidatus* Phytoplasma pruni. This has long been known to infect stone fruit species, including peach and cherry (Davis et al. 2013) in eastern Canada, but was only first reported on *Trillium* spp. in North America in London, Ontario, Canada, in 2016 (Montano and Rosete 2019). This disease typically causes the petals to take on a green coloration, similar to the shade of the rest of the plant, although the edges of the petals may remain white. The petals will also commonly have more of a rounded shape at the terminal end and wavy margins. Infected plants can survive for several years, although they will eventually die from the infection (Voss and Reznicek 2012). This disease was first documented in 2013 on SMI by author Gehring.

The fact that we found an increase in avoided species on the ML, but not on NMI is, perhaps, not surprising. We would generally expect to see this only after prolonged browse impacts, when marked decreases in preferred species create a niche with sufficient light and nutrient availability. Then, only after enough time for dispersal, germination, and establishment can avoided species become more dominant. We may be observing this on the mainland as a result of the longer, consistent history of overabundant deer there, compared with NMI, which supported relatively smaller populations in the early 2000s (Hurley and Flaspohler 2005). This could also reflect diet preferences of the island herd, where opportunities for dispersing elsewhere are limited and survival necessitates eating suboptimal species.

A final unanticipated finding was that species richness did not change in any of the sampling zones, but particularly on NMI. A post hoc analysis using the Wilcoxon signed rank test to compare the number of nonnative species between the two sampling events provides some context (Table 3). On NMI, we found an increase in the number of nonnative species per site from 0.92 ± 0.29 to 1.75 ± 0.37. Subtracting this from the total species richness to obtain native species richness, we see a drop of 26.4 to 25.3 species per site. Perhaps this decline would not have been significant, but it does partially explain the findings on NMI and suggests that deer may, indeed, be having some degree of impact to native species richness there.

A reduction in the deer herd, either on the mainland or NMI may, given enough time, allow regeneration of hardwoods and a recovery of groundlayer populations, but the extent that legacy effects will play is unclear. The ability of desirable species to recover is a function of the size of the remaining population, dispersal ability of the affected species, and distance to source plants, as well as the level of continued browse pressure. It is unlikely that populations on NMI and the ML can recover without a reduction in the deer herd. In a heavily invaded forest in western Pennsylvania, where deer densities were 14–29 deer km^{-2}, Pendergast et al. (2016) found herbaceous species richness in deer exclosures did not increase, relative to unfenced controls, until 7 y after their construction, at which time only a modest increase of 2 species/site was noted. In the same study, density of preferred browse species did not differ between fenced and control sites until sometime between 5 and 11 y post-fencing. Also, in northwestern Pennsylvania, Royo et al. (2010) observed increases of select indices (height, abundance, cover) of certain preferred browse species only after intensified hunting reduced deer densities from 10.4 to 4.9 individuals km^{-2}. Here, *Trillium* spp. were 60% more abundant and 46% taller at the conclusion of the study in 2007 than in 2003, when intensified hunting began. Despite this, overall site species richness had yet to increase by 2007.

The role that BBD plays in the browse dynamic at SLBE is uncertain, although it is clear that it will be significant. As the disease progresses and large trees die, vigorous sprouting from infected stumps ensues, turning aftermath forests into dense beech thickets (Ostrofsky 2004). Loss of overstory beech will, at least temporarily, result in more light reaching the forest floor, which can promote survival of sugar maple saplings (Hane 2003), as well as some herbs (Nelson et al. 2007). Ultimately, however, intense stump sprouting and thicket formation can lead to loss of groundlayer cover of non-beech species, and reduced species richness and diversity (Cale et al. 2013). In effect, BBD exacerbates the stressors within the understory. This disease, in combination with severe browse in the park, is a one–two punch against those species that deer choose to browse, whether highly preferred, or simply occasionally selected.

Management Recommendations

While definitive thresholds of deer density, as triggers for management action, generally do not exist, both historical and current knowledge of deer densities and impacts can inform management decisions. In the hardwoods of northern Wisconsin, pre-European settlement densities of white-tailed deer were likely lower than 4 deer km^{-2} (McCabe and McCabe 1984). Other research in northern hardwood forests (Balgooyen and Waller 1995) suggests deer densities be held to below 5 deer km^{-2} if management objectives are to preserve the full complement of herbaceous species in northern hardwood forests. On NMI, with a land mass of 57.9 km^2, this equivalates to a herd of no larger than 289 individuals. This value is consistent with the initial objective, established in the 1985 NMI deer management plan, of managing for 300 deer on the island (SLBE 1985). Ultimately, however, for the successful regeneration of preferred browse species, several years, and perhaps decades, may be needed.

We suggest managers be cognizant of sample size when factoring outcomes of statistical tests (or lack thereof) into management decisions, since sample size can strongly impact significance (Royall 1986). Indeed, of the eight Wilcoxon signed-rank tests comparing change between years, none for SMI (four sites) were significant, while five for ML (20 sites) were. While these comparisons provide sound, scientific evidence of browse impacts, ultimately, park biologists are the best able to piece together the influences of the interacting suite of drivers and stressors within the systems where they work.

We feel that our use of indirect measures, looking at changes in plant abundance and height over time, is a more suitable approach than using direct measures, such as bite marks. Our ultimate goal is to ascertain the impacts of deer on the forest understory and the indirect approach, in and of itself, accomplishes this goal. In this sense, the plants are *phytometers* (Clements and Goldsmith 1924; Dietrich et al. 2013), directly used to gauge environmental conditions. The drawback with this approach is the investment (time, funding, labor) required to carry it out. In situations where this is not realistic, measuring bite marks directly visible on woody species can be a proxy. Unfortunately, while these results would serve as an index of deer impacts, they would not be informative on herbaceous layer impacts.

Our approach here provides a thorough assessment of browse impacts to both woody and herbaceous species, and examines species and groups known to be preferred browse by white-tailed deer, as well as those that are avoided. We recognize that datasets containing the level of detail analyzed here are not available for most natural areas and maintain that the institutional knowledge in many state and county parks and nature preserves may be great, and equally of value. Provided managers incorporate indirect impacts of browse, such as changes in abundance and height, ultimately, personal observations, details of park history, and prior management actions can allow informed decision making.

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