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A COMPARATIVE STUDY OF THE FLORA AND SOILS OF
GREAT DUCK AND LITTLE DUCK ISLANDS,
MAINE, USA

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ABSTRACT. Strong environmental gradients and varied land-use practices have generated a mosaic of habitats harboring distinct plant communities on islands on the coast of Maine. Botanical studies of Maine's islands, however, are generally limited in number and scope. Baseline studies of Maine's islands are necessary for assessing vegetation dynamics and changes in habitat conditions in relation to environmental impacts imposed by climate change, rising sea levels, invasive species, pests and pathogens, introduced herbivores, and human disturbance. We conducted a survey of the vascular plants and soils of forest, field, and ocean-side communities of Great Duck and Little Duck Islands, ME. These islands differ in environmental and land-use features, and in particular the presence of mammalian herbivores; Great Duck Island has had over a century of continuous mammalian herbivory while Little Duck Island has been largely free of mammalian herbivores over the last 100 years. We recorded 235 vascular plant species in 61 families on the Duck Islands, 106 of which were common to both islands. The composition, abundances, and diversity of plant species substantially differed within similar plant communities between the islands. These differences were particularly evident in the forest communities where Little Duck Island had significantly greater sapling regeneration and a more recent peak in tree recruitment. Soil properties also significantly differed between these islands, with a higher pH in all three communities and higher P, Ca, and K in field, forest, and ocean-side communities, respectively, on Little Duck Island, and higher soluble salts in forest and ocean-side communities of Great Duck Island. Together, our findings suggest that soil characteristics and the dominance and regeneration of

vascular plant species can differ substantially even between adjacent islands with otherwise similar geologic characteristics and glacial history, and that mammalian herbivory along with other ecological factors may be important drivers of these differences.

Key Words: coastal ecology, insular ecology, baseline survey, mammalian herbivory, Gulf of Maine, vascular plants, edaphic features

The coastline of northeastern North America includes a mosaic of islands with varied topography, climate, bedrock and surface geology, and with complex postglacial and post-settlement histories (McMaster 2005; Turcotte and Butler 2006). The strong environmental gradients, along with historical factors, have produced varied habitats harboring a wide range of species and vegetation types on islands of the region (Clayden et al. 2010; Greene et al. 2005). The state of Maine, located at the intersection of temperate and boreal bioclimatic zones in northeastern North America, is home to 2103 vascular plant taxa (Campbell et al. 1995) and 104 natural plant communities (Gawler and Cutko 2010). Although more than 3000 islands hug the coastline of Maine, botanical studies of the state's islands are limited in number and scope, with the vast majority focusing on floristics (Folger and Wayne 1986; Greene et al. 2005; Lesser 1977; Lewis 1983; Mulligan 1980; Pike and Hodgdon 1962; Rand 1900; Rappaport and Wesley 1985; Redfield 1885, 1893; Stebbins 1929; Wise 1970), and a few on plant-habitat relations (Ellis et al. 2006, 2011; Hodgdon and Pike 1969; Nichols and Nichols 2008; Rajakaruna et al. 2009; Wherry 1926). Long-term and systematic floristic studies on Maine's islands are necessary for assessing long-term vegetation dynamics, including changes in habitat conditions, especially in light of significant environmental impacts imposed by climate change, rising sea levels, invasive species, pests and pathogens, introduced herbivores, and human disturbances on island ecosystems (Caujapé-Castells et al. 2010; Harris et al. 2012).

The Great Duck and Little Duck Islands, ME, provide an important setting for establishing a baseline ecological study to assess long-term changes to plant diversity, community composition, and habitat conditions. The environmental factors that differ between these islands may offer some insights into the current and future ecologies of these islands. For example, Great Duck Island has had over a century of continuous mammalian herbivory in the form of sheep and hares, whereas Little Duck Island has been largely free of mammalian herbivores. Introduced mammalian herbivores are a major conservation concern, especially in predator-free habitat fragments such as islands where herbivores can severely limit tree recruitment (Peterson et

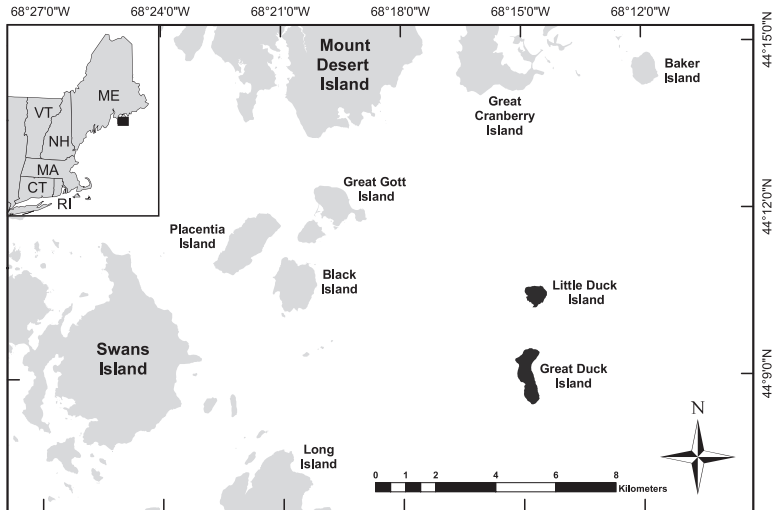


Figure 1. Study area, showing location of Great Duck and Little Duck Islands, Maine, USA.

al. 2005; Terborgh et al. 2001). These islands also differ in topography and other aspects of land-use history, which may in turn drive plant communities and edaphic features. In this study, we conducted a survey to describe the vascular flora and associated soils of the islands' natural plant communities. We compared species composition and diversity, tree demography, and sapling regeneration to assess the potential impact of long-term herbivory and other environmental and human factors on plant communities of the two islands.

MATERIALS AND METHODS

Site description. The Duck Islands, ME (44.16°N, 68.25°W) are composed of Little Duck Island (LDI, 35 ha) and Great Duck Island (GDI, 91 ha), located about eight kilometers south of Mount Desert Island in the Gulf of Maine (Figure 1). The climate of the region is typically characterized by cool summers and mild winters (McMahon 1990). Average high and low annual temperatures for the nearby town of Mount Desert are 11.9 and 0.1°C, respectively, with an average annual precipitation of 114.7 cm (between 1981 and 2010; US Climate Data 2015).

The Duck Islands have similar bedrock geology and glacial history (Osberg et al. 1985), with parent material typically composed of coarse

acidic glacial till (Jordan 1988). Parent material varies in depth, with occasional exposed bedrock, especially near the ocean. The islands were connected to the mainland for about 500 y following glacial retreat around 11,000 YBP; sea-level has increased since, reaching close to current levels around 4000 YBP (Barnhardt et al. 1995). The islands are partially covered by forests dominated by *Picea* spp. and *Abies balsamea* and old-fields dominated by a variety of forbs, shrubs, and graminoids. Each island also harbors a saline wetland with a different assemblage of species. Redfield (1885, 1893), Rand (1900), Lesser (1977), Rappaport and Wesley (1985), and Folger and Wayne (1986) offered preliminary accounts of vascular plants of the Duck Islands.

These islands differ substantially in their history of recent human use, particularly regarding mammalian herbivory. Although both islands have been under conservation protection since the 1970s, LDI has been protected as a bird sanctuary since 1908 (McLane 1989). The last record of sheep grazing on LDI—a common practice on Maine islands (Conkling 2011)—was in the late 19th century, and no permanent populations of grazing mammals have been reported on LDI in the past 100 y (McLane 1989). Great Duck Island, however, had a history of permanent human habitation and sheep grazing until 1986, when the lighthouse at the south end of the island became automated and lighthouse keepers were no longer needed. In addition, both European hare (*Lepus europaeus*) and snowshoe hare (*L. americanus*) were introduced to GDI in the late 1940s for recreational hunting. The hare populations have since expanded and were estimated at 500 individuals or, about 6 hares per ha in 1985 (Folger and Wayne 1986). We made numerous sightings during our fieldwork in 2011, indicating the hares on GDI were still abundant. This is in contrast to LDI, where we observed no signs of any mammalian herbivores in 2010. Both GDI and LDI also harbor large populations of nesting seabirds, including black guillemot (*Cepphus grille*), common eider (*Somateria mollissima*), double-crested cormorant (*Phalacrocorax auritus*), great cormorant (*P. carbo*), great black-backed gull (*Larus marinus*), and herring gull (*L. argentatus*), as well as the threatened Leach's storm-petrel (*Oceanodroma leucorhoa*; Allen et al. 2012).

Vegetation survey. We established and surveyed sixty 20 m² plots on LDI during June–August of 2010 and on GDI during June–August of 2011. Plots (10 × 2 m) were randomly located within three strata: communities dominated by a woody canopy (forest), mostly herbaceous vegetation without a woody canopy (field), and the vegetation found within proximity of the ocean (excluding the rocky berm; ocean-side). These were the most conspicuous natural communities found on

both islands. Prior to fieldwork, we delineated these vegetation communities from aerial photographs (North American Proficiency Testing Program 2009) and later refined the maps based on field observations. The forest community was defined by the presence of a woody canopy at least 2 m in height and at least 10 m from the rocky shoreline. The field community was defined by the presence of herbs, the absence of a woody canopy greater than 2 m in height, and by a distance of at least 10 m from the rocky shoreline. The ocean-side community was defined as the vegetation within 10 m of the rocky shoreline. To randomly select plot locations in the forest and field vegetation communities, we first generated a geo-referenced map of the island and overlaid a series of plots based on a 0.40 ha grid. Plots were excluded from consideration if they occurred within community transition zones on our delineated maps. Using a GPS unit (Garmin eTrex Venture HC, Olathe, KS), we navigated to each randomly selected plot within each stratum. Based on our field interpretations, plots that occurred at the edges of community transition zones were moved away from the transition edges. These plots were moved 30 m in the cardinal direction (north, east, south, or west) that put them farthest into the community they represented. The long sides of all plots were oriented north-south. Ocean-side plots were systematically placed around the perimeter of each island. These ocean-side plots were oriented perpendicular to the shoreline, beginning at the first occurrence of 100% vegetation cover from the rocky shore. In total, we established 60 plots on LDI (29 forest, 20 field, 11 ocean-side), and 60 plots on GDI (29 forest, 19 field, 12 ocean-side).

We subdivided each 10×2 m plot into five 2×2 m subplots to allow for easier estimation of percent cover of each vascular plant species below a height of 2 m. Percent cover was estimated for each species within each subplot to the nearest one percent. Species represented by less than one percent were recorded as 0.5%, and species represented by one or only a few seedlings were recorded as 0.1%. Percent cover data from the five subplots were averaged to represent each plot. All individuals > 5 cm diameter at breast height (DBH) in each plot were counted and cored at breast height, and the age of each tree was estimated in the field by counting rings with a loupe and adding 10 to conservatively account for age at breast height. Saplings (< 5 cm DBH, and $>$ than 20 cm height) of each tree species were counted within each plot.

Although the plot surveys provided a measure of species abundances on the islands, this method is likely to miss rare plants. Our plot surveys also did not include transitional habitats such as between forest and field, saline wetlands, or the rocky berm where some species were

exclusively found. Thus, in addition to our plot surveys we traversed the islands, spending time in other habitats in order to generate complete species lists for each island. Plants within and outside of plots were identified in the field to the species level, if possible, or collected and identified in the lab with a dissecting microscope and taxonomic key (Haines 2011). Several taxa were identified only to the genus level due to missing reproductive structures necessary for identification. Intraspecific taxa were not considered in our study. All vascular nomenclature follows Haines (2011). A complete list of vascular taxa for each island is presented in the Appendix. Voucher specimens have been deposited at the herbarium of College of the Atlantic, Bar Harbor, ME (HCOA). We compared the list of vascular plant species tallied on the Duck Islands to those of historic surveys of these islands (Folger and Wayne 1986; Lesser 1977; Rappaport and Wesley 1985; Redfield 1885, 1893) as a preliminary assessment of historic change in the species composition of these islands.

Soil analyses. Soil samples were collected from the top 10 cm of mineral soil, in two opposing corners of each 10×2 m plot, and these were combined to form a single 200 g sample for each plot. Samples were air dried in the laboratory and then sent to A&L Western Laboratories Inc. (Modesto, CA) where they were tested for nitrogen (N, NO_3^-), phosphorus (P, Weak-Bray), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), sulfur (S, SO_4^-), pH, percent organic matter (OM), estimated nitrogen release (ENR), soluble salts (SS), and cation exchange capacity (CEC). All soil testing procedures followed the Soil and Plant Analytical Methods of the North American Proficiency Testing Program (NAPT 2011).

Statistical analyses. Data were analyzed to describe and compare species diversity, edaphic features, and woody regeneration between islands within similar vegetation communities. All statistical analyses were conducted using the R language and environment for statistical computing (R Core Team 2014).

We compared soil features between the two islands using two methods. First, we conducted a principal components analysis (PCA) as a way to visually inspect soil differences in multivariate space and to extract the soil features most important for describing this variation. The PCA was calculated using soil data that were log-transformed to aid with assumptions of normality. For each community, the two primary axes—those that explained the most multivariate variation—were plotted and were labeled with the soil features important for driving this variation (features with loadings greater than 0.3 were included). Second, we tested for differences in soil features within communities and

between islands, using two-tailed Mann-Whitney tests for each comparison. The Mann-Whitney test is a non-parametric analog to the t-test, appropriate for comparisons of non-normally distributed data such as our soil data. We adjusted p-values using the Hochberg method to reduce the chance of Type I errors in repeated testing, generating more conservative comparisons (Hochberg 1988).

Finally, we compared the diversity, composition, abundance, and regeneration of the common species on each island. Understory species composition (species with vegetation cover within 2 m from the ground) was assessed using plot mean percent cover data in each vegetation type. Forest overstory composition was assessed using stem counts of each species (individuals > 5 cm DBH). We also compared woody regeneration between islands by qualitatively comparing tree demography. Estimates of tree ages were binned by decade, and plotted as a density histogram where all bins for an island sum to one. We tested for differences in sapling numbers (< 5 cm DBH, and > than 20 cm height) in forests between islands and accounted for differences in soil features by using negative binomial models of the form:

Model 1. $Sapling\ count_{plot} \sim soil\ PCA1_{plot} + soil\ PCA2_{plot}$

Model 2. $Sapling\ count_{plot} \sim soil\ PCA1_{plot} + soil\ PCA2_{plot} + island$

in which the primary axes of soil variation from our PCA were used to generate a null model of sapling count as a function of soil features (Model 1). Our second model included island as an explanatory variable for sapling counts (Model 2). We then used a likelihood-ratio test to assess the importance of including island as an explanatory variable for sapling count. This approach allowed us to test for differences in regeneration between islands while accounting for soil differences. Finally, diversity indices were calculated for each community on each island. Alpha diversity was calculated as the species richness within each plot. The Shannon-Wiener diversity index, calculated using base e , additionally accounted for species evenness as determined by percent cover of each species in plots. Evenness tests the extent to which species abundance distributions are skewed towards few dominant species versus many evenly abundant species. A plot represented by species with equal relative cover is equivalent to the natural log of alpha diversity.

RESULTS

In total, we identified 235 plant taxa in 61 families on the Duck Islands—189 in 56 families on GDI and 151 in 47 families on LDI

(Appendix). There were 83 species unique to GDI and 46 unique to LDI, with 106 common between both islands (45%). In the 60 vegetation plots on each island, we found 130 species in 42 families on GDI and 84 species in 38 families on LDI. Thirty-one species were non-native, 27% of species on LDI and 24% on GDI. Furthermore, 31 species were newly recorded for GDI, and 44 were newly recorded on LDI. A total of 62 species were previously recorded on GDI (from multiple surveys dating between 1885 to 1986), but not found in the current study. A total of 30 species were previously recorded on LDI, but not found in the current study.

Forest. The forest community of GDI was dominated by an overstory of *Picea* spp. with *Betula papyrifera*, *Sorbus* spp., and *Abies balsamea* found in only one or two forest plots (Figure 2). The overstory on LDI was dominated by both *A. balsamea* and *Picea* spp., and included a greater richness and abundance of broad-leaved deciduous species such as *Acer pensylvanicum*, *A. spicatum*, and *B. papyrifera* (Figure 2). We also found a significantly greater number of regenerating tree saplings per plot on LDI (17.97 ± 4.37 SEM) than on GDI (2.41 ± 1.78 SEM), even after allowing for differences in soils ($p < 0.001$; $\chi^2(1) = 12.17$). This included greater richness of both coniferous and deciduous sapling species on LDI (Figure 3), including *Abies balsamea* and *Acer spicatum*, with occasional *Sorbus* spp. and *Acer pensylvanicum*. The saplings on GDI mainly consisted of *B. papyrifera* and *S. americana*, though these saplings were only encountered in one or very few forest plots (Figure 3). The understory of each island was dominated by *Dryopteris* spp. (Figure 4). Other than wood fern, the understory of GDI was mainly composed of *Chamaepericlymenum canadense*, *Maianthemum canadense*, and *Oclemena acuminata*, whereas *A. balsamea* and *A. spicata* dominated the understory cover on LDI. *Clintonia borealis* and *Streptopus lanceolatus* were also frequently encountered in the forest understory community of LDI (Figure 4). A mean alpha diversity of 11.85 (± 0.84) species was encountered in forest plots on GDI, and a mean alpha diversity of 14.14 (± 0.64) species was encountered in forest plots on LDI (Table 2). See Table 2 for the Shannon-Wiener diversity index. Tree recruitment peaked in the 1940s for GDI, when close to 25% of the trees surveyed had reestablished (Figure 5). Tree recruitment on LDI, in contrast, peaked in the 1960s, when over 25% of trees surveyed had reestablished (Figure 5).

Field. The field community on both islands consisted of a mix of forbs, graminoids, and shrubs. The field community on GDI was

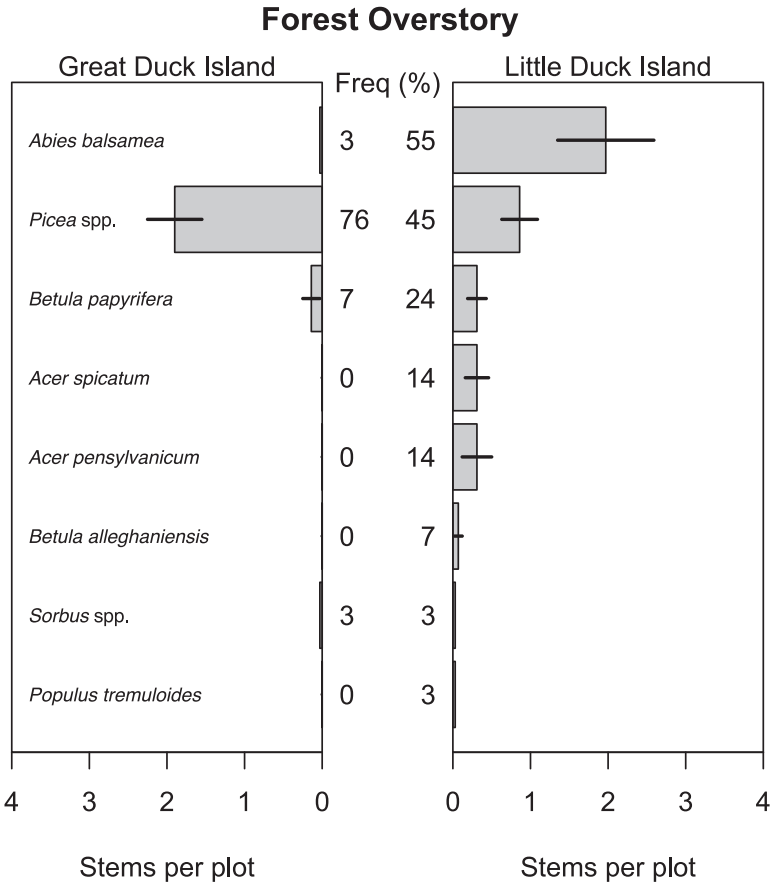


Figure 2. Tree composition of the forest community on Great Duck and Little Duck Islands during the summers of 2010–2011. Relative species abundance is determined as mean stem count (individuals > 5 cm DBH; \pm standard error). Frequency refers to the percent of plots on each island occupied by stems.

characterized by a dominant layer of *Festuca rubra*, with occasional *Vaccinium angustifolium*, *Deschampsia flexuosa*, and *Rubus hispidus*, and with the less dominant, but frequent occurrence of *R. idaeus*, *Achillea millefolium*, *Rumex acetosella*, and *Fragaria virginiana* (Figure 6). The field on LDI was dominated by *Poa pratensis*. Other abundant or frequent species on LDI included *Rubus idaeus*, *Elymus repens*, *F. virginiana*, *Moehringia lateriflora*, *Chamerion angustifolium*, and *Soli-*

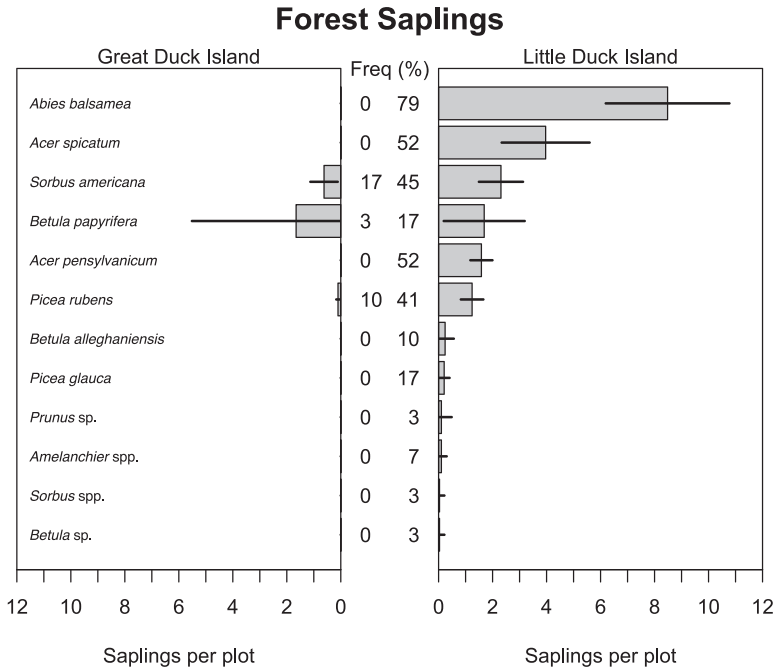


Figure 3. Saplings found in each vegetative community on Great Duck and Little Duck Islands, during the summers of 2010–2011. Saplings are defined as trees > 20 cm in height but < 5 cm DBH. Frequency refers to the percent of plots on each island occupied by stems. Overall, sapling counts within each plot differed significantly between islands in the forest community even when accounting for edaphic differences; $p < 0.001$; $\chi^2(1) = 12.17$.

dago rugosa (Figure 6). A mean alpha diversity of 19 (± 1.57) species was encountered in field plots on GDI, and a mean alpha diversity of 12.65 (± 0.81) species was encountered in field plots on LDI (Table 2). See Table 2 for the Shannon-Wiener diversity index.

Ocean-side. The GDI ocean-side community was characterized by its dominant field species, *Festuca rubra* and *Symphyotrichum novibelgii*, and a generally sparse cover of *Agrostis* spp. and *Calystegia sepium* (Figure 7). In contrast to the ocean-side community on LDI, several salt-tolerant or wetland species were occasionally encountered, including *Argentina egedii*, *Bolboschoenus maritimus*, *Juncus balticus*, *J. gerardii*, *Plantago maritima*, and *Impatiens capensis* (Figure 7). The LDI ocean-side community was also dominated by the abundant and frequent species found in its field community, followed by an abundance

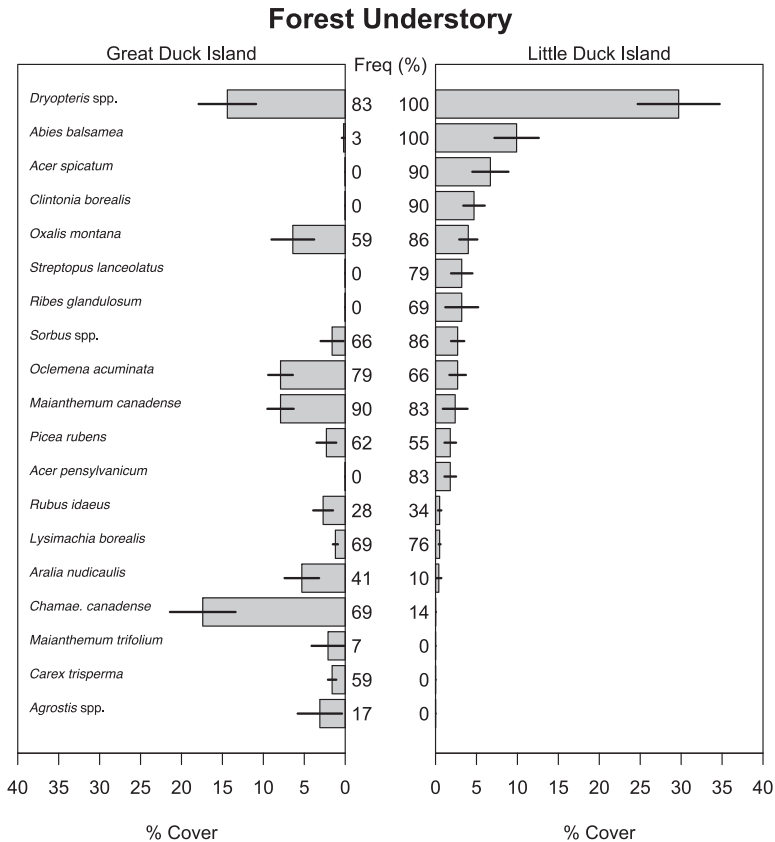


Figure 4. Forest community species with the 10 highest abundance and frequency ranks on Great Duck and Little Duck Islands, during summers 2010–2011. Abundance was determined as mean percent cover (\pm SE). Frequency refers to the percent of plots on each island occupied by each species. Additional species were included to account for ties in abundance or frequency.

of *Lathyrus japonicus*, *Elymus repens*, *Rubus idaeus*, *C. sepium*, and *Angelica lucida* (Figure 7). A mean alpha diversity of 14 (\pm 1.34) species was encountered in ocean-side plots on GDI, and a mean alpha diversity of 13.27 (\pm 1.42) species was encountered in ocean-side plots on LDI (Table 2). See Table 2 for the Shannon-Wiener diversity index.

Soils. Visual inspection of soil PCA ordinations for each community indicated that LDI and GDI generally differed in their soil properties (Figure 8). The greater overall extent of GDI plots in multivariate

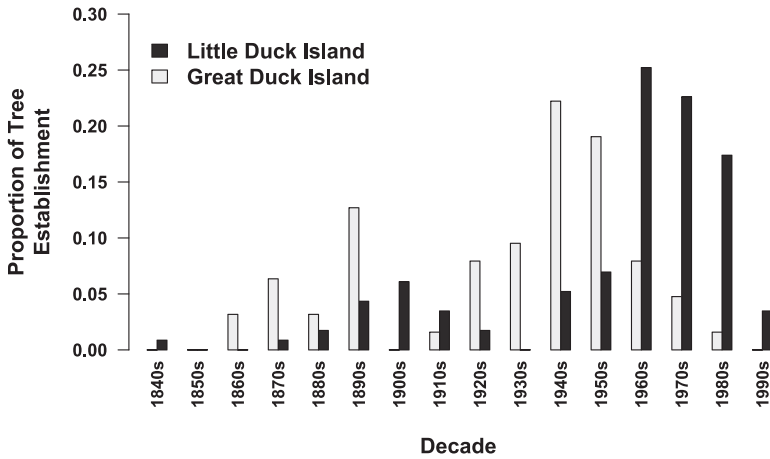


Figure 5. Tree recruitment history of Great Duck and Little Duck Islands. Tree ages were determined by coring all trees greater than 5 cm DBH in plots and adding 10 to ring count to account for age at breast height. Tree age was then subtracted from 2010 (LDI) or 2011 (GDI) to determine recruitment decade ($n = 115$ for LDI, $n = 63$ for GDI).

ordination space suggested that GDI generally had a greater variation in soil features between plots (Figure 3). The primary two PCA axes explained 60% of the variation in soil properties in forest soils, 66% of the variation in field soils, and 65% of the variation in ocean-side soils. The first axis of variation in forest soils was primarily driven by a gradient of physical properties related to CEC, organic matter, and associated nutrient availabilities. The second axis of variation in forest soils explained more of the soil variation between GDI and LDI, and was primarily associated with pH, nutrients, and soluble salts. Similar to forest soils, the first axis of variation in field soils was primarily driven by physical properties related to CEC, organic matter, and associated nutrient availabilities, whereas the second axis better differentiated between the islands and was driven by pH and essential nutrients. The first axis of variation in the ocean-side soils was similar to the first axis of other communities, but with the additional variation in soluble salts and S. The second axis of variation in ocean-side soils was similar to field soils but with the addition of Mg. Overall, PCA results suggested that axes related to pH and essential nutrient concentrations best explained the variation between islands, though salinity and S were also important for differences between ocean-side soils of the islands. Through pairwise comparisons, we found pH to be higher on LDI in all three communities.

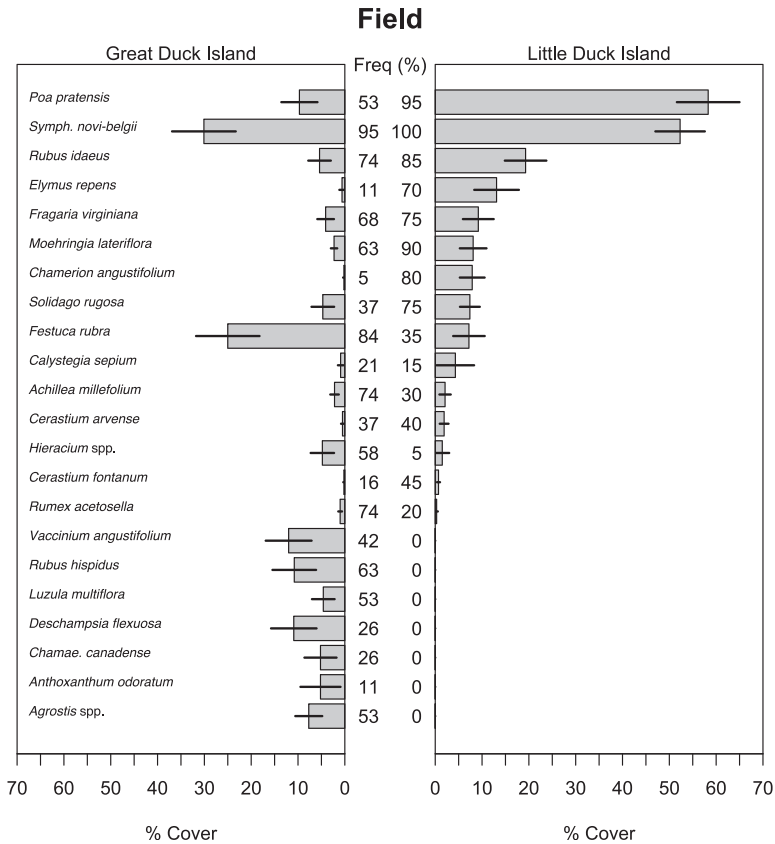


Figure 6. Field community species with the 10 highest abundance and frequency ranks on Great Duck and Little Duck Islands, during summers 2010–2011. Abundance is determined as mean percent cover (\pm SE). Frequency refers to the percent of plots on each island occupied by each species. Additional species were included to account for ties in abundance or frequency.

In addition, P was higher on LDI in fields, Ca was higher in LDI forests, and K was higher in LDI ocean-side sites (Table 1). Soluble salt was higher in GDI forests and ocean-side communities (Table 1). No other soil features differed significantly between islands (Table 1).

DISCUSSION

Our study is among the first floristic studies of Maine's islands to generate baseline ecological information for vascular plant species

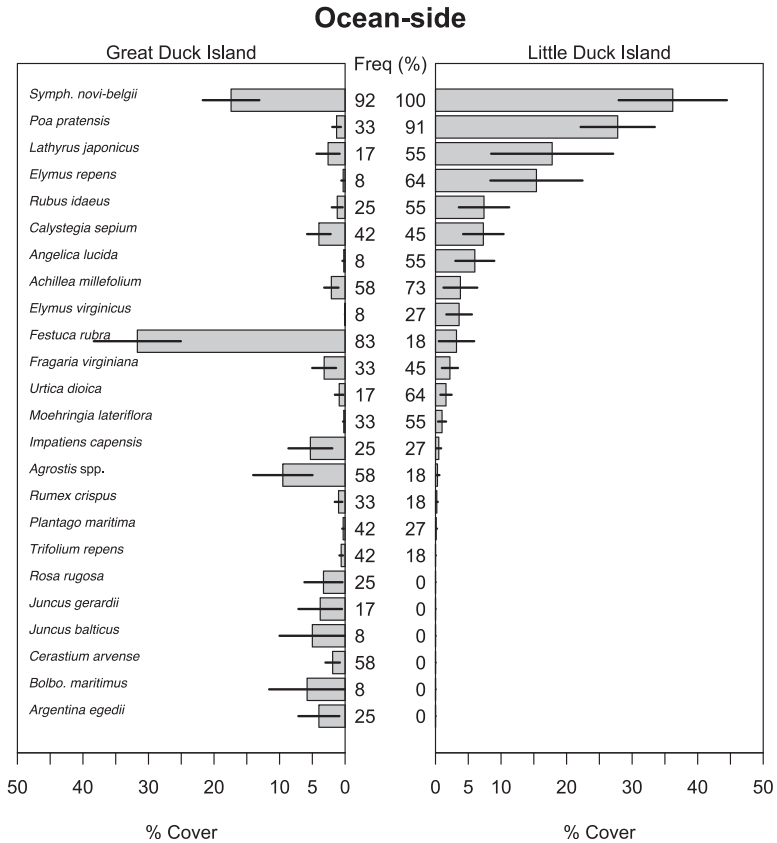


Figure 7. Ocean-side community species with the 10 highest abundance and frequency ranks on Great Duck and Little Duck Islands, during summers 2010–2011. Abundance is determined as mean percent cover (\pm SE). Frequency refers to the percent of plots on each island occupied by each species. Additional species were included to account for ties in abundance or frequency.

diversity, abundance, and associated edaphic features. Our findings suggest that soil characteristics and the dominance and regeneration of vascular plant species can differ substantially, even between adjacent islands with otherwise similar geologic characteristics and glacial history. Differences in vegetation structure were especially apparent in the forest communities. The overstory on LDI was dominated by *Abies balsamea* and had a greater diversity of both coniferous evergreen and broad-leaf deciduous trees, despite the overall greater diversity of

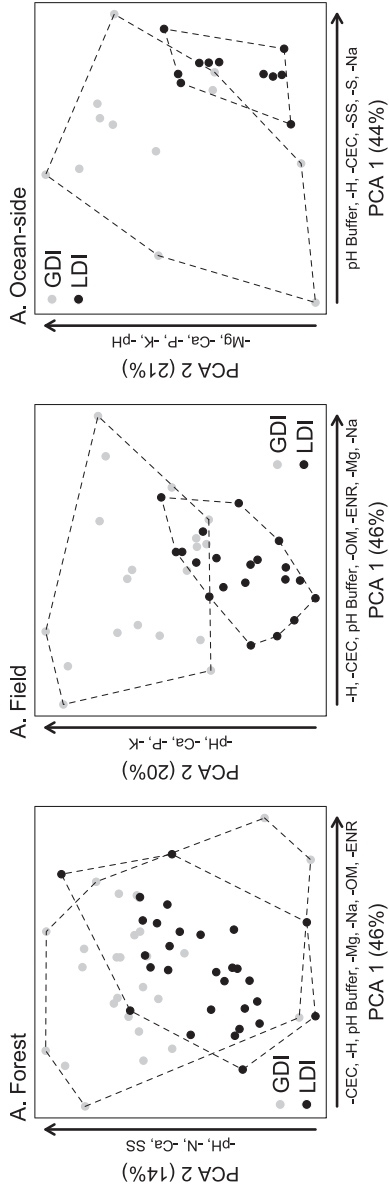


Figure 8. Principal components analysis of edaphic features within communities on Great Duck and Little Duck Islands, during summers 2010–2011. Each ordination presents the primary two axes of variation, with the percent variation explained by each axis in parentheses. Edaphic features with the greatest loadings on each principal component (greater than 0.3) are labeled on each axis. A minus sign (–) before a feature indicates an inverse relationship with axis arrows.

species on GDI. The historic recruitment of the overstory on LDI peaked more recently than on GDI, and the greater abundance of saplings on LDI suggests that, at the time of this study, the tree species found on this island were successfully regenerating. In contrast, the forest on GDI was almost exclusively dominated by *Picea* spp., which peaked in recruitment in the 1940s and for which few saplings were recorded in the current study. The overall significantly lower sapling count on GDI was evident even when accounting for differences in soil features.

A number of abiotic and biotic factors may have contributed to the documented vegetation and soils differences between LDI and GDI. For example, GDI has a maximum elevation of about 18 m compared to 27 m on LDI. The lower elevation on GDI could expose inland habitats to more salt spray. This can explain the significantly greater soluble salt concentrations in the forest and ocean-side community, and the greater diversity of halophyte (salt-tolerant) species in the ocean-side community on GDI. It may also explain why *Festuca rubra*, a more salt-tolerant species than *Poa pratensis* (Torello and Symington 1984), was the dominant graminoid in the open communities on GDI. However, sapling counts in GDI forests were lower even when accounting for the edaphic differences.

Another factor that contributed to the vegetation differences is the land-use history of these islands. GDI has a long history of introduced mammalian herbivores, including at least 100 y of sheep and 60 y of European and Snowshoe hares, compared to LDI, which has been largely free of mammalian herbivores for at least the last 100 y (McLane 1989). Mammalian herbivores can have drastic impacts on plant communities (Crawley 1997; Donlan et al. 2002; McLaren et al. 2004; Nuñez et al. 2010; Peterson et al. 2005; Terborgh et al. 2001), so it seems plausible that the long-term history of mammalian habitation on GDI could have played a role in the vegetation and soil differences between these islands. Herbivory may shift the composition of plant species through preferential browsing and grazing of more palatable or noticeable species. Over time, this can lead to communities composed of species that are more tolerant, or less palatable, to herbivores (Díaz et al. 2001; Gillham 1955; McInnes et al. 1992). For example, *Clintonia borealis* and *Streptopus lanceolatus* have been shown to be particularly vulnerable to mammalian herbivory (Balgooyen and Waller 1995; Kraft et al. 2004; Lapointe et al. 2010), which suggests why these species may be lacking on GDI, though frequently encountered in plots on LDI.

Table 1. Soil features of Great Duck and Little Duck Islands, Maine during summers 2010–2011. All values are means \pm standard error. Elemental concentrations are reported as ppm ($\mu\text{g/g}$ dry soil). ENR (estimated nitrogen release) is reported as lbs/acre. Cation exchange capacity (CEC) and hydrogen (H) are reported as meq/100g. Soluble salts are reported as mmhos/cm. The soil features that differed significantly between islands within each community are identified by bold font (Mann-Whitney two-tailed tests; p-values adjusted with Hochberg method; $\alpha_{\text{pooled}} = 0.05$). Note: $n = 27$ for GDI Forest due to missing soil samples from two plots.

Soil Feature	Forest			Field			Ocean-side		
	GDI (n=27)	LDI (n=29)		GDI (n=19)	LDI (n=20)		GDI (n=12)	LDI (n=11)	
% Organic Matter	52.3 (± 5.97)	38.7 (± 3.29)		33.7 (± 6.31)	18.6 (± 1.42)		62.4 (± 6.79)	38.0 (± 5.45)	
ENR	1076 (± 119)	803 (± 65.9)		704 (± 126)	401 (± 28.5)		1278 (± 136)	789 (± 109)	
P	12.6 (± 2.71)	14.0 (± 1.79)		17.5 (± 4.09)	40.0 (± 4.19)		9.95 (± 2.78)	28.3 (± 4.59)	
pH	3.74 (± 0.05)	3.93 (± 0.04)		4.37 (± 0.09)	4.79 (± 0.07)		4.49 (± 0.16)	5.14 (± 0.12)	
K	66.1 (± 4.29)	74.5 (± 5.1)		69.0 (± 6.14)	89.9 (± 7.99)		90.8 (± 15.7)	176 (± 27.2)	
Mg	241 (± 19.5)	231 (± 17.2)		201 (± 25.0)	245 (± 31.4)		542 (± 83.9)	617 (± 76.4)	
Ca	312 (± 29.5)	371 (± 24.2)		411 (± 48.4)	976 (± 111)		632 (± 90.2)	1006 (± 158)	
Na	181 (± 25.8)	145 (± 9.04)		105 (± 18.4)	115 (± 18.6)		801 (± 270)	372 (± 65.5)	
H	12.9 (± 1.01)	12.6 (± 0.75)		8.22 (± 1.34)	6.63 (± 0.45)		19.1 (± 6.43)	7.23 (± 0.99)	
CEC	17.4 (± 1.34)	17.1 (± 0.99)		12.5 (± 1.73)	14.2 (± 0.99)		30.5 (± 8.10)	19.4 (± 2.01)	
Nitrate (N)	1.33 (± 0.35)	1.95 (± 0.53)		23.5 (± 5.97)	16.6 (± 4.37)		20.2 (± 7.51)	14.4 (± 3.66)	
S	18.9 (± 3.60)	14.9 (± 1.01)		16.7 (± 1.94)	16.6 (± 2.34)		287 (± 177.2)	16.2 (± 1.43)	
Soluble Salts (SS)	0.51 (± 0.05)	0.30 (± 0.02)		0.52 (± 0.05)	0.33 (± 0.03)		3.96 (± 2.41)	0.4 (± 0.06)	

Table 2. Species diversity indices for Great Duck and Little Duck Islands, Maine, during summers 2010–2011. The Shannon-Wiener diversity index is calculated using base e .

	Forest		Field		Ocean-side	
	GDI (n=29)	LDI (n=29)	GDI (n=19)	LDI (n=20)	GDI (n=12)	LDI (n=11)
Diversity Index						
Alpha (\pm SD)	11.85 (\pm 0.84)	14.14 (\pm 0.64)	19 (\pm 1.57)	12.65 (\pm 0.81)	14 (\pm 1.34)	13.27 (\pm 1.42)
Shannon-Wiener (\pm SD)	1.68 (\pm 0.08)	1.57 (\pm 0.05)	1.94 (\pm 0.07)	1.72 (\pm 0.05)	1.78 (\pm 0.09)	1.58 (\pm 0.09)

Herbivory can also affect forest succession by, directly or indirectly, suppressing or supporting the growth of certain woody species (Angell and Kielland 2009; Heinen and Currey 2000; McInnes et al. 1992; Peterson et al. 2005). *Betula papyrifera* was the primary regenerating species in forests on GDI, congruent with a study that found young *B. papyrifera* individuals to be more resistant to snowshoe hare herbivory by reducing palatability through a high resin content in juvenile twigs (Bryant et al. 1983). Almost no *Picea* spp. recruitment was encountered on GDI, consistent with a study comparing forest regeneration on two Maine islands that differed in long-term snowshoe hare herbivory (Peterson et al. 2005). This study concluded that hares were actively inhibiting the regeneration of northern spruce-fir forest through seedling browsing, reflected by a decline in tree recruitment following the introduction of the hares. We found a similar result with our histogram of tree recruitment on the Duck Islands over the last century, in which tree recruitment on GDI has declined since the introduction of hares in the 1940s (Figure 5). Lacking a better alternative hypothesis, we suggest the reduced sapling regeneration and decline in tree recruitment on GDI is due to the introduction of hares. However, future experimental work (i.e., long-term hare exclosures that track regenerating individuals to maturity) is necessary for directly testing this hypothesis (Clark et al. 1999). This is because the effect of herbivory on plant community succession may be highly context dependent—in some cases accelerating woody succession (Davidson 1993).

Vegetation differences may also be driven by soil processes, in some cases, to a greater extent than by herbivory (Turkington et al. 2002). This may be especially important when extrinsic factors such as nesting seabirds drive essential nutrient and heavy metal concentrations in the soil (Ellis 2005; Rajakaruna et al. 2009). Essential nutrient concentrations of P and Ca were about two-fold greater in the field community on LDI, and K was about two-fold greater in the ocean-side community on LDI. This may reflect a longer history of seabird nesting on LDI, which would lead to an increase in nutrient concentrations (Ellis 2005). Finally, the plants are key drivers of soil properties, and feedbacks make it impossible to distinguish cause from effect without adequate experimental data (Chapin et al. 2011).

Little Duck Island and GDI also differ in other aspects of their land-use history. Humans have not inhabited LDI over the last century, whereas GDI had at least three families with multiple dwellings, including a schoolhouse for thirty children, at its peak habitation in the early 20th century (McLane 1989). Although the primary human

impact may be directly linked to grazing by introduced sheep and browsing by introduced hares, localized agricultural plots, trail compaction, an airplane landing strip, and timber harvest may have also had important impacts on the soils and vegetation of GDI. Timber harvest may have influenced the tree demography by removing certain age classes and reducing the diversity of hardwoods in the canopy (Figures 2, 5). Human habitation of GDI has largely declined over the last century and especially, since 1986, when the lighthouse became automated. Thus, it seems unlikely that human history had a confounding influence on the most recent decline in tree recruitment. Those trees would have likely been too young to be worth harvesting until at least the 1970s and, by then, human habitation had declined. Furthermore, any human impact by trail compaction, localized agriculture, or the airplane landing strip is unlikely to be evident in our plot data since we avoided placing plots in areas with evident human disturbance. Overall species lists for the Duck Islands, however, may reflect some of these human effects. For example, several species of orchids such as *Malaxis unifolia* and *Platanthera clavellata* were found growing on the airplane landing strip on GDI and were otherwise absent from the rest of the island. Finally, it is important to acknowledge prehistoric differences in human-use between GDI and LDI and the potential impacts of shell middens on soil nutrients and vegetation structure (Cook-Patton et al. 2014). Future work may consider available archaeological history as an additional factor.

Repeated resurveys are important for gauging long-term changes in communities and ecosystems, though it would be important that a similar survey effort be made in order to yield comparable results. Most earlier surveys of the Duck Islands were not as thorough as the current study (but see Folger and Wayne 1986). For example, efforts by Redfield (1885, 1893) and Rand (1900) were based on single- or several-day surveys and, by Rappaport and Wesley (1985), on only five days. Lesser (1977) did not include any graminoids or other cryptic species. Thus, the extant surveys are not ideal for drawing conclusions about factors contributing to any documented changes. Nonetheless, some interesting anecdotes may be gleaned from historic surveys. For example, *Capsella bursa-pastoris*, an otherwise common ruderal species, was not encountered in the current study of the Duck Islands, yet it was commonly recorded on both islands in historic surveys of lesser effort. The disappearance of *C. bursa-pastoris* suggests the potential role of stochastic population drift in communities (Vellend 2010), especially as it may affect short-lived species such as *C. bursa-pastoris* on islands. Overall, 73 species were historically recorded but not found in the

current survey, which supports the idea of the dynamic nature of island community turnover as described by MacArthur and Wilson's (1967) theory of island biogeography (but see Nilsson and Nilsson 1983). Future resurveys should also include quantitative records of species abundances in order to gauge relevant changes in ecosystem properties that are otherwise lost in the coarse scale of basic floristic surveys.

Limitations of the study. We chose to avoid plant-community transition zones in our vegetation survey. Although this approach was necessary for characterizing particular plant communities, it ignores the unique characteristics of the transition zones. Several species were most common in the transition zone between forest and field, rather than in either community. These, and other species missed in plots, were captured on the total species list (Appendix). The transition between forest and field may also harbor a greater number of regenerating trees due to proximity to seed sources and increased light availability, though such data were unavailable from our study. Although our plot design does not account for all regeneration, composition, and diversity of each island, it does offer data that are comparable between these and, hopefully, future island surveys.

Our study is among the first to incorporate edaphic features and vascular plant species abundances into a robust baseline description of island ecosystems in the Gulf of Maine (but see Rajakaruna et al. 2009). Our study provides an important baseline from which to gauge future changes in coastal Maine habitats, and our causal understanding of island ecosystems will increase as more surveys are conducted and their data made available. We suggest that future island inventories incorporate plot surveys to estimate the abundance of plant species, as well as to quantify associated edaphic properties. Such baseline data and future re-surveys will be essential for better understanding the potential direct and indirect effects of climate change, rising sea levels, herbivory, and other human impacts.

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APPENDIX

CHECKLIST OF THE VASCULAR FLORA OF THE DUCK ISLANDS, MAINE, DURING SUMMERS OF 2010–2011

For each species, the table shows presence (X), absence (–), and frequency of species recorded during the 2010 (Little Duck Island; LDI) and 2011 (Greater Duck Island; GDI) surveys of the two islands. Nativity (Nativ.) is in reference to eastern North America (N = native, E = exotic). X* = species not previously recorded; X = species recorded both previously and in the current study; O = species previously recorded but not encountered in the current study (Folger and Wayne 1986; Lesser 1977; Rappaport and Wesley 1985; Redfield 1885, 1893). Plot frequency refers to the number of plots occupied by each species of vascular flora on each island (N = 60 plots for each island). Voucher specimens are deposited at the College of the Atlantic Herbarium, Bar Harbor, ME (HCOA). Nomenclature is based on Haines (2011). Rand (1900) did not distinguish between the islands so his study is excluded.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2011	LDI 2010	Frequency	
						GDI Plot	LDI Plot
ADOXACEAE	<i>Sambucus racemosa</i> L.	N	X*		X	0	1
	<i>Viburnum lantanoides</i> Michx.	N	O		–	0	0
	<i>Viburnum nudum</i> L.	N	X		X	0	0
ALLIACEAE	<i>Allium schoenoprasum</i> L.	N	X*		–	0	0
	<i>Allium</i> sp.	N/E	O		–	0	0
AMARANTHACEAE	<i>Atriplex prostrata</i> Boucher ex DC.	N	–		X	0	0
	<i>Atriplex subspicata</i> (Nutt.) Rydb.	N	–		X*	0	0
	<i>Chenopodium album</i> L.	E	X		X	3	2
	<i>Chenopodium berlandieri</i> Moq.	N	–		X*	0	0
AMARYLLIDACEAE	<i>Narcissus</i> sp.	E	X		–	0	0
ANACARDIACEAE	<i>Rhus glabra</i> L.	N	–		O	0	0
APIACEAE	<i>Angelica lucida</i> L.	N	X		X	3	12
	<i>Aralia hispida</i> Vent.	N	X		X*	2	1

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Aralia nudicaulis</i> L.	N	X	X	12	3
	<i>Daucus carota</i> L.	E	O	—	0	0
	<i>Ligusticum scoticum</i> L.	N	X	X*	1	0
APOCYNACEAE	<i>Apocynum androsaemifolium</i> L.	N	—	X	0	0
AQUIFOLIACEAE	<i>Ilex verticillata</i> (L.) Gray	N	X	X*	0	0
	<i>Ilex mucronata</i> (L.) M. Powell, Savol. & S. Andrews	N	O	—	0	0
ASTERACEAE	<i>Achillea millefolium</i> L.	N	X	X	24	14
	<i>Anaphalis margaritacea</i> (L.) Benth. & Hook. f.	N	X*	—	1	0
	<i>Cirsium arvense</i> (L.) Scop.	E	X	X	5	1
	<i>Cirsium vulgare</i> (Savi) Ten.	E	X	X*	0	0
	<i>Doellingeria umbellata</i> (P. Mill.) Nees	N	X	X	14	3
	<i>Eurybia radula</i> (Aiton) G.L. Nesom	N	O	—	0	0
	<i>Euthamia graminifolia</i> (L.) Nutt.	N	X	X*	3	0
	<i>Gnaphalium uliginosum</i> L.	E	O	—	0	0
	<i>Hieracium aurantiacum</i> L.	E	X	X*	0	0
	<i>Hieracium caespitosum</i> Dumort.	E	X	X	0	0
	<i>Hieracium kahnia</i> L.	N	O	—	0	0
	<i>Hieracium pilosella</i> L.	E	X	O	0	0
	<i>Hieracium</i> sp.	N/E	X*	X	14	2
	<i>Matricaria discoidea</i> DC.	E	X	X	0	0
	<i>Nabalus altissimus</i> (L.) Hook.	N	X	X	0	0
	<i>Nabalus serpentarius</i> (Pursh) Hook.	N	O	—	0	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Nabulus trifoliolatus</i> Cass.	N	—	X	2	15
	<i>Oclemena acuminata</i> (Michx.) Nesom	N	X	X	26	19
	<i>Oclemena nemoralis</i> (Aiton) Greene	N	X	—	0	0
	<i>Scorzoneroideis autumnalis</i> (L.) Moench	E	X	X	6	0
	<i>Senecio viscosus</i> L.	E	—	X*	0	0
	<i>Senecio vulgaris</i> L.	E	X	O	1	0
	<i>Solidago canadensis</i> L.	N	X	—	2	0
	<i>Solidago puberula</i> Nutt.	N	X	—	2	0
	<i>Solidago rugosa</i> P. Mill.	N	X	X	11	20
	<i>Solidago sempervirens</i> L.	N	X	X	0	4
	<i>Sonchus arvensis</i> L.	E	X*	X	1	1
	<i>Sonchus asper</i> (L.) Hill	E	X	—	3	0
	<i>Sonchus oleraceus</i> L.	E	—	X*	0	1
	<i>Synphytochium novi-belgij</i> (L.) Nesom	N	X	X	34	31
	<i>Tanacetum vulgare</i> L.	E	X	—	0	0
	<i>Taraxacum laevigatum</i> (Willd.) DC.	E	—	O	—	—
	<i>Taraxacum officinale</i> G.H. Weber ex Wiggers	E	X	X	3	7
BALSAMINACEAE	<i>Impatiens capensis</i> Meerb.	N	X	X	5	4
	<i>Impatiens pallida</i> Nutt.	N	O	—	0	0
BETULACEAE	<i>Betula alleghaniensis</i> Britton	N	X	X	0	6
	<i>Betula cordifolia</i> Regel	N	—	X*	0	0
	<i>Betula papyrifera</i> Marshall	N	X	X	6	11
BORAGINACEAE	<i>Symphytum officinale</i> L.	E	X	—	0	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
BRASSICACEAE	<i>Barbarea vulgaris</i> Aiton f.	E	—	O	0	0
	<i>Cakile edentula</i> (Bigelow) Hook.	N	X	X	1	0
	<i>Capsella bursa-pastoris</i> (L.) Medik.	E	O	O	0	0
	<i>Cardamine parviflora</i> L.	N	O	—	0	0
	<i>Cardamine pensylvanica</i> Muhl. ex Willd.	N	—	O	0	0
	<i>Rorippa palustris</i> (L.) Bess.	N	—	O	0	0
	<i>Sisymbrium officinale</i> (L.) Scop.	E	X*	X	1	0
	<i>Campanula rotundifolia</i> L.	N	—	X*	0	0
	<i>Diervilla lonicera</i> P. Mill.	N	X	X	0	3
	<i>Linnæa borealis</i> L.	N	X	X	1	8
CAMPANULACEAE	<i>Lonicera canadensis</i> Bartram ex Marshall	N	—	X	0	11
	<i>Valeriana officinalis</i> L.	E	—	X*	0	2
	<i>Cerastium arvense</i> L.	E	X	X	16	8
	<i>Cerastium fontanum</i> Baumg.	E	X	X	4	12
	<i>Cerastium glomeratum</i> Thuill.	E	O	—	0	0
	<i>Moehringia lateriflora</i> (L.) Fenzl	N	X	X	18	24
	<i>Sagina procumbens</i> L.	N	X	X*	2	0
	<i>Spergularia marina</i> (L.) Griseb.	N	X*	X	1	0
	<i>Spergularia rubra</i> (L.) J. & K. Presl	E	X	—	2	0
	<i>Stellaria graminea</i> L.	E	X	X	1	0
CONVOLVULACEAE	<i>Stellaria media</i> (L.) Vill.	E	X	X	1	3
	<i>Calystegia sepium</i> (L.) R.Br.	N	X*	X	9	8
	<i>Cuscuta gronovii</i> Willd. ex J.A. Schultes	N	X*	X	3	6

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
CORNACEAE	<i>Ipomoea purpurea</i> (L.) Roth	E	—	O	0	0
	<i>Chamaepericlymenum canadense</i> (L.) Aschers. & Graebn.	N	X	X	27	4
CUPRESSACEAE	<i>Juniperus communis</i> L.	N	X	—	0	0
CYPERACEAE	<i>Bolboschoenus maritimus</i> (L.) Palla	N	X	X*	1	0
	<i>Carex atlantica</i> Bailey	N	X*	—	1	0
	<i>Carex brunnescens</i> (Pers.) Poir.	N	X	X*	1	1
	<i>Carex canescens</i> L.	N	O	O	0	0
	<i>Carex debilis</i> Michx.	N	O	O	0	0
	<i>Carex folliculata</i> L.	N	—	X*	0	0
	<i>Carex gymandra</i> Schwein.	N	—	X	0	0
	<i>Carex hormathoides</i> Fernald	N	—	X*	3	0
	<i>Carex mackenziei</i> Kreez.	N	X	—	0	0
	<i>Carex magellanica</i> Lam.	N	O	—	0	0
	<i>Carex nigra</i> (L.) Reichard	N	X	—	7	0
	<i>Carex paleacea</i> Schreb. ex Wahlenb.	N	O	—	0	0
	<i>Carex pallescens</i> L.	N	O	—	0	0
<i>Carex pensylvanica</i> Lam.	N	X	—	1	0	
<i>Carex stipata</i> Muhl. ex Willd.	N	—	X*	0	0	
<i>Carex stricta</i> Lam.	N	O	—	0	0	
<i>Carex trisperma</i> Dewey	N	X	—	18	0	
<i>Eleocharis</i> sp.	N/E	O	O	X*	0	0
<i>Eleocharis tenuis</i> (Willd.) J.A. Schultes	N	X*	—	—	0	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
DENNSTAEDTIACEAE	<i>Eleocharis uniglumis</i> (Link) J.A. Schultes	N	O	-	0	0
	<i>Eriophorum angustifolium</i> Honckeny	N	X	-	0	0
	<i>Dennstaedtia punctilobula</i> (Michx.) T. Moore	N	X	-	2	0
	<i>Pteridium aquilinum</i> (L.) Kuhn	N	-	X	0	0
	<i>Drosera rotundifolia</i> L.	N	X	-	3	0
	<i>Dryopteris campyloptera</i> (Kunze) Clarkson	N	-	X	0	0
	<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs	N	X	O	0	0
	<i>Dryopteris</i> sp.	N	X*	X	24	32
	<i>Elaeagnus angustifolia</i> L.	E	O	-	0	0
	<i>Equisetum arvense</i> L.	N	X	X	1	1
ERICACEAE	<i>Empetrum nigrum</i> L.	N	X	-	0	0
	<i>Gaultheria hispida</i> (L.) Muhl. ex Bigelow	N	O	O	0	0
	<i>Kalmia angustifolia</i> L.	N	X	-	1	0
	<i>Moneses uniflora</i> (L.) Gray	N	X	X	2	0
	<i>Monotropa uniflora</i> L.	N	X	X	5	4
	<i>Rhododendron canadense</i> (L.) Torr.	N	X*	-	0	0
	<i>Vaccinium angustifolium</i> Aiton	N	X	X	13	1
	<i>Vaccinium macrocarpon</i> Aiton	N	X	O	3	0
	<i>Vaccinium oxycoccos</i> L.	N	X	-	0	0
	<i>Vaccinium vitis-idaea</i> L.	N	X	X*	9	0
FABACEAE	<i>Lathyrus japonicus</i> Willd.	N	X	X	2	9
	<i>Lathyrus palustris</i> L.	N	X	X	1	2
	<i>Trifolium arvense</i> L.	E	-	X*	0	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Trifolium aureum</i> Pollich	E	X	X*	0	0
	<i>Trifolium pratense</i> L.	E	X	—	0	0
	<i>Trifolium repens</i> L.	E	X	X	13	5
	<i>Vicia cracca</i> L.	E	X	X	0	0
GERANIACEAE	<i>Geranium robertianum</i> L.	N	X	X	1	5
GROSSULARIACEAE	<i>Ribes glandulosum</i> Grauer	N	X	X	0	27
	<i>Ribes hirtellum</i> Michx.	N	O	X*	0	1
	<i>Ribes lacustre</i> (Pers.) Poir.	N	X*	—	0	0
	<i>Ribes triste</i> Pallas	N	—	O	0	0
HEMEROCALLIDACEAE	<i>Hemerocallis fulva</i> (L.) L.	E	X	—	0	0
HUPERZIACEAE	<i>Huperzia lucidula</i> (Michx.) Trevisan	N	—	X	0	0
HYPERICACEAE	<i>Hypericum canadense</i> L.	N	X	—	0	0
	<i>Hypericum perforatum</i> L.	E	—	X*	0	0
	<i>Triadenum virginicum</i> (L.) Raf.	N	X	—	0	0
IRIDACEAE	<i>Iris hookeri</i> Penny ex D. Don	N	O	—	0	0
	<i>Iris</i> sp. (cultivated)	N/E	O	—	0	0
	<i>Iris versicolor</i> L.	N	X	X	5	0
	<i>Sisyrinchium angustifolium</i> Mill.	N	O	—	0	0
	<i>Sisyrinchium atlanticum</i> Bicknell	N	O	—	0	0
	<i>Sisyrinchium montanum</i> Greene	N	X	—	1	0
JUNCACEAE	<i>Juncus balticus</i> Willd.	N	X	—	2	0
	<i>Juncus brevicaudatus</i> (Engelm.) Fernald	N	X*	—	1	0
	<i>Juncus bufonius</i> L.	N	O	X*	0	1

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Juncus effusus</i> L.	N/E	-	X	0	0
	<i>Juncus gerardii</i> Loisel.	N	X	X	2	0
	<i>Juncus pelocarpus</i> E. Mey.	N	O	-	0	0
	<i>Juncus tenuis</i> Willd.	N	X	-	2	0
	<i>Luzula multiflora</i> (Ehrh.) Lej.	N	X	X*	12	0
JUNCAGINACEAE	<i>Triglochin maritima</i> L.	N	X	-	2	0
LAMIACEAE	<i>Galeopsis bifida</i> Boenn.	E	X*	X*	2	4
	<i>Galeopsis tetrahit</i> L.	E	X	O	2	0
	<i>Lycopus americanus</i> Muhl. ex W. Bart.	N	X	-	4	0
	<i>Lycopus virginicus</i> L.	N	X	-	1	0
	<i>Mentha arvensis</i> L.	E	X	-	0	0
	<i>Scutellaria galericulata</i> L.	N	X	X	4	1
LILIACEAE	<i>Clintonia borealis</i> (Aiton) Raf.	N	O	X	0	27
	<i>Streptopus lanceolatus</i> (Aiton) Reveal	N	X	X	0	24
LINACEAE	<i>Linum radiola</i> L.	E	O	-	0	0
LYCOPODIACEAE	<i>Lycopodiella inundata</i> (L.) Holub	N	X*	-	0	0
	<i>Lycopodium clavatum</i> L.	N	X	O	1	0
LYTHRACEAE	<i>Lythrum salicaria</i> L.	E	O	-	0	0
MENYANTHACEAE	<i>Menyanthes trifoliata</i> L.	N	O	-	0	0
MYRICACEAE	<i>Comptonia peregrina</i> (L.) Coult.	N	O	-	0	0
	<i>Morella carolinensis</i> (P. Mill.) Small	N	X	-	0	0
	<i>Myrica gale</i> L.	N	X	-	1	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
MYRSINACEAE	<i>Lysimachia borealis</i> (Raf.) U. Manns & A. Anderb.	N	X	X	23	22
	<i>Lysimachia maritima</i> (L.) Galasso, Banfi & Soldano	N	X	—	0	0
	<i>Lysimachia terrestris</i> (L.) Britton, Sterns & Poggenb.	N	X	—	3	0
ONAGRACEAE	<i>Chamerion angustifolium</i> (L.) Scop.	N	X	X	3	17
	<i>Circea alpina</i> L.	N	X	X	5	1
	<i>Epilobium ciliatum</i> Raf.	N	X	X	2	2
	<i>Epilobium coloratum</i> Biehler	N	O	—	0	0
	<i>Epilobium leptophyllum</i> Raf.	N	X	—	0	0
	<i>Epilobium palustre</i> L.	N	O	—	0	0
	<i>Oenothera biennis</i> L.	N	X	—	0	0
	<i>Oenothera perennis</i> L.	N	X	—	1	0
ONOCLEACEAE	<i>Onochea sensibilis</i> L.	N	X	—	0	0
OPHIGLOSSACEAE	<i>Botrychium</i> sp.	N	X*	—	0	0
ORCHIDACEAE	<i>Cypripedium acaule</i> Aiton	N	X	—	1	0
	<i>Malaxis unifolia</i> Michx.	N	X	—	1	0
	<i>Platanthera clavellata</i> (Michx.) Luer	N	X	—	4	0
	<i>Platanthera lacera</i> (Michx.) G. Don	N	X	—	2	0
	<i>Pogonia ophioglossoides</i> (L.) Ker-Gawl.	N	X	—	0	0
	<i>Spiranthes cernua</i> (L.) L.C. Rich.	N	X	—	0	0
OROBANCHACEAE	<i>Euphrasia nemorosa</i> (Pers.) Wallr.	N	X	—	3	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Euphrasia randii</i> B.L. Robins.	N	X	-	0	0
	<i>Euphrasia stricta</i> D. Wolff ex J.F. Lehm.	E	O	-	0	0
OSMUNDACEAE	<i>Osmundastrum cinnamomeum</i> (L.) C. Presl	N	X	X	5	1
OXALIDACEAE	<i>Oxalis montana</i> Raf.	N	X	X	17	25
	<i>Oxalis stricta</i> L.	N	O	O	0	0
PINACEAE	<i>Abies balsamea</i> (L.) P. Mill.	N	X	X	1	29
	<i>Picea glauca</i> (Moench) Voss	N	X	X	8	5
	<i>Picea rubens</i> Sarg.	N	X	X	18	16
PLANTAGINACEAE	<i>Hippuris vulgaris</i> L.	N	O	-	0	0
	<i>Plantago major</i> L.	E	X	X	0	0
	<i>Plantago maritima</i> L.	N	X	X	5	3
	<i>Veronica arvensis</i> L.	E	-	O	0	0
	<i>Veronica peregrina</i> L.	N	O	-	0	0
POACEAE	<i>Agrostis scabra</i> Willd.	N	X	-	5	0
	<i>Agrostis</i> sp.	N/E	X	X	22	2
	<i>Agrostis stolonifera</i> L.	E	X*	X	0	0
	<i>Alopecurus pratensis</i> L.	E	X*	-	1	0
	<i>Anthoxanthum nitens</i> (Weber) Y. Schouten & Veldkamp	N	X	-	1	0
	<i>Anthoxanthum odoratum</i> L.	E	X	-	2	0
	<i>Calamagrostis canadensis</i> (Michx.) Beauv.	N	X	X*	7	0
	<i>Cinna latifolia</i> (Trev. ex Goepf.) Griseb.	N	-	X*	0	2
	<i>Dactylis glomerata</i> L.	E	O	-	0	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Danthonia spicata</i> (L.) Beauv. ex Roemer & J.A. Schultes	N	O	—	0	0
	<i>Deschampsia flexuosa</i> (L.) Trin.	N	X	—	10	0
	<i>Dichanthelium boreale</i> (Nash) Freckmann	N	X*	—	0	0
	<i>Elymus repens</i> (L.) Gould	E	X*	X	3	21
	<i>Elymus trachycaulis</i> (Link) Gould ex Shinners	N	—	O	0	0
	<i>Elymus virginicus</i> L.	N	X	X*	1	4
	<i>Festuca rubra</i> L.	N/E	X	X	29	9
	<i>Hordeum jubatum</i> L.	N	O	—	0	0
	<i>Panicum</i> sp.	N/E	O	—	0	0
	<i>Phleum pratense</i> L.	E	X	X*	5	0
	<i>Poa alsodes</i> Gray	N	—	X*	0	0
	<i>Poa compressa</i> L.	E	O	X	0	0
	<i>Poa palustris</i> L.	N	—	X	0	4
	<i>Poa pratensis</i> L.	N/E	X	X	17	29
	<i>Poa trivialis</i> L.	E	—	X*	0	0
	<i>Schedonorus pratensis</i> (Huds.) Beauv.	E	O	—	0	0
	<i>Spartina pectinata</i> Link	N	O	—	0	0
	<i>Fallopia cilioidis</i> (Michx.) Holub	N	—	X	0	0
	<i>Fallopia convolvulus</i> (L.) A. Löve	E	—	X*	0	0
	<i>Fallopia scandens</i> (L.) Holub	N	—	O	0	0
	<i>Polygonum aviculare</i> L.	E	O	O	0	0
	<i>Polygonum buxiforme</i> Small	N	X*	X*	1	0

POLYGONACEAE

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Rheum rhabarbarum</i> L.	E	X*	-	0	0
	<i>Rumex acetosella</i> L.	E	X	X	20	5
	<i>Rumex crispus</i> L.	E	X	X	6	5
	<i>Rumex longifolius</i> DC.	E	-	X*	0	4
	<i>Rumex obtusifolius</i> L.	E	-	X	0	0
	<i>Rumex pallidus</i> Bigelow	N	-	O	0	0
	<i>Polypodium virginianum</i> L.	N	-	X	0	11
POLYPODIACEAE	<i>Montia fontana</i> L.	N	O	-	0	0
PORTULACACEAE	<i>Coptis trifolia</i> (L.) Salisb.	N	X	X	9	0
RANUNCULACEAE	<i>Ranunculus acris</i> L.	E	X	X	9	1
	<i>Ranunculus bulbosus</i> L.	E	-	O	0	0
	<i>Ranunculus cymbalaria</i> Pursh	N	O	-	0	0
	<i>Ranunculus repens</i> L.	E	O	-	0	0
	<i>Thalictrum pubescens</i> Pursh	N	X	X	3	4
	<i>Amelanchier laevis</i> Wiegand	N	O	X*	0	0
ROSACEAE	<i>Amelanchier</i> sp.	N	X*	X	0	4
	<i>Argentina anserina</i> (L.) Rydb.	N	O	O	0	0
	<i>Argentina egedii</i> (Wormsk.) Rydb.	N	X*	X*	3	0
	<i>Aronia floribunda</i> (Lindl.) Spach	N	X	-	0	0
	<i>Aronia melanocarpa</i> (Michx.) Elliott	N	X	-	1	0
	<i>Fragaria virginiana</i> Duchesne	N	X	X	25	20
	<i>Malus pumila</i> P. Mill.	E	X	X	0	0
	<i>Potentilla argentea</i> L.	E	O	-	0	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Potentilla argentea</i> L.	E	O	—	0	0
	<i>Potentilla canadensis</i> L.	N	O	O	0	0
	<i>Potentilla norvegica</i> L.	N	X	X	0	3
	<i>Potentilla simplex</i> Michx.	N	X	—	8	0
	<i>Prunus pennsylvanica</i> L. f.	N	—	X	0	0
	<i>Rosa nitida</i> Willd.	N	X	—	3	0
	<i>Rosa rugosa</i> Thunb.	E	X	X*	3	0
	<i>Rosa</i> sp. (cultivated)	N/E	O	—	0	0
	<i>Rosa virginiana</i> P. Mill.	N	X*	—	1	0
	<i>Rubus hispидus</i> L.	N	X	—	17	0
	<i>Rubus idaeus</i> L.	N/E	X	X	25	33
	<i>Rubus pubescens</i> Raf.	N	X	X	7	0
	<i>Sibbaldopsis tridentata</i> (Aiton) Rydb.	N	X	—	0	0
	<i>Sorbus americana</i> Marshall	N	X	X	0	0
	<i>Sorbus aucuparia</i> L.	E	—	O	0	0
	<i>Sorbus decora</i> (Sargent) Schneid.	N	—	X*	0	0
	<i>Sorbus</i> sp.	N/E	X*	X	20	26
	<i>Spiraea alba</i> Du Roi	N	X	—	7	0
	<i>Spiraea tomentosa</i> L.	N	X*	—	0	0
RUBIACEAE	<i>Galium aparine</i> L.	N	X	X	1	3
	<i>Galium triflorum</i> L.	N	O	—	0	0
	<i>Galium triflorum</i> Michx.	N	X	X*	1	1
RUPPIACEAE	<i>Ruppia maritima</i> L.	N	O	—	0	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
RUSCACEAE	<i>Maianthemum bifolium</i> (L.) F. W. Schmidt	N	O	-	0	0
	<i>Maianthemum canadense</i> Desf.	N	X	X	37	32
	<i>Maianthemum trifolium</i> (L.) Sloboda	N	X	-	2	0
SALICACEAE	<i>Populus grandidentata</i> Michx.	N	-	O	0	0
	<i>Populus tremuloides</i> Michx.	N	-	X	0	1
	<i>Salix bebbiana</i> Sargent	N	-	O	0	0
	<i>Salix discolor</i> Muhl.	N	-	X	0	0
	<i>Salix</i> sp.	N/E	X	-	0	0
SAPINDACEAE	<i>Acer pensylvanicum</i> L.	N	-	X	0	25
	<i>Acer platanoides</i> L.	E	-	X*	0	0
	<i>Acer rubrum</i> L.	N	X	X	2	0
	<i>Acer spicatum</i> Lam.	N	-	X	0	26
	<i>Selaginella selaginoides</i> (L.) P. Beauv. ex Mart. & Schrank	N	-	O	0	0
SOLANACEAE	<i>Solanum dulcamara</i> L.	E	X	X	2	8
	<i>Solanum nigrum</i> L.	E	O	-	0	0
THELYPTERIDACEAE	<i>Thelypteris palustris</i> Schott	N	O	-	0	0
TYPHACEAE	<i>Typha latifolia</i> L.	N	X	-	0	0
URTICACEAE	<i>Urtica dioica</i> L.	N/E	X*	X	2	8
	<i>Urtica</i> sp.	N/E	O	-	0	0
VIOLACEAE	<i>Viola blanda</i> Willd.	N	-	X	0	0
	<i>Viola cucullata</i> Aiton	N	-	O	0	0
	<i>Viola lanceolata</i> L.	N	X	-	3	0

APPENDIX. Continued.

Family	Scientific Name	Nativ.	GDI 2011	LDI 2010	Frequency	
					GDI Plot	LDI Plot
	<i>Viola pallens</i> (Banks ex DC.) Brainerd	N	X	—	0	0
	<i>Viola sororia</i> Willd.	N	X	—	0	0
	<i>Viola</i> sp.	N/E	X	X	17	5
	<i>Athyrium angustum</i> (Willd.) C. Presl.	N	—	X	0	0
	<i>Deparia acrostichoides</i> (Sw.) M. Kato	N	—	X	0	0
	<i>Gymnocarpium dryopteris</i> (L.) Newman	N	—	X*	0	0

WOODSIACEAE