Habitat associations of macrolichens on a boreal island in the Bay of Fundy, New Brunswick, Canada

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ABSTRACT. Compared to the mainland, boreal oceanic islands would be expected to have a depauperate lichen biota because of their isolation, small area, exposure to salt spray and structurally simple habitats. We surveyed the macrolichens (non-crustose lichens) and quantified habitat associations on Kent Island, an 80-hectare island that lies at the mouth of the Bay of Fundy, New Brunswick, Canada. A total of 43 species in 13 genera were identified, which represents 19% of the macrolichen species richness of Fundy National Park on the mainland coast of New Brunswick. Cyanolichens were not found on Kent Island. Nearly 75% of Kent Island's macrolichen species had boreal biogeographical affinities, despite the island's temperate latitude (44°35′N) and low elevation, due to the chilling influence of the locally upwelling Labrador Current. Multi-response Permutation Procedures and Indicator Species Analysis demonstrated non-random habitat associations among Kent Island's macrolichen species and moderate but significant differences in lichen communities among five forest types on the island.

KEYWORDS. Macrolichens, Kent Island, New Brunswick, Canada, Bowdoin Scientific Station, island biogeography, boreal, habitat associations, communities, indicator species, Multi-response Permutation Procedures.

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The isolation and small area of islands reduce colonization rates and increase the probability of local extinction of most taxa, and islands tend to have reduced habitat diversity compared to the mainland (MacArthur & Wilson 1967; Simberloff 1974). As a result, lichen communities on islands would be expected to have fewer species and a greater proportion of habitat generalists than mainland lichen communities.

Boreal oceanic islands present particular challenges for many species because of their harsh physical environment (e.g., low summer temperatures, strong winds, reduced solar radiation, dense and acidic fog, salt spray; Cunningham 1998).

THE BRYOLOGIST 112(4), pp. 762–772 0007-2745/09/$1.25/0

Although such factors may not pose problems for lichens (except for acidity and salt spray), extreme environmental conditions limit the diversity of tree species and the structural complexity of potential habitats for lichens.

Lichen communities have been surveyed in a few archipelagoes (Jüriado et al. 2006; Seaward & Aptroot 2000; Talbot et al. 2002) and the predictions of island biogeography theory have been tested in lichen communities on the mainland in boreal forest fragments (Berglund & Jonsson 2001) and on rock outcrops (Armesto & Contreras 1981; Lawrey 1992). However, the community ecology of lichens on boreal oceanic islands remains poorly known.

We studied foliose and fruticose lichens (macrolichens) on Kent Island, a boreal oceanic island in the Bay of Fundy, New Brunswick, Canada. The only previous published study of lichens in the Bay of Fundy was conducted on the mainland, in Fundy National Park (Gowan & Brodo 1988), although collections from local islands made by earlier lichenologists are included in taxonomic works. The main goals of our study were to survey the macrolichen biota of Kent Island, characterize its biogeographical affinities, describe habitat associations and gain insights about lichen community structure under simple island conditions. We were particularly interested in whether lichens on a boreal island showed significant habitat preferences among forest types or tree species in spite of reduced habitat diversity and predicted generalist lichen colonists. We also compared Kent Island's lichen biota with similar-sized islands differing in isolation and latitude. Finally, by describing the abundance and distribution of lichens on Kent Island, we aimed to provide baseline data for monitoring possible long-term changes in lichen communities in response to climate change, eradication of introduced herbivores or other disturbances (Holt et al. 2008; McCune 2000).

METHODS

Study area. We measured the distribution of macrolichens in five distinct forest types on Kent Island, New Brunswick, Canada (44°35′N, 66°46′W) in June and July 2007. Kent Island, site of the Bowdoin Scientific Station, is 80 ha in area, 3 km long and 0.5 km wide at the widest point. Oriented north-south, its highest elevation is only about 20 m above sea level. It is the largest island in the Three Islands Archipelago, which is located 9 km south of Grand Manan Island and isolated in the Bay of Fundy by more than 29 km from the mainland of Maine, New Brunswick and Nova Scotia. The island's bedrock, predominantly granite with mafic dykes, is covered in glacial till except where exposed along the shore and in a few hilltop outcrops in the southern end of the island. Several limestone-dolomite assemblages with large quartz veins are visible on the west side of the island (Ritchie 1985). Soil pH averages 5.5, although soils are more acidic (pH 4.9) on the south hill, presumably due to defecation by herring gulls (*Larus argentatus*) which for centuries have bred there by the thousands (Cannell & Maddox 1983; McCain 1975).

Kent Island has a boreal climate despite its temperate latitude and low elevation. Mean temperatures in June and July are only 12.3°C, which is substantially cooler than the mainland (unpubl. data 1938–2008, Bowdoin Scientific Station). Precipitation averages less than 10 cm/month, but because thick fog (visibility less than 0.5 km) occurs on an average of 15.9 days/month in the summer, the island is typically damp. Cool, moisture-laden winds blow predominantly from the south, southwest or west (62% of observations) at mean maximum daily wind speeds of 27.2 km/hr.

Of the 280 species of vascular plants that occur on Kent Island, about 10% are woody plants, mostly shrubs (McCain 1975; McIlraith 1986). Just six tree species dominate the island's forests, which cover the northern half of the island (see below). The unforested southern half of the island is comprised mostly of open shoreline habitats and abandoned agricultural fields which were farmed from the early 19th century until the 1930s for root crops, hay production and sheep-grazing. Secondary succession in the fields has been largely arrested due to the harsh climate, competition by aggressive plants such as mountain wood fern (*Dryopteris campyloptera*), rough goldenrod (*Solidago rugosa*) and raspberry (*Rubus idaeus*), trampling and plucking of plants by nesting herring gulls and intense browsing of tree seedlings by snowshoe hares (*Lepus americanus*)

(Peterson et al. 2005). Introduced to the archipelago in 1959, the hares were finally eradicated in 2007. This study will permit an evaluation of the effect of habitat change on lichen communities as the forest recovers in the absence of hares. Other than bats, the only other mammal species on Kent Island are muskrats (*Ondatra zibethicus*).

Lichen communities and habitat associations. We compared macrolichen communities in 25 plots representing five distinct forest types on Kent Island. The forest types differed in dominant tree species, age and physical structure: (1) heartleaf birch (*Betula cordifolia*), (2) mountain ash (*Sorbus americana*), (3) white spruce (*Picea glauca*), (4) balsam fir (*Abies balsamea*) and (5) mixed coniferous-deciduous forest dominated by balsam fir, red spruce (*P. rubens*), yellow birch (*B. alleghaniensis*) and heartleaf birch with scattered mountain ash (**Table 1**). (The few other tree species that occur on Kent Island are represented by no more than 10 individuals (*Larix larcina*, *Acer spicatum*, *Amalanchier* sp.) or just a single individual (*Betula populifolia*, *Salix* sp., *Alnus viridis*), other than the relatively common small wetland tree, *Alnus incana*.) Except for the mixed forest, the forest patches were small (0.2–0.5 ha), even-aged, mostly monospecific stands of similar height that became established following local disturbances (mountain ash patches by a wildfire in 1946; balsam fir stands by a logging operation in the early 1950s), or that were the only trees able to recruit on forest edges after the introduction of snowshoe hares (heartleaf birch, white spruce invading field edges). The mixed forest was the only forest type on Kent Island that had not been substantially altered during the last century. The understory of each forest type was structurally simple and species-poor, with a dense cover of wood ferns and whorled aster (*Oclemena acuminata*) in more open forests (heartleaf birch, mountain ash), mosses and herbaceous plants such as common wood sorrel (*Oxalis montana*) in forests with closed canopies (balsam fir, mixed forest) and a thick layer of dead needles with little or no understory vegetation in the densely shaded white spruce forests. We collected bark samples from three trees of each of the major species and, using a pH meter, measured bark pH from pulverized dry bark samples in deionized water,

Table 1. Characteristics and macrolichen species richness of different forest types on Kent Island. Notes: *p*-values based on one-way ANOVA (*), t-test (+) and one-sample chi-square test (−). Values in parentheses = 1 S.E.

	Forest types						
	Deciduous			Coniferous			
	Heartleaf Birch	Mountain Ash	Mixed Forest	White Spruce	Balsam Fir	*P* forest types	*P* deciduous vs. coniferous
Number of quadrats	123	123	123	123	100		
Mean bark pH	4.5 (± 0.4)	4.8 (± 0.003)	4.6 (± 0.2)	4.3 (± 0.01)	4.3 (± 0.02)	*<0.001**	0.24$^+$
Forest age (years)	30–45	61	> 110	30–45	55		
Light levels/canopy openness	medium-high	medium	low	very low	very low		
Tree density	low	low	medium	high	high		
Mean number of macrolichen species/plot	13.8 (± 1.0)	14.0 (± 0.7)	13.2 (± 0.7)	11.6 (± 1.1)	12.4 (± 0.8)	0.32*	0.07$^+$
Total number of macrolichen species	24	24	21	23	20	0.96$^-$	0.13$^-$

following Frati et al. (2007). The dominant tree species differed in the pH of their bark, with mountain ash having a significantly higher pH than other species (one-way ANOVA, $P<0.001$; **Table 1**).

Within each forest type, we selected five 5 × 5 m replicate plots, each of which was separated from other plots by at least 50 m (total N = 25 plots). Within each plot, we haphazardly chose three representative live trees with a diameter at breast height (DBH) greater than 10 cm. We used 25 × 25 cm quadrats to determine the presence or absence of lichen species on the ground, and 62.5 × 10 cm quadrats to determine presence or absence on higher branches and on the trunk of the tree at two heights, 0–62.5 cm and 62.5–125 cm above the ground (N = 1–4/location/tree). Additional quadrats were haphazardly sampled on the ground away from the tree, resulting in a total of 20–43 sampled quadrats per plot (total N = 592 quadrats, each 625 cm^2). We also conducted general surveys of each forest type to record lichens found outside of quadrats, on dead standing and fallen trees and in the upper canopy. Because of the three-dimensional nature and densely overlapping spatial distribution of macrolichens on Kent Island, we did not estimate percent cover, nor did we attempt to measure specific microhabitat variables (e.g., stratum, trunk diameter, bark vs. bare wood, upper vs. lower branch or trunk surfaces; McCune et al. 2000).

Table 1 summarizes the physical characteristics of each forest type. Although light levels differed appreciably among forest types, temperatures varied little because of the overwhelming thermal influence of the ocean and the narrowness of the island (**Table 1**).

In addition to measuring frequency of occurrence of macrolichens in different forest types, we conducted surveys in open fields (N = 8 plots) and on rock outcrops along the shore (N = 6 plots) using quadrat and transect sampling. Fields were dominated by native and introduced grasses, woody shrubs such as lowbush blueberry (*Vaccinium angustifolium*) and raspberry, and various herbaceous plants (McCain 1975), with lichens occurring on living and dead wood, rock outcrops and the ground. The shoreline was mostly exposed granite covered with *Verrucaria* spp., other crustose lichens and cyanobacteria (*Calothrix* spp.).

Lichens were identified in the laboratory using a 10×-dissecting microscope and chemical spot tests (Brodo et al. 2001). Nomenclature followed Brodo et al. (2001), Gowan and Brodo (1988) and Hinds and Hinds (2007). Voucher specimens are housed at the Bowdoin Scientific Station on Kent Island and at Bowdoin College. We assigned biogeographical zones for each species based on information in Ahti (1964, 1977, 1983), Brodo et al. (2001) and Hinds and Hinds (2007), as follows: circumpolar boreal (normally restricted to the boreal zone, or widespread throughout the boreal zone and with its center of distribution there), oceanic boreal (limited to coastal boreal habitats with relatively mild winters and cool foggy summers), temperate (widespread, especially in hardwood-dominated forests with cool winters and warm summers) and oceanic temperate.

Data analysis. Frequency of occurrence of a particular lichen species in a given forest type (a measure of the lichen's abundance and habitat preference) and in all forest types combined was calculated by dividing the number of quadrats in which the species occurred by the total number of quadrats sampled (**Table 2**). Non-metric Multi-response Permutation Procedures (MRPP; McCune & Mefford 2005) was performed to compare lichen species composition among forest types. Frequencies of the 23 identified lichen species qualified in forest (as opposed to open or shoreline) habitats were relativized by the maximum value for each species across forest types. MRPP compared observed versus randomly generated frequencies to determine the probability that differences in species composition among forest types could have occurred by chance (McCune et al. 2000). The statistic A reflects the chance-corrected within-group agreement between sampling units (i.e., effect size, or similarity of lichen species composition in plots within versus between forest types). $A = 0$ indicates that lichen communities in distinct forest types are no more different than expected by chance, and $A = 1$ indicates that plots within a forest type are identical to each other in lichen species composition but completely distinct from plots in other forest types; $A > 0.1$ is interpreted as showing biologically significant differences among forest types (McCune & Grace 2002).

Table 2. Mean frequency of occurrence of macrolichen species in 25 × 25 cm quadrats (N = 592) in five different forest types on Kent Island, New Brunswick, Canada. Species occurring in at least 10% of quadrats within one or more forest types are denoted in **bold**. Lichen biogeographical zones (after Ahti 1964; Brodo 2001; Gowan & Brodo 1988): A = circumpolar boreal, B = oceanic boreal, C = widespread temperate, D = oceanic temperate, U = unknown. Notes: [1]recorded also in 1993 survey (Wheelwright 1993); [2]recorded also in 1996 survey (Wheelwright 1996); [+]infrequently encountered outside quadrats; [R]found only on granite bedrock along the shore; [O]found only in open field plots. *p*-values based on Monte Carlo Test from Indicator Species Analysis; significant habitat associations *italicized* (alpha = 0.05).

		Frequency of occurrence in different forest types						
		Deciduous		**Coniferous**				
Species	**Range**	**Heartleaf Birch**	**Mountain Ash**	**Mixed Forest**	**White Spruce**	**Balsam Fir**	**Overall Frequency**	***P***
Alectoria sarmentosa	B					+		
Bryoria fuscescens	A	0.02		0.05	0.01	+	0.02	*0.02*
B. nadvornikiana	C	0.06	0.01	0.10	+	0.02	0.04	0.68
B. trichodes [1]	B	0.20	0.11	0.46	0.12	0.31	0.24	0.28
Cladonia arbuscula [2, O]	A							
C. cenotea	A		0.01				0.002	1.00
C. chlorophaea [1]	A	0.02	0.06				0.02	0.11
C. coniocraea	A	0.18	0.32	0.31	0.13	0.47	0.28	*0.05*
C. cristatella	C			+				
C. digitata	D	0.10	0.14	0.07	0.05	0.06	0.08	0.74
C. fimbriata	A	0.06	0.04	0.02	0.10	0.04	0.05	0.91
C. maxima [O]	B				+			
C. ochrochlora	D					+		
C. pleurota	A				+			
C. pyxidata [O]	A							
C. rangiferina [O]	A							
C. squamosa [1]	A	0.02		0.11	0.02	0.32	0.09	*<0.01*
C. sp.	U	+	+	+	+	+		
Hypogymnia physodes [1]	A	0.74	0.56	0.86	0.70	0.67	0.71	0.12
H. tubulosa [2]	A					+		
Melanelia subaurifera [2, O]	A							
Parmelia saxatilis [O]	A							
P. squarrosa [2]	B	0.91	0.91	0.82	0.91	0.84	0.88	0.65
P. sulcata [1, 2]	A	0.02			0.01		0.01	1.00
Physcia tenella [2, R]	D							
Platismatia glauca [1]	B	0.17	0.19	0.26	0.26	0.64	0.30	*<0.01*
Punctelia subrudecta (= *P. perreticulata* in Hinds & Hinds 2007)	C	0.05	0.06	0.02	0.13	0.01	0.06	0.16
Pyxine sorediata [R]	C							
Ramalina americana	C	0.01	0.02	0.01	0.02	0.03	0.02	0.46
R. farinacea	B	0.02	0.07	0.03	0.11	0.03	0.05	0.82
R. roesleri [1, 2]	B	0.28	0.30	0.19	0.51	0.16	0.29	*0.03*
R. thrausta	B	0.08	0.01	0.10	0.05	0.06	0.06	0.36
Usnea ceratina	D	0.49	0.47	0.39	0.11	0.18	0.33	0.22
U. filipendula [2]	A	0.63	0.44	0.57	0.35	0.51	0.50	0.45
U. hesperina	B	+						
U. longissima	B	0.01	0.01	0.07	0.02	0.01	0.03	0.12
U. rubicunda	D	0.23	0.07	0.07	0.10	0.05	0.10	0.08
U. subfloridana [1, 2]	A	0.01	0.03			+	0.008	0.31

Table 2. Continued.

		Frequency of occurrence in different forest types						
		Deciduous		Coniferous				
Species	Range	Heartleaf Birch	Mountain Ash	Mixed Forest	White Spruce	Balsam Fir	Overall Frequency	*P*
U. sp.	U			+				
Xanthoria elegans R	A							
X. parietina 1, 2, R	D							
X. polycarpa 1, 2, R	B			+				
X. sorediata R	A							

We used Indicator Species Analysis to determine whether individual lichen species differed in their frequency of occurrence among forest types (Dufrêne & Legendre 1997). An indicator value for each species represents the likelihood of finding the particular species in each forest type. Monte Carlo simulations (4999 permutations) were conducted to test the significance of observed indicator values (alpha = 0.05). MRPP and Indicator Species Analysis were performed using PC-ORD software (McCune & Mefford 2005).

To illustrate habitat associations of particular lichen species and similarities in lichen communities between the five forest types (as well as between the 25 individual forest plots), we used hierarchical cluster analysis (SPSS 13 for Macintosh). Because rare species can reduce the reliability of clustering (McCune et al. 2000), we included only species found in more than 10% of the quadrats within at least one forest type (N = 13 common species). Frequency data were arcsine-square root transformed to improve normality (Sokol & Rohlf 1995). Ward's method using a Euclidean distance matrix was used for hierarchical cluster analysis (McCune et al. 2000).

RESULTS

Lichen biota. We recorded 43 species of macrolichens in 13 genera on Kent Island (**Table 2**). In comparison, a study of Fundy National Park, a 20,000-ha area at the head of the Bay of Fundy on the mainland coast of New Brunswick, found 221 macrolichen species in 47 genera—about five times as many species and 3.5 times as many genera as 80-ha Kent Island (Gowan & Brodo 1988). In terms of growth form, 15 of Kent Island's macrolichen species (35%) were fruticose and 28 species (65%) were foliose, whereas 45% of Fundy National Park's macrolichens were fruticose and 55% were foliose (chi-square test comparing the frequency of lichen growth forms in the two sites: $p = 0.30$).

Throughout Kent Island, macrolichens grow thickly on tree branches and trunks, covering virtually 100% of dead coniferous branches and twigs in particular. The two most species-rich and common lichen genera on Kent Island were *Cladonia* (14 spp.) and *Usnea* (7 spp.). Although only 14% of the species of *Cladonia* found in Fundy National Park were recorded on Kent Island, 50% of Fundy National Park's *Usnea* species were present. Two species of *Usnea* found on Kent Island (*U. ceratina* and *U. hesperina*) had not previously been reported in Fundy National Park or southern New Brunswick. None of the lichens found on Kent Island was a cyanolichen.

We did not attempt to survey crustose lichens on Kent Island. However, 53% of the 470 lichen species recorded in Fundy National Park were crustose (Gowan & Brodo 1988). Assuming a similar proportion on Kent Island, a rough estimate of the total number of lichen species on Kent Island would be 91. We used that figure to compare total lichen species richness (i.e., including crustose lichens) on Kent Island to the results of the few published lichen surveys of oceanic islands (Jüriado et al. 2006; Seaward & Aptroot 2000; Talbot et al. 2002). Taking into account island area, Kent Island had fewer lichen species than temperate-zone islands in West Estonia in the Baltic Sea (Jüriado et al. 2006) but many more than tropical islands in the isolated Chagos Archipelago in the Indian Ocean (Seaward & Aptroot

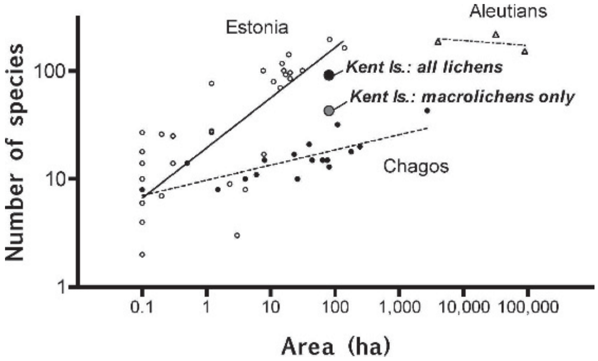

Figure 1. Number of lichen species on oceanic islands of different sizes. Open circles: West Estonian Archipelago (Jüriado et al. 2006); open triangles: Aleutian Islands (Talbot et al. 2002); filled circles: Chagos Archipelago (Seaward & Aptroot 2000). The estimated number of lichen species (including crustose lichens; see *Lichen biota*, above) of Kent Island (large filled circle) was less than predicted based on the species-area relationship of the West Estonian Archipelago but greater than predicted based on the Chagos Archipelago.

2000; **Fig. 1**). If crustose lichens made up as much as 75% of Kent Island's lichen biota (a figure characteristic of some well-studied European sites; J. Hinds, pers. comm.), Kent Island would still have fewer lichen species than similar-sized islands in West Estonia.

Despite Kent Island's temperate-zone latitude, nearly three-quarters of its identified macrolichen species had primarily boreal biogeographical affinities (**Table 2**). The boreal influence was especially apparent among the most common species: 11 of 13 species found in more than 10% of quadrats in at least one forest type were boreal in origin, as were 8 of 9 species found in more than 25% of quadrats (**Table 2**). All three species found in more than 50% of quadrats overall were boreal in origin. The lichen biota of Fundy National Park, by comparison, consisted of 33% boreal and 56% temperate species (the remaining 11% being Arctic or tropical; Gowan & Brodo 1988) (chi-square test comparing lichen biogeographical affinities in the two sites: $p < 0.0001$); 41% of Kent Island species were classified as oceanic in distribution.

Lichen communities and habitat associations. The mean number of lichen species found in individual forest plots on Kent Island was 13.0 ± 0.4 (± S.E.). Although there was no difference in species richness among the five forest types, species richness in deciduous plots collectively (heartleaf birch, mountain ash) was marginally greater than in coniferous plots (t-test: t_{23}=1.90, $p = 0.07$) (**Table 1**). In terms of lichen species composition, forest types differed from each other (MRPP, $A > 0.11$, $p = 0.0002$). Species compositions of deciduous plots collectively were also significantly different from coniferous plots and, among coniferous plots, white spruce plots had significantly different lichen species composition than balsam fir plots (MRPP pairwise comparisons, $A > 0.11$, $p < 0.04$). Hierarchical cluster analysis demonstrated that eight of ten deciduous forest plots were tightly clustered and separated from coniferous forest plots (the sole exceptions, heartleaf birch plots 1 and 4, may have been different because they were located on the periphery of the forested parts of Kent Island in relatively narrow and wind-exposed strands of forest) (**Fig. 2**).

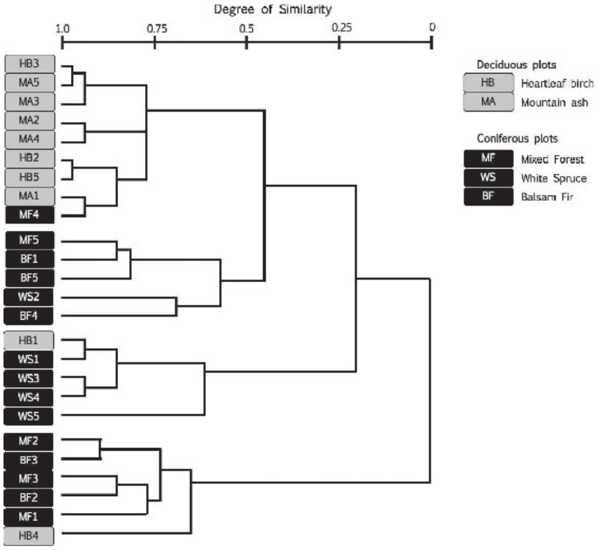

Figure 2. Hierarchical cluster analysis illustrating the similarity of macrolichen communities in 25 plots representing five forest types on Kent Island. Branch lengths indicate degree of similarity between plots as determined by Ward's method using a Euclidean distance matrix.

Based on Indicator Species Analysis, five lichen species were significantly more likely to be found in certain forest types. *Platismatia glauca*, *Cladonia coniocraea* and *C. squamosa* were particularly common in balsam fir forest, *Ramalina roesleri* in white spruce forest and *Bryoria fuscescens* in mixed coniferous forest (Monte Carlo Test, $p < 0.05$;

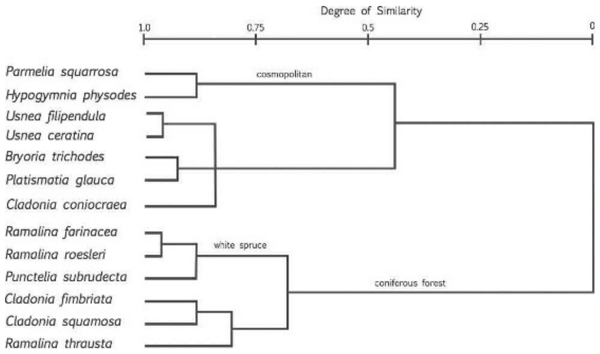

Figure 3. Hierarchical cluster analysis illustrating similarity in habitat preferences of the 13 most common macrolichen species in five forest types on Kent Island. Branch lengths indicate degree of similarity between lichen species as determined by Ward's method using a Euclidean distance matrix.

Table 2). The cluster analysis and the Indicator Species values suggested three distinct lichen groups based on species' preferred forest types: (1) widely distributed and abundant generalist species (*Parmelia squarrosa*, *Hypogymnia physodes*); (2) common species that have a preference for heartleaf birch (*Usnea ceratina*, *U. filipendula*); and (3) species that have a preference for white spruce (*Ramalina roesleri*, *R. farinacea* and *Punctelia subrudecta*) (*P. subrudecta* = *P. perreticulata*; Hinds & Hinds 2007) (**Fig. 3**). Note, however, that the three balsam fir specialists identified in the Indicator Species Analysis did not form a distinct group in the cluster analysis (**Fig. 3**). Moreover, although five lichen species appeared to have non-random distributions with respect to forest type, Bonferronni corrections for multiple comparisons were not applied, and the majority of lichens (24 of 29 forest species [83%]) did not show significant habitat preferences.

DISCUSSION

The number of species of macrolichens on Kent Island is only about 19% of that found on the mainland of New Brunswick in Fundy National Park (Gowan & Brodo 1988). The island's reduced lichen species richness is presumably the result of several factors: its small area, isolation, limited habitat diversity, even-aged forests and harsh physical environment. A similar pattern is reflected in the diminished species richness of other taxa on Kent Island (mosses: Futamura & Wheelwright 2000; vascular plants: McCain 1975; McIlraith 1986; ground beetles: Apigian & Wheelwright 2000; butterflies: Maddox & Cannell 1982; syrphid flies: Wheelwright et al. 2006).

A comparison of 80-ha Kent Island with the few other similar-sized oceanic islands that have been surveyed suggests the possibility of a reversed latitudinal gradient in lichen species richness. For example, Kent Island has only about half as many lichen species as Hanikatsi Island (82-ha) in the West Estonian Archipelago, which is located at a much higher latitude (59°N; Jüriado et al. 2006). On the other hand, Kent Island has about seven times as many lichen species as Nelson Island (81-ha) in the tropical Chagos Archipelago (5°S; Seaward & Aptroot 2000). Note that this preliminary analysis does not control for habitat diversity or isolation from the mainland. Kent Island has slightly lower habitat diversity and is more isolated than the West Estonian Archipelago (29 km vs. 5 km from the mainland) but has greater habitat diversity and is far less isolated than the Chagos Archipelago (ca. 2000 km). A survey of a Pacific Northwest forest similar to Kent Island's in terms of latitude (45°N), canopy tree species richness and dominance by conifers (although much taller and structurally more complex) yielded 97 lichen species, about the same as estimated for Kent Island despite the small area of the study site (2.3-ha; McCune et al. 2000). At a boreal forest site on Mt. Katahdin, Maine, Hinds and Hinds (2007) recorded 81 macrolichen species, 40 of which (49%) had boreal biogeographical affinities. Reversed latitudinal gradient in species richness has recently been demonstrated in other cryptogamic species such as mosses and liverworts in southern South America, where peak species richness actually occurs on sub-Antarctic islands (Rozzi et al. 2008; Shaw et al. 2005).

A distinctive feature of the macrolichen biota of Kent Island is its dominance by boreal species. Kent Island has more than twice the percentage of boreal species than nearby Fundy National Park (Gowan & Brodo 1988). Although Kent Island is located at a temperate latitude and is due east of midcoast Maine, the cooling influence of upwelling of the Labrador Current in the Bay of Fundy gives the island a much more northerly climate, which is reflected in boreal biogeographical affinities of other plant and animal taxa on the island (e.g., mosses: Futamura & Wheelwright 2000; ground beetles: Apigian & Wheelwright 2000; songbirds: Eliason 1986). Not surprisingly, species characterized as oceanic in distribution comprise almost half of Kent Island's lichen biota. Species in the genus *Usnea* appear to be especially successful at colonizing under Kent Island's conditions, based on the relatively high proportion of species shared with Fundy National Park (Gowan & Brodo 1988). We found no association, however, between growth form *per se* (fruticose vs. foliose) and the probability of occurrence on Kent Island.

Despite its small area, Kent Island has several different forest types. We found no difference between forest types in macrolichen species richness; on average individual 5 × 5 m plots had about a dozen species. Yet forest types varied significantly in terms of the species composition of their lichen communities. Two separate analyses (Multi-response Permutation Procedures, hierarchical cluster analysis) showed that deciduous and coniferous forests had quantitatively different lichen communities, although they shared many of the same species. White spruce forest plots in particular were distinctive. Deciduous trees appear to host different compositions of lichen species than coniferous trees in Fundy National Park and other sites as well (Ahti 1977; Gowan & Brodo 1988).

Indicator Species Analysis demonstrated that about one-sixth of Kent Island's macrolichens show significant habitat preferences. Likely factors explaining species-specific habitat associations on Kent Island are variation in forest light levels, the morphology and chemistry of the bark of different tree species and moisture (e.g., Antoine & McCune 2004; Frati et al. 2007; O'Hare 1974). The two most abundant and widespread species on Kent Island, *Hypogymnia physodes* and *Parmelia squarrosa*, are equally common in other boreal forests (Ahti 1983; Cameron 2002; Gowan & Brodo 1988); *H. physodes* was found in 76 of 90 survey plots in northern Maine and *P. squarrosa* in 43 of 92 (Hinds & Hinds 2007). Among the balsam fir specialists on Kent Island, *Platismatia glauca* is known to favor conifers elsewhere, while *Cladonia coniocraea* and *C. squamosa* often occur in shady habitats like Kent Island's balsam fir forest (Ahti 1983; Hinds & Hinds 2007). It is less obvious why *Ramalina roesleri* apparently favors white spruce on Kent Island and *Bryoria fuscescens* mixed coniferous forest.

Although cyanolichens are normal components of the four floristic categories found on Kent Island (circumpolar boreal, oceanic boreal, widespread temperate, oceanic temperate), we did not observe any macrolichens with cyanobacteria photobionts during our two-month survey in 2007 or in earlier preliminary surveys. The structure and conditions of Kent Island's forest may explain the absence of cyanolichens there. Most of Kent Island's forest communities are relatively young (50–60 yr), structurally simple and subjected to disturbance (storm-induced treefalls, seedling herbivory by snowshoe hares, historic fires); cyanolichens tend to be associated with old growth forests (McCune 1993; Sillett & Neitlich 1996; Wolseley 1991). Moreover, epiphytic cyanolichens are particularly sensitive to acidity (Gilbert 1986) and tend to be found in greatest abundance on tree species with bark pH greater than 5.0 (Gauslaa 1985). Most trees sampled on Kent Island had bark pH lower than 5.0, and the island is regularly bathed in highly acidic fog (Cunningham 1998). Although cyanolichens can flourish in young forests and on trees with low bark pH as a result of allochthonous nutrient enrichment and increase in bark pH due to a "dripzone effect" from *Populus* branches (Goward & Arsenault 2000), such a mechanism is unlikely on Kent Island because of the absence of a forest overstory or of *Populus* spp. However, farming and forestry activity on Kent Island during the 19th and early 20th centuries may have eliminated or disturbed the island's few old-growth forest patches, a necessary feature for most members of the Lobarion community. Evidence for this is the fact that cyanolichens occur on Grand Manan Island and small islands off the coast of Maine.

Among the macrolichens of Kent Island are a number of species of possible conservation concern. Hinds and Hinds (2007, table 9) list *Alectoria sarmentosa*, *Bryoria fuscescens*, *B. trichodes*, *Ramalina americana*, *Usnea ceratina* and *U. longissima* as R3 (found in more than 20 sites in New England but with evidence of declines in the last quarter century), *R. farinacea*, *R. thrausta* and *Xanthoria sorediata* as R2 (found in 6–20 sites and with evidence of recent declines) and *U. rubicunda* as R1 (found in fewer than 6 sites and with good evidence of recent declines).

In conclusion, compared to the mainland of New Brunswick the macrolichen biota of Kent Island is depauperate and dominated by species with boreal and oceanic biogeographical affinities. Despite the island's small area and the simplicity of its habitats, its lichen communities are subtly distinctive between forest types. Although most of Kent Island's lichen species are generalists, a few show significant habitat preferences. In the face of climate change, isolated boreal islands like Kent Island may provide a refuge for lichen species declining on the mainland of New England and the Maritime Provinces.

ACKNOWLEDGMENTS

We thank John Lichter and Barry Logan for useful comments on earlier drafts, Anna Bender, Liz Carlton, Bob Mauck, Kendra Neff, Nancy Olmstead and Jaret Reblin for lab and field assistance, Donald McAlpine for conducting a preliminary lichen survey on Kent Island in 1992, Stephen Clayden for identifying specimens collected in 1996 and James and Patricia Hinds for confirmation of identification of specimens collected in this study and in 1993. We are particularly grateful to Bruce McCune for providing some of the multivariate analyses and helpful comments on the manuscript. This represents Contribution No. 194 from the Bowdoin Scientific Station and was supported by NSF Grant IBN-0116139.

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ms. received December 4, 2008; accepted April 23, 2009.