Vegetation composition, structure and soil properties across coastal forest–barren ecotones

Burley, Scott T.[1]; **Harper, Karen A.**[2] & **Lundholm, Jeremy T.**[3*]

[1]Biology Department, Saint Mary's University, 923 Robie St., Halifax, NS; E-mail: scott.burley@amec.com;
[2]School for Resource and Environmental Studies, Dalhousie University, 6100 University Ave., Halifax, NS; E-mail: Karen.Harper@dal.ca; [3]Biology/Environmental Studies Department, Saint Mary's University, 923 Robie St., Halifax, NS; *Corresponding Author; Fax: +902-420-5046; E-mail: Jeremy.Lundholm@smu.ca;

Abstract

Coastal barrens support rare plant species but may be threatened by forest encroachment. We determined whether trees spread into coastal barrens from forest patches and assessed plant species composition and soil properties across the forest – barren ecotone. We quantified tree age and height, soil properties, and vascular plant, bryophyte and lichen species composition along transects perpendicular to the edges of tree patches within the forest-barren ecotone in coastal Nova Scotia. Randomization tests assessed whether the vegetation and environmental characteristics were significantly different in the transition zone compared to one or both adjoining ecosystems. We used ordination to examine trends in species composition across the ecotone and the relationship to environmental variables. Tree age and height decreased continuously from the forest towards the edge of the forest patches. There were also trends in vegetation composition and structure from the forest into the open barrens. Many species were most abundant within the transition zone, although not always significantly. Soil properties were relatively uniform across the ecotone. The structure and vegetation of the forest-barren ecotone suggests that forest patches act as nuclei for forest expansion on barrens with a typical successional pathway where coastal barrens vegetation is gradually replaced by forest species. This encroachment may pose a threat to rare barrens communities. While landscape factors such as salt spray and wind exposure may determine the general locations where forest can establish, biotic processes of growth and dispersal appear to govern the fine-scale expansion of tree patches.

Keywords: forest succession, rock barrens, heathland, landscape dynamics, nucleation, contagion, forest edges

Introduction

Along the Atlantic coast of Nova Scotia and northeastern United States, there are patches of nonforested ‘coastal barrens’ scattered on areas with exposed bedrock or little soil cover within a forested landscape. More extensive barrens occur in Newfoundland and further north in mainland Canada (Meades 1983). These barren habitats are open, low growing shrub communities with sparse tree cover dominated by ericaceous species such as *Gaylussacia baccata* and *Vaccinium angustifolium* (Dunwiddie et al. 1996; Oberndorfer and Lundholm 2009). Dynamic open habitats represent an early successional stage following disturbance that removes the canopy and alters the vegetation composition of the area (Bazzaz 1979; Saldarriaga et al. 1988; Nova Scotia Museum of Natural History 1997). These openings can persist for many years and even decades before they become forested during post-disturbance succession (Ehrenfeld et al. 1995; Mallik 1995, 2003; Latham et al. 1996; Bradley et al. 1997; Faison et al. 2006). Other rocky habitats persist as islands in a forested landscape and have been shown to last for hundreds of years without significant soil development or succession into forest (Stark et al. 2003, 2004). Aerial photo analysis on coastal barrens in Nova Scotia suggests that these areas contain both persistent barrens that have not undergone forest encroachment over the last 70 years, as well as other areas that have become forested (Burley 2009). In coastal barrens in Nova Scotia, rare plant species are typically only found in low shrub barrens where tree species are absent (Oberndorfer and Lundholm 2009); therefore forest encroachment represents a potential threat to rare plant species in this system.

Succession from open barrens to forest could occur either simultaneously throughout the entire disturbed area or along a spatial gradient from the edges of the forested areas surrounding the disturbance. In Nova Scotia, barrens are more likely to succeed to forest when they occur inland or in topographically sheltered areas near the coast with some protection from wind and salt spray (Burley 2009). It is not clear whether forest patches, once established in a landscape of open barrens, act as sources of propagules for colonization of more exposed areas (Burley 2009). Maurice et al. (2004) found that proximity to forest edge accelerates forest succession into open shrubland habitats, therefore barrens located within a forest matrix exposed to high amounts of forest edge may be less persistent than more exposed barrens. Edge influence from nearby trees alters local environmental conditions through shading and increased water or nutrient availability (Breshears 2006; Duarte et al. 2006), potentially enabling the spread of tree species.

Edges of forest patches in coastal barrens, whether or not they are expanding, may harbour greater biotic diversity. The concept of an increase in biotic diversity within edge environments has been suggested by a number of studies (e.g. Harris 1988; Fraver 1994). However, more recent studies have found little to no effect of edges on species richness at some forest edges (Lloyd et al. 2000; Harper and Macdonald 2002).

Coastal barrens in northeastern North America have high cultural, aesthetic, and biological values and are important habitats for rare species such as *Solidago multiradiata*, *Empetrum eamsii* and *Prenanthes nana* (Oberndorfer & Lundholm 2009). Understanding the extent and effects of forest expansion into coastal barrens is required for conservation planning in this habitat. The first goal of this study was to determine if these forest patches are expanding into coastal barrens by quantifying tree age and size across the edges of forest patches. Our second goal was to characterize gradients in plant species composition and soils across the forest-barren transition zone. We were specifically interested in the pattern of plant diversity and individual vascular and nonvascular plant species distributions across the ecotone.

Methods

Study area

Forests surrounding coastal barrens in Nova Scotia are generally dominated by coniferous tree species including *Picea glauca*, *Picea rubens*, *Larix laricina*, and *Abies balsamea* (Neily et al. 2004; Oberndorfer and Lundholm 2009). In Nova Scotia, the majority of coastal barrens habitat consists of isolated patches located along the Atlantic coast. Extant patches of forest within the barrens tend to be found at greater distances from the coast and in more topographically sheltered areas than extant barren patches (Burley 2009). Three coastal barrens study sites were chosen in Nova Scotia (Figure 1): Peggy’s Cove (44° 29' 35" N and 63° 55' 00" W), Taylor’s Head Provincial Park (44° 49' 06" N and 62° 33' 46" W), and Canso Coastal Barren Wilderness Area (45° 17' 12" N and 61° 05' 21" W). Regional climate is cool maritime with 1200-1600 mm of precipitation annually (15% snow), frost-free period of approximately 130-150 days, mean January temperature of around -5 ºC, and mean July temperature around 16 ºC. Soils are shallow over bedrock, acidic and have thick organic layers (Oberndorfer and Lundholm 2009).

Forest patches within the barrens varied in size and shape both within and among the three study sites. These patches ranged from small clumps of a few individual trees developing in topographical depressions to large forest stands extending over many hectares. The majority of forest patches within the study sites consisted primarily of densely packed coniferous tree species including *Picea rubens*, *Picea glauca*, and *Abies balsamea* with sub-dominants including *Acer rubrum* and *Betula papyrifera*. Outward expansions of these patches appeared to have no directional preference (inland vs coast) but patch shape was often influenced by topographical features such as steep-sided ravines and low-lying bogs.

Data collection

At each of the three study sites, aerial photos were used to randomly select three forest patches within 500m of the coast and three patches between 500m and 1000m of the coast for a total of six patches at each site (n=18). For the purpose of this study, forest patches chosen had to cover a minimum area of 50 m^2. In order to assess changes in soil properties and vegetation patterns across the forest-barren ecotone at the edges of the patches, transects were established perpendicular to the south-facing forest patch edge, which was always the ocean-facing side (Figure 2).

Each transect was at least 18 m long and started in the forest at 0 m with the limit of the continuous forest canopy (the edge of the forest patch) at 6 m (Figure 2). This starting point did not necessarily represent the center of the forest patch as these patches varied in size. Five 2 x 5m plots were established along each transect at 0-2 m (reference forest plot), 4-6, 8-10 and 12-14 m (transition plots), and 16-18 m or more (barrens reference plot). The last plot was sometimes located further along the transect to reach an area classified as open coastal barrens (less than 1% tree canopy cover for the entire plot).

Within each plot, soil depth was measured at five sampling points, at each corner and in the middle of each plot, using a soil auger that was driven into the ground until it reached bedrock (or resistance prevented it from going any further down). Soil development was assessed using these cores and classified as: **0 -** no soil development (*i.e*. bare rock, litter, or humus (O_f) only); **1 –** decomposed organic (O_m or O_h) layer present; **2 -** 'A' horizon present; or **3 -** 'B' horizon present. Soils only containing 'A' horizons consisted of a layer of leached mineral soil over bedrock, whereas soils that were classified as further developed ('B' horizon) consisted of a differentiated horizon under the leached 'A' horizon. Soil was collected for analysis of nutrient content from these same five points, to a maximum depth of 1.15m (length of auger), and combined into a single sample per plot. At least 250 ml of soil was collected where possible from each plot from the lowest layer of soil present at each sampling location. At sample locations where no mineral soil was encountered only the organic layer (O_m or O_h) was collected and no sample was collected from areas with neither organic nor mineral soil. Samples were sent to the Agricultural College in Truro, Nova Scotia for chemical analysis (%N, pH, % organic matter, P, K, Ca, Mg, Na, S, Fe, Mn, Cu, Zn, B).Organic matter content was determined by loss on ignition after 1 h at 450 ◦C. Soil pH was determined following the Adams-Evans buffer method (COEC, 1992) and a pH meter (Accumet AR25: Fisher Scientific, Ottawa, Canada). To quantify the soil content of P, K, Ca, Mg, Na, Mn, Cu and Zn, Mehlich 3 extraction was used, followed by the inductively coupled argon plasma method. Total nitrogen was analysed using a Leco (Mississauga, Canada) FP528 Nitrogen Analyzer. Cation exchange capacity (CEC) was determined by calculating the sum of the milliequivalents of sodium, calcium, potassium, magnesium, and hydrogen per 100 g of soil (Baird, 1999).

At each distance, the two closest trees (>1.6 cm dbh) to each of six 1 m intervals (0 to 5 m inclusive across each plot) were selected for sampling. Each tree was cored using a Swedish increment borer as near to the base of the tree as possible. Age of the selected tree was assessed by counting the annual growth rings of each tree under a dissecting microscope. For each tree, diameter was measured at breast height (1.3 m) and tree height was estimated using a clinometer.

At the southwest and northeast corners of each plot, canopy cover was estimated using a convex densiometer. Maximum vegetation height was measured in the centre and at these two corners. Two 1 x 1m subplots were established in these corners to measure herbaceous layer composition using the point intercept method with a grid of 25 evenly spaced points 20 cm apart, with a 10 cm buffer around the edge of the plot. Vascular plants, mosses and ground macrolichens touching a metal rod, placed vertically at each intercepting point, were identified to species. Nomenclature follows Roland & Smith (1963) for vascular plants, Crum (1983) for mosses, and Brodo et al. (2001) for lichens. Frequencies (# intercepts per subplot) of each species were determined for plant species composition. All measurements were averaged per plot.

Statistical Analysis

All six patches at each site (regardless of distance to coast) were analyzed together, as preliminary analyses suggested no relationships between distance to coast and patch characteristics. Randomization tests (using an Excel AddIn, K.A. Harper and S.E. Macdonald unpublished) were used to detect differences in abiotic variables, vegetation composition and structure between plots located at various distances along transects and reference forest and barrens plots. This analysis was used in Mascarua et al. (2006) and consists of an updated version of the Critical Values Approach (Harper and Macdonald 2001). The difference between the mean of reference conditions and the mean at a given distance from the edge is compared to a distribution of randomized differences of the entire data set. We used 5000 permutations and compared the percentile of the observed difference within the distribution of randomized distributions with the 5th and 95th percentiles which were the critical values for a two-tailed test ($\alpha = 0.10$). These analyses were conducted separately using the forest plots as the reference and using coastal barrens plots as the reference in order to detect differences between the edge of forest patches and both adjacent habitats. The abundances of frequent individual species (found in five or more plots) across the transition were also analyzed with randomization tests. The false discovery rate was used to account for multiple testing (Verhoeven et al. 2005) for all tests conducted on abiotic variables and forest structure and composition (192 tests), and separately for all individual species (488 tests).

Frequent species were classified based on the pattern of their abundance across the forest-tundra ecotone. Graphs of abundance vs. distance across the ecotone were visually examined to classify each species into one of the five groups. Forest and barrens species were those that were more abundant in one of the reference habitats. Transition species and transition avoiders were more and less abundant, respectively, in one or more of the transition plots compared to both reference habitats. The final category, ubiquitous species, was for species that showed no obvious pattern across the ecotone.

Detrended Correspondence Analyses (DCA) were conducted to visually examine differences in species composition among plots. The site scores from the first two DCA axes were also analyzed using randomization tests as described above to test the difference in overall species composition between the edge and adjacent communities. Canonical Correspondence Analyses (CCAs) were conducted to examine potential relationships between species composition and environmental gradients along transects. Data from all 18 environmental variables sampled in the field were initially analysed using a CCA. Results of the initial CCA were examined to determine weak predictors as well as potential redundant variables that could be removed in order to simplify the analysis while maintaining a similar proportion of inertia explained by the model. Seven environmental variables were chosen for the final CCA that best explained the distribution of vegetation including two structural variables: tree height and canopy cover, and five soil properties: iron content, cation exchange capacity, calcium content, percent organic matter, and soil depth. Both ordination techniques were done using the vegan package in R version 2.5.1 (2007).

Results

There were a number of significant gradients in forest structure across the forest –barren ecotone including decreasing tree age, tree height, vegetation height and canopy cover from the forest to the barrens (Table 1). Tree age and height were significantly different throughout the transition area compared to both the forest and the barrens whereas in the transitional plot nearest the forest vegetation height and canopy cover were not significantly different from the forest. Soil depth, development, organic matter, pH and most nutrients were not significantly different across the transition compared to either the forest or the barrens. Species richness was significantly lower in two of the three transition plots as compared to the barrens but not the forest. Site scores along the first two DCA axes continually decreased or increased, indicating a continual change in species composition from the forest into the barrens. Along the first axis, scores for the two transitional plots nearest the barrens were significantly different from both barrens and forest plot scores; the score for the transitional plot nearest the forest was significantly different from the barrens plot score only. Along the second DCA axis, site scores in the transition plots were significantly different from either the barrens or forest plot scores, but not both.

We found a total of 61 vascular species, 19 lichen species, and 27 moss and liverwort species (Appendix 1). Overall, there were vascular species in all five categories of patterns of abundance across the transition, while most lichens were barrens species and bryophytes were either forest species, transition species or transition avoiders (Table 2). There were slightly more barrens species than forest species but only about a third each of the barrens and forest species had significantly greater abundances in their respective habitats. Most of the forest species with significant trends were mosses or liverworts. We were surprised at the number of transition species, a total of 13 vascular plants and 2 mosses. However, the five transition avoider species that had significant trends were only significantly different from one of the adjacent ecosystems. Therefore the appearance that these species' abundances had greater abundances in both forest and barrens compared with the transition locations was never statistically significant.

Species composition changed across the forest-barren ecotone as illustrated in the ordination (Figure 3a). The DCA shows some separation between the extremes of barrens vs. forest plots, mainly along axis 1, with much overlap with the transition zone in between. Species classified as barrens, transition or forest species (Table 2) also fall out along this same gradient (Figure 3b). Species classified as "transition avoiders" were found in several plots near the upper end of Axis 2, whereas "ubiquitous" species (unsurprisingly) had intermediate scores on both axes. In the CCA conducted to examine potential relationships between understory vascular species composition and environmental gradients, canopy cover, tree height, soil depth, cation exchange capacity, percent organic matter, iron, and calcium were found to have the highest loadings of the 18 abiotic variables sampled (Figure 4). The first two CCA axes represent the majority (17.3%) of inertia explained by the model where the entire model explains 19.8% of the total inertia (5.5696). The first axis ($\lambda = 0.396$) represents an "openness" gradient, with higher values being associated with lower canopy cover and tree height; forest understory species such as *Oclemena acuminata, Rhus typhina, Linnaea borealis, Clintonia borealis, Gaultheria hispidula, Osmunda cinnamomea* and many mosses had low values on this axis (Figure 4). Shade intolerant species such as *Corema conradii, Empetrum nigrum, Gaylussacia dumosa, Rubus chamaemorus, Scirpus cespitosus* and some *Cladonia* spp. were found to be positively correlated with this gradient and tended to occur in more open areas with less canopy cover.

The second CCA axis (λ = 0.239) represents gradients of soil depth and CEC, perpendicular to the main barrens-forest ecotone gradient. Species associated with shallow soils and high CEC values include *Arctostaphylos uva-ursi, Corema conradii,* and *Myrica gale*. These species were generally found extending clonally over rocks encountered along the transects in areas with very shallow soils; mosses and lichens common on rocks were also found in these areas (e.g. *Cladonia boryi*). Species associated with deep soils and low CEC values include *Carex trisperma, Rubus chamaemorus, Sarracenia purpurea, Scirpus cespitosa, Sphagnum fuscum, S. magellanicum* and *Vaccinium oxycoccos.* These species were associated with bog habitats occasionally encountered in our transects which generally had deep peat and organic accumulation.

Discussion

Forests appear to be expanding outward into coastal barrens habitat from patches as evidenced by continually decreasing age and height across the edges of the patches towards the barrens. If tree ages were similar across the gradient, this would suggest that the trees in patches recruited as a single cohort after a disturbance such as a fire or wind storm, and expansion is restricted by the post-disturbance environment. Uniform soil conditions across the gradient provides additional evidence that the forest patches are indeed expanding and are not delimited by distinct edaphic conditions or microenvironments. While soil variables were important in explaining some of the variation in species composition in the CCA, this variation was orthogonal to the main forest-barren ecotone which was the subject of the edge analysis. Homogeneous soil depth was also found across forest-savanna ecotones where forest was encroaching onto savanna with a similar spatial trend in age structure (Hennenberg et al. 2005). This pattern suggests that these forest patches may be acting as nuclei or seed and propagule sources for forest expansion into barrens habitat.

At the landscape level, aerial photo analysis in a previous study suggested that forest expansion into barrens over the last 70 years was more likely to occur in topographically sheltered locations or farther from the coastline (Burley 2009). The current study shows expansion from isolated forest patches that may have established originally due to relatively favorable conditions within a harsher barrens matrix. Since soil conditions were similar across the ecotone, this suggests that trees may be acting as “landscape modulators” (Shachak et al. 2008) and the vegetation gradient across the ecotone is not due to pre-existing edaphic heterogeneity but is a response to shade created by the tree canopy (positive feedback). While forest expansion into other open ecosystems can be associated with soil chemistry changes (McKinley and Blair 2008), such changes have yet to happen in the ~60 years since these patches became established, possibly because open barrens are also characterized by acid soils with deep litter (Oberndorfer and Lundholm 2009). Forest expansion in this system appears to be governed by abiotic factors that slow or inhibit tree establishment such as salt spray, wind, rock outcrops or depressions with wet conditions at coarse spatial scales (Burley 2009) together with biotic processes of dispersal and growth that determine the spread of trees at finer scales.

There was a gradual vegetation gradient across the edges of the forest patches rather than an abrupt switch between forests and barrens. This general vegetation transition across the forest - barren ecotone represents a typical forest successional pathway from barrens to forest where creeping or ground shrubs give way to short shrubs, which are then outcompeted by taller shrubs and finally tree species (Bazzaz 1979; Saldarriaga et al. 1988). Similar species richness between the two reference habitats indicates that forest encroachment does not so much represent a loss of total number of species as it is more of a shift or replacement of low growing, open-ground species such as *Arctostaphylos uva-ursi*, *Chamaedaphne calyculata*, *Corema conradii* and *Gaylussacia dumosa* by shade tolerant forest understory species and canopy tree species including *Acer rubrum*, *Betula papyrifera* and *Drepanocladus fluitans*. The presence of forest patches on the barrens landscape thus adds to overall species diversity at the landscape level, as it does in other systems (Manning et al. 2006). Other work on these coastal barrens, however, shows that rare species are consistently associated with the low shrub communities (Oberndorfer and Lundholm 2009) that are replaced as forest vegetation spreads out from treed patches, as in other grassland or heathland systems (Andrés & Ojeda 2002; Rhoades et al. 2005; Linneman and Palmer 2006; Price and Morgan 2008). Therefore further tree expansion may pose a threat to these rare species.

The greater spread of plots and species along axis 2 in the CCA in barrens areas scoring high on axis 1 indicates that open barrens habitats are more heterogeneous than forest patches, containing bog and rock outcrop vegetation in edaphic extremes. Forest encroachment is a homogenizing force for coastal barrens. Increased canopy cover would negatively impact rock outcrop species such as *Arctostaphylos uva-ursi*, *Corema conradii*, and *Sibbaldiopsis tridentata* as these species are generally found in open, full light environments. These species were strongly associated with shallow soil depth found on exposed rock outcrops but orthogonal (unrelated) to canopy cover and tree height. *Pinus banksiana*, and *Picea* sp. stands that contained exposed outcrops with species such as *Corema conradii*, and *Sibbaldiopsis tridentata* were found within the study sites (S. Burley pers. obs.), but not in the sampled forest patches (Appendix 1). This mosaic of forest and rock outcrops may represent a lag in vegetation response to forest encroachment where rock species such as *S. tridentata* are able to persist in spite of increased canopy cover. As soil develops over these exposed rocks as a result of litter accumulation and decomposition from the surrounding trees, rock outcrop species may be replaced by more typical forest understory species such as *Linnaea borealis* and *Clintonia borealis*. A more detailed examination of species interactions between rock outcrop species and forest understory species within forests is needed to further explain this pattern.

Species richness within transition zones was not significantly different from reference forest plots and was significantly lower than the reference coastal barrens. Our findings concur with recent studies that found little difference in species richness at forest edges compared to forested areas (Harper and MacDonald 2002; Lloyd et al. 2000) and provide further evidence against the concept of increased diversity within edge environments (e.g. Harris 1988; Fraver 1994). In our study area, the transition zones consisted of very dense shrub cover which may have resulted in reduced abundance of transition avoiders such as *Carex trisperma* and *Cornus canadensis* and lower number of species due to thick accumulations of leaf litter and dense shrubby stems. Despite lower species richness there were more transition species than transition avoiders which may be explained by the greater abundance of barrens species than transition species across the ecotone. Nevertheless, the differentiation in community composition across the ecotone and the presence of species unique to each of the three zones suggests again that these forest patches act to increase beta-diversity in the barrens landscape (e.g. Manning et al. 2006; Brooker et al. 2008). In particular, the apparent peaks in abundance of transition species are an interesting phenomenon; more study is needed to determine if these trends represent a real phenomenon and what its biological significance may be.

Conclusions and implications

Coastal barrens communities in Nova Scotia are important for their rare plant species and unique vegetation types. This study determined that forest patches located within coastal barrens are not static relicts of pre-disturbance conditions, but show signs of expansion into the surrounding vegetation over time. These forest patches represent seed and propagule sources from which forest expansion may increase the extent of forest into coastal barrens habitat. However, we do not suggest that forest patches will expand into coastal barrens habitat indefinitely, as the rate and amount that each forest patch can expand is determined by the local environment and species interactions within the forest-barren ecotone (Breshears 2006; Maurice et al. 2004). Although forest patch expansion poses a potential threat to the uncommon assemblages and rare species occurring on coastal barrens, a moderate amount of forest patches increases beta diversity over the landscape. Forest expansion seems to be controlled by abiotic vs. biotic processes at different spatial scales as tree patch expansion relies on processes of dispersal and growth within a landscape where abiotic factors such as wind and salt spray dictate the possible limits of forest encroachment.

Acknowledgments

Tyler Smith provided invaluable help with the statistical components. We thank Kat Dillon, Crystal Hillier, Molly Simons, Sarah Robinson and Jenn Lau for assistance with field work. Sean Basquill and Philip Giles provided critical comments on an earlier version of the paper. Financial support for this project is from NSERC (CGS to S. Burley, Discovery Grant to J. Lundholm) and Saint Mary’s University.

Appendix 1. Species, family, S-rank, frequency (# plots) and mean # intersection points (out of 25) in 1m x 1m plots within each distance, ± 1 SE for 61 vascular species, 19 lichen species and 27 moss and liverwort species sampled from 18 transects across the transition area between coastal barrens and forest patches. S Ranks (where available) are from the Atlantic Canada Conservation Data Centre (2008a). The S rank indicates the Nova Scotia rarity status where; S1- extremely rare, 5 or fewer occurrences; S2 – rare, 6 to 20 or fewer occurrences; S3 – uncommon, 21-100 occurrences; S4 – widespread, fairly common, >100 occurrences; S5 – abundant, demonstrably widespread (ACCDC 2008b**).** Distance is from the centre of the forest plot. Significant differences from either the forest or barrens plots are both were determined using randomization tests to assess edge influence (see Methods for details). Multiple testing for the 488 tests was accounted for using the false discovery rate (Verhoeven et al. 2005). Species present in less than 5 plots were not tested. Nomenclature was based on Roland and Smith (1963) for vascular plants, Brodo et al. (2001) for lichens and Crum (1983) for mosses and liverworts.

				Distance (m)				
Species	Family	S-rank	# plots	0 Forest	4	8	12	16 Barrens
VASCULAR PLANTS								
Abies balsamea	Pinacea	S5	29	5.7 ± 0.18	9.3 ± 0.23*	6.2 ± 0.20	4.9 ± 0.17	0.1 ± 0.03
Acer rubrum	Aceraceae	S5	3	0.4 ± 0.08	0.3 ± 0.06	0.1 ± 0.03	0 ± 0	0 ± 0
Alnus viridis	Betulaceae	S5	26	0.3 ± 0.06	1.4 ± 0.9	3.4 ± 0.16	2.4 ± 0.13	1.4 ± 0.10
Amelanchier sp.	Rosaceae	N.A.	3	0 ± 0	0 ± 0	0.1 ± 0.03	0 ± 0	0.2 ± 0.05
Aralia hispida	Araliaceae	S5	2	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.03	0.2 ± 0.05
Aralia nudicalus	Araliaceae	S5	47	1.7 ± 0.09	1.9 ± 0.10	4.1 ± 0.12	2.3 ± 0.09	1.3 ± 0.09
Arctostaphylos uva-ursi	Ericaceae	S4	7	0 ± 0	0 ± 0	0.9 ± 0.11	0.2 ± 0.06	1.4 ± 0.11
Betula papyrifera	Betulaceae	S5	4	0.1 ±	0.2 ± 0.05	0 ± 0	0.1 ± 0.04	0 ± 0
Calamagrostis pickeringii	Poaceae	S4S5	3	0 ± 0.04	0 ± 0	0 ± 0	0.6 ± 0.09	0.2 ± 0.05
Carex nigra	Cyperaceae	S5	1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.7 ± 0.16
Carex trisperma	Cyperaceae	S5	18	4.2 ± 0.2	3.2 ± 0.18	0.1 ± 0.03	1.6 ± 0.12	2.7 ± 0.17
Carex sp. 1	Cyperaceae	N.A.	1	0 ± 0.0	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0
Chamaedaphne calyculata	Ericaceae	S5	9	0 ± 0	0 ± 0	0.4 ± 0.07	1.1 ± 0.11	0.7 ± 0.08
Clintonia borealis	Liliaceae	S5	11	0.8 ± 0.08	0.2 ± 0.04	0.4 ± 0.07	0 ± 0	0.4 ± 0.05**
Coptis trifolia	Ranunculaceae	S5	8	0.1 ± 0.03	0.1 ± 0.03	0 ± 0	0.3 ± 0.05	0.4 ± 0.06
Corema conradii	Empetraceae	S4	15	0 ± 0*	0 ± 0*	0.7 ± 0.10*	1.8 ± 0.15	8.3 ± 0.21
Cornus canadensis	Cornaceae	S5	54	3.3 ± 0.16	2.4 ± 0.11	2.2 ± 0.10	2.9 ± 0.14	3.8 ± 0.11
Deschampsia flexuosa	Poaceae	S5	1	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0

				Distance (m)				
Species	Family	S-rank	# plots	0 Forest	4	8	12	16 Barrens
Drosera rotundifolia	Droseraceae	S5	4	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.05	0.2 ± 0.04
Empetrum eamesii	Empetraceae	S2S3	1	0 ± 0	0 ± 0	0.1 ± 0.03	0 ± 0	0 ± 0
Empetrum nigrum	Empetraceae	S5	25	0.4 ± 0.07*	0.2 ± 0.05*	4.7 ± 0.19	6.6 ± 0.20	10.4 ± 0.23**
Gaultheria hispidula	Ericaceae	S5	13	1.7 ± 0.10	1.2 ± 0.11	0.6 ± 0.08	0.1 ± 0.04	0.1 ± 0.03
Gaultheria procumbens	Ericaceae	S5	36	0.9 ± 0.11	0.1 ± 0.03*	1.4 ± 0.09	2.1 ± 0.09	3.3 ± 0.12
Gaylussacia baccata	Ericaceae	S5	61	1.7 ± 0.11*	9.8 ± 0.20***	16.5 ± 0.23**	18.2 ± 0.23**	22.4 ± 0.22**
Gaylussacia dumosa	Ericaceae	S4	8	0 ± 0	0 ± 0	0.3 ± 0.07	0.2 ± 0.04	1.1 ± 0.09
Hamamelis virginiana	Hamamelidaceae	S5	1	0.2 ± 0.05	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Ilex verticillata	Aquifoliaceae	S5	22	0.9 ± 0.08	1.3 ± 0.09	1.7 ± 0.11	0.4 ± 0.05	0.1 ± 0.03
Juniperus communis	Cupressaceae	S5	25	0 ± 0*	0 ± 0*	3.7 ± 0.19	5.6 ± 0.18	9.9 ± 0.22**
Kalmia angustifolia	Ericaceae	S5	82	8.2 ± 0.2	13.9 ± 0.20	17.7 ± 0.19	16.8 ± 0.20	13.9 ± 0.19
Kalmia polifolia	Ericaceae	S5	13	0 ± 0	0.1 ± 0.04	0.3 ± 0.06	1.1 ± 0.09	1.1 ± 0.09
Larix laricina	Pinacea	S5	1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.04
Linnaea borealis	Caprifoliaceae	S5	18	2.6 ± 0.12	1.4 ± 0.11	1.1 ± 0.09	0.8 ± 0.10	0.1 ± 0.03
Maianthemum canadense	Liliaceae	S5	51	2.2 ± 0.11	1.7 ± 0.08	1.4 ± 0.08	0.9 ± 0.06	1.7 ± 0.08
Maianthemum stellatum	Liliaceae	S4	1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.04
Melampyrum lineare	Scrophulariaceae	S5	4	0.1 ± 0.03	0.1 ± 0.03	0 ± 0	0 ± 0	0.1 ± 0.03
Myrica gale	Myricaceae	S5	5	0 ± 0	0 ± 0	0.2 ± 0.05	0.2 ± 0.05	0.4 ± 0.08
Myrica pensylvanica	Myricaceae	S5	27	0.4 ± 0.08	0.1 ± 0.04*	2.6 ± 0.12	2.5 ± 0.11**	1.3 ± 0.08
Nemopanthus mucronatus	Aquifoliaceae	S5	33	3.0 ± 0.15	1.9 ± 0.10	3.7 ± 0.14	5.0 ± 0.16	1.2 ± 0.09
Oclemena acuminata	Asteraceae	S5	8	0.8 ± 0.09	0.4 ± 0.06	0 ± 0	0 ± 0	0.1 ± 0.04
Osmunda cinnamomea	Osmundaceae	S5	20	3.8 ± 0.18	4.2 ± 0.19	2.1 ± 0.15	3.1 ± 0.05	1.2 ± 0.13
Photinia floribunda	Rosaceae	S5	35	0 ± 0*	0.3 ± 0.05*	2.3 ± 0.12**	1.6 ± 0.08**	2.6 ± 0.09**
Picea glauca	Pinacea	S5	6	1.0 ± 0.12	0.1 ± 0.04	0.2 ± 0.05	0.4 ± 0.08	0.1 ± 0.04
Picea mariana	Pinacea	S5	9	4.3 ± 0.19	2.6 ± 0.15	0.3 ± 0.06	0 ± 0	0 ± 0
Picea rubens	Pinacea	S5	30	12.4 ± 0.21*	13.7 ± 0.24*	3.4 ± 0.16	5.8 ± 0.20	0.3 ± 0.07**
Prenanthes trifoliolata	Asteraceae	S5	1	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.03	0 ± 0
Prunus pensylvanica	Rosaceae	S5	9	0.1 ± 0.03	1.1 ± 0.10	0.3 ± 0.06	0.7 ± 0.19	0 ± 0
Pteridium aquilinum	Dennstaedtiaceae	S5	39	0.9 ± 0.09	3.1 ± 0.13	5.6 ± 0.18	4.6 ± 0.15	5.1 ± 0.16
Rhododendron canadense	Ericaceae	S5	38	1.4 ± 0.12	2.3 ± 0.12	8.7 ± 0.21	5.6 ± 0.16	3.3 ± 0.14
Rhododendron groenlandicum	Ericaceae	S5	46	1.8 ± 0.12	2.4 ± 0.13	8.4 ± 0.19	5.1 ± 0.15	3.8 ± 0.14
Rhus typhina	Anacardiaceae	S4S5	5	0.6 ± 0.07	0.1 ± 0.03	0.2 ± 0.05	0.3 ± 0.06	0 ± 0

				Distance (m)				
Species	Family	S-rank	# plots	0 Forest	4	8	12	16 Barrens
Rubus chamaemorus	Rosaceae	S4	6	0 ± 0	0 ± 0	0.1 ± 0.04	0.1 ± 0.04	0.6 ± 0.07
Sarracenia purpurea	Sarraceniaceae	S5	10	0.1 ± 0.03	0.2 ± 0.06	0.2 ± 0.06	1.6 ± 0.13	0.8 ± 0.08
Scirpus cespitosus	Cyperaceae	S5	8	0 ± 0	0.6 ± 0.09	1.1 ± 0.13	1.9 ± 0.13	4.1 ± 0.20
Sibbaldiopsis tridentata	Rosaceae	S5	2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.3 ± 0.06
Sorbus americana	Rosaceae	S5	3	0.1 ± 0.03	1.0 ± 0.12	0.1 ± 0.03	0 ± 0	0 ± 0
Symphyotrichum novi-belgii	Asteraceae	S5	9	0 ± 0	0.2 ± 0.05	0 ± 0*	0.1 ± 0.03	0.4 ± 0.05
Trientalis borealis	Primulaceae	S5	61	2.1 ± 0.11	1.6 ± 0.09	1.9 ± 0.08	2.0 ± 0.08	3.1 ± 0.08
Vaccinium angustifolium	Ericaceae	S5	66	1.1 ± 0.08*	3.3 ± 0.12	8.2 ± 0.18**	7.5 ± 0.17**	6.1 ± 0.14**
Vaccinium oxycoccos	Ericaceae	S5	9	0 ± 0	0.2 ± 0.05	0.3 ± 0.06	0.9 ± 0.09	0.9 ± 0.09
Vaccinium vitis-idaea	Ericaceae	S5	42	2.7 ± 0.12	1.6 ± 0.09	1.6 ± 0.08	3.0 ± 0.13	0.8 ± 0.07
Viburnum nudum var. cassinoides	Caprifoliaceae	S5	39	2.3 ± 0.12	4.5 ± 0.14*	4.5 ± 0.16	2.1 ± 0.11	0.3 ± 0.06
LICHENS								
Cladina multiformis	Cladoniaceae	N.A.	1	0 ± 0	0.1 ± 0.04	0 ± 0	0 ± 0	0 ± 0
Cladina rei	Cladoniaceae	N.A.	2	0.1 ± 0.03	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0
Cladina turgida	Cladoniaceae	N.A.	1	0 ± 0	0 ± 0	0.1 ± 0.03	0 ± 0	0 ± 0
Cladina umbricola	Cladoniaceae	N.A.	2	0 ± 0	0.2 ± 0.06	0 ± 0	0.1 ± 0.04	0 ± 0
Cladonia boryi	Cladoniaceae	N.A.	7	0 ± 0	0 ± 0	1.0 ± 0.12	0.4 ± 0.06	1.1 ± 0.11
Cladonia cenotea	Cladoniaceae	N.A.	2	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.03	0.1 ± 0.03
Cladonia chlorophaea	Cladoniaceae	N.A.	2	0 ± 0	0.1 ± 0.03	0 ± 0	0 ± 0	0.1 ± 0.04
Cladonia crispata	Cladoniaceae	N.A.	2	0.1 ± 0.03	0 ± 0	0.1 ± 0.03	0 ± 0	0 ± 0
Cladonia maxima	Cladoniaceae	N.A.	13	0.5 ± 0.06	0.4 ± 0.06	0.2 ± 0.06	0.3 ± 0.05	0.1 ± 0.04
Cladonia mitis	Cladoniaceae	N.A.	16	0.4 ± 0.08	0.1 ± 0.03	0.3 ± 0.05	1.1 ± 0.10	0.9 ± 0.08
Cladonia rangiferina	Cladoniaceae	N.A.	26	0.4 ± 0.08*	0 ± 0*	4.0 ± 0.20	3.7 ± 0.14	7.2 ± 0.19**
Cladonia squamosa	Cladoniaceae	N.A.	3	0 ± 0	0 ± 0	0.1 ± 0.03	0.2 ± 0.06	0.1 ± 0.03
Cladonia stellaris	Cladoniaceae	N.A.	3	0 ± 0	0.1 ± 0.03	0.1 ± 0.04	0 ± 0	0.1 ± 0.04
Cladonia uncialis	Cladoniaceae	N.A.	16	0.1 ± 0.03	0.3 ± 0.06	0.2 ± 0.04	0.6 ± 0.07	0.4 ± 0.05
Parmelia sulcata	Parmeliaceae	N.A.	1	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.05	0 ± 0
Umbilicaria muehlenbergii	Umbilicariaceae	N.A.	2	0 ± 0	0 ± 0	0 ± 0	0.7 ± 0.10	0.4 ± 0.08
Usnea trichodea	Parmeliaceae	N.A.	1	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Usnea sp. 1	Parmeliaceae	N.A.	1	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Crustose lichen sp	-	N.A.	2	0 ± 0	0 ± 0	0.1 ± 0.03	0.1 ± 0.04	0 ± 0

				Distance (m)				
Species	Family	S-rank	# plots	0 Forest	4	8	12	16 Barrens
MOSSES, LIVERWORTS								
Conordia compacta	Amblystegiaceae	S1	2	0.1 ± 0.03	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0
Cratoneuron filicinum	Amblystegiaceae	S2	1	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Dicranum condensatum	Dicranaceae	N.A.	1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.5 ± 0.09
Dicranum fuscesens	Dicranaceae	N.A.	16	0.5 ± 0.06	0.8 ± 0.08	0.2 ± 0.04	0.2 ± 0.05	0.1 ± 0.03
Dicranum polysetum	Dicranaceae	N.A.	14	0.6 ± 0.06	0.3 ± 0.05	0.1 ± 0.03	0.3 ± 0.05	0.2 ± 0.04
Dicranum scoparium	Dicranaceae	N.A.	16	1.4 ± 0.09*	0.7 ± 0.08	0.2 ± 0.04	0.2 ± 0.05	0 ± 0**
Dicranum undulatum	Dicranaceae	N.A.	1	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.03	0 ± 0
Drepanocladus fluitans	Amblystegiaceae	N.A.	1	0.2 ± 0.06	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Herzogiella striatella	Hypnaceae	N.A.	2	0.4 ± 0.08	0.3 ± 0.07	0 ± 0	0 ± 0	0 ± 0
Hylocomium splendens	Hylocomiaceae	N.A.	27	2.1 ± 0.10*	4.4 ± 0.15*	1.0 ± 0.09	0.7 ± 0.07	0.2 ± 0.05**
Hypnum pallescense var. *protuberans*	Hypnaceae	N.A.	4	0.1 ± 0.03	0.3 ± 0.06	0.1 ± 0.04	0 ± 0	0 ± 0
Leucobryum glaucum	Leucobryaceae	N.A.	4	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.05	0.3 ± 0.06
Moss 1	-	N.A.	4	0.9 ± 0.12	1.2 ± 0.11	0.2 ± 0.05	0 ± 0	0 ± 0
Pleurozium schreberi	Hylocomiaceae	N.A.	63	18.9 ± 0.22*	13.2 ± 0.17*	5.8 ± 0.18**	5.2 ± 0.16**	2.4 ± 0.13**
Ptilium crista-castrenscens	Hylocomiaceae	N.A.	21	0.9 ± 0.08	1.0 ± 0.07*	0.6 ± 0.07	0.8 ± 0.10	0.1 ± 0.03
Racomitrium fasiculare	Grimmiaceae	N.A.	1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.08
Sphagnum angustifolium	Sphagnaceae	S1	9	0.4 ± 0.05	0.1 ± 0.03	0.6 ± 0.07	0.2 ± 0.06	0 ± 0
Sphagnum capillifolium	Sphagnaceae	N.A.	17	2.2 ± 0.14	1.1 ± 0.08	0.7 ± 0.08	1.7 ± 0.13	2.7 ± 0.15
Sphagnum fuscum	Sphagnaceae	N.A.	11	0.4 ± 0.05	1.4 ± 0.12	0.6 ± 0.09	0.4 ± 0.08	0.3 ± 0.06
Sphagnum girgensohnii	Sphagnaceae	N.A.	7	1.0 ± 0.11	0.2 ± 0.05	0 ± 0	0.1 ± 0.03	0.3 ± 0.06
Sphagnum magellanicum	Sphagnaceae	N.A.	18	4.2 ± 0.18	2.4 ± 0.13	0.2 ± 0.05	0.7 ± 0.08	1.7 ± 0.13
Sphagnum russowii	Sphagnaceae	N.A.	2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.3 ± 0.06
Tetraphis pelucidia	Tetraphidaceae	N.A.	2	0.1 ± 0.03	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0
Bazzania trilobata	Liverwort	N.A.	27	6.9 ± 0.20*	2.2 ± 0.11*	1.1 ± 0.10	0.4 ± 0.06**	0.1 ± 0.03**
Lepedoza repens	Liverwort	N.A.	1	0 ± 0	0.1 ± 0.03	0 ± 0	0 ± 0	0 ± 0
Liverwort spp	Liverwort	N.A.	1	0 ± 0	0 ± 0	0.1 ± 0.03	0 ± 0	0 ± 0
Ptilidium pulcherimum	Liverwort	N.A.	3	0 ± 0	1.2 ± 0.12	0 ± 0	0 ± 0	0 ± 0

N.A. = Not available or not applicable.

* Significantly different from the barrens.

** Significantly different from the forest.

*** Significantly different from both the barrens and the forest.

Appendix 2. Species scores for the DCA and CCA ordinations for species listed in Appendix 1 that were included in the ordination. See methods for details.

Species	DCA axis 1	DCA axis 2	CCA axis 1	CCA axis 2
VASCULAR PLANTS				
Abies balsamea	-1.58	1.18	-1.05	0.33
Acer rubrum	0.29	2.16	-1.46	-0.04
Alnus viridis	-0.16	-0.94	0.56	0.03
Amelanchier sp.	-0.09	-1.54	0.90	0.46
Aralia hispida	0.54	-1.66	0.65	-0.10
Aralia nudicalus	-0.67	-0.23	-0.32	0.45
Arctostaphylos uva-ursi	1.66	-2.47	0.84	1.53
Betula papyrifera	-0.40	1.13	-0.71	0.30
Calamagrostis pickeringii	2.36	1.94	0.53	-0.62
Carex nigra	3.30	-1.59	1.21	0.27
Carex trisperma	0.88	2.43	-0.48	-1.45
Carex sp. 1	-3.14	0.46	-1.83	1.32
Chamaedaphne calyculata	2.03	1.75	0.62	-0.85
Clintonia borealis	-0.66	0.35	-0.44	0.24
Coptis trifolia	1.04	0.69	0.47	-0.10
Corema conradii	1.82	-2.50	0.96	1.08
Cornus canadensis	0.25	0.34	-0.02	0.19
Deschampsia flexuosa	-2.77	1.59	-1.81	0.01
Drosera rotundifolia	2.50	1.90	0.80	-1.10
Empetrum eamesii	-0.78	1.09	-0.25	0.19
Empetrum nigrum	2.32	0.79	0.88	-0.77
Gaultheria hispidula	-1.13	0.97	-0.49	0.11
Gaultheria procumbens	0.63	-1.73	0.60	0.02
Gaylussacia baccata	0.55	-1.35	0.46	0.15
Gaylussacia dumosa	1.57	-1.37	0.88	-0.33
Hamamelis virginiana	-5.72	-0.09		
Ilex verticillata	-0.83	0.74	-0.33	-0.03
Juniperus communis	2.06	-1.63	0.86	0.34
Kalmia angustifolia	0.22	0.17	0.20	-0.17
Kalmia polifolia	2.02	1.62	0.63	-0.71
Larix laricina	2.43	-2.37	0.85	0.00
Linnaea borealis	-1.70	1.31	-1.24	0.33
Maianthemum canadense	-0.35	0.16	-0.35	0.25
Maianthemum stellatum	2.69	2.13	1.05	0.42
Melampyrum lineare	0.40	-1.45	-0.01	0.75
Myrica gale	1.06	-1.39	0.89	0.56
Myrica pensylvanica	1.02	0.22	0.51	-0.13
Nemopanthus mucronatus	-0.32	0.34	-0.06	-0.10
Oclemena acuminata	-3.35	-0.21	-1.21	0.95
Osmunda cinnamomea	-1.13	1.30	-0.88	0.40
Photinia floribunda	0.93	-0.99	0.62	0.08
Picea glauca	-1.53	0.31	-1.32	0.45
Picea mariana	0.29	2.58	-0.97	-1.18

Species	DCA axis 1	DCA axis 2	CCA axis 1	CCA axis 2
Picea rubens	-1.81	-0.73	-0.55	0.16
Prenanthes trifoliolata	0.31	1.34		
Prunus pensylvanica	-1.16	-1.54	-0.01	0.62
Pteridium aquilinum	-0.38	-1.44	0.43	0.17
Rhododendron canadense	-0.27	-0.03	0.22	0.05
Rhododendron groenlandicum	0.65	0.64	0.23	-0.36
Rhus typhina	-3.75	0.22	-2.04	0.84
Rubus chamaemorus	2.35	1.78	1.00	-1.53
Sarracenia purpurea	2.24	1.89	0.52	-1.02
Scirpus cespitosus	2.33	1.59	0.80	-1.08
Sibbaldiopsis tridentata	1.95	-2.82	1.04	1.67
Sorbus americana	-2.85	-2.06	-0.44	0.88
Symphyotrichum novi-belgii	1.71	0.25	0.68	-0.99
Trientalis borealis	0.22	-0.02	0.01	0.16
Vaccinium angustifolium	0.43	-0.95	0.40	0.18
Vaccinium oxycoccos	2.15	1.89	0.61	-1.20
Vaccinium vitis-idaea	-0.37	0.25	-0.02	0.22
Viburnum nudum var. cassinoides	-0.57	0.60	-0.19	-0.07
LICHENS				
Cladina multiformis	-0.49	0.07	-0.44	0.67
Cladina rei	0.18	2.24	-1.64	-0.52
Cladina turgida	-1.18	-1.34	-0.46	0.37
Cladina umbricola	0.49	2.26	-0.24	-1.09
Cladonia boryi	1.61	-2.47	0.81	1.56
Cladonia cenotea	0.99	-2.10	0.88	0.46
Cladonia chlorophaea	-2.73	-0.06	-1.64	0.93
Cladonia crispata	0.65	-1.95	0.12	-0.56
Cladonia maxima	-1.21	0.16	-0.33	0.05
Cladonia mitis	1.30	0.16	0.51	-0.19
Cladonia rangiferina	1.92	-1.68	0.95	0.00
Cladonia squamosa	0.74	-1.98	0.92	0.45
Cladonia stellaris	1.24	-2.66	0.72	1.63
Cladonia uncialis	0.94	-1.44	0.62	0.38
Parmelia sulcata	-4.56	0.01	-0.18	0.85
Umbilicaria muehlenbergii	-1.17	-1.33	0.21	1.05
Usnea trichodea	-3.97	0.96	-1.78	0.51
Usnea sp. 1	-0.91	2.04	-1.25	0.25
Crustose lichen sp	-1.49	-1.60	0.09	1.17
MOSSES, LIVERWORTS				
Conordia compacta	-0.46	-0.02	-0.85	0.61
Cratoneuron filicinum	-2.77	1.59	-1.81	0.01
Dicranum condensatum	2.20	-3.43	1.14	1.92
Dicranum fuscesens	-1.22	1.27	-1.01	0.22
Dicranum polysetum	-0.85	0.93	-0.35	-0.06
Dicranum scoparium	-2.41	1.53	-1.36	0.22
Dicranum undulatum	2.19	-2.89	0.94	1.72

Species	DCA axis 1	DCA axis 2	CCA axis 1	CCA axis 2
Drepanocladus fluitans	-4.73	1.35	-2.34	0.96
Herzogiella striatella	-1.20	-0.62	-0.79	0.32
Hylocomium splendens	-2.02	0.70	-0.63	0.50
Hypnum pallescense var. *protuberans*	-1.71	1.46	-1.49	0.18
Leucobryum glaucum	0.86	-1.86	0.71	0.53
Moss 1	-2.67	1.71	-1.55	0.03
Pleurozium schreberi	-1.72	0.52	-0.79	0.12
Ptilium crista-castrenscens	-2.04	1.04	-0.99	0.20
Racomitrium fasiculare	1.02	-2.14	0.82	0.47
Sphagnum angustifolium	-0.06	1.39	-0.45	-0.04
Sphagnum capillifolium	1.40	2.19	-0.19	-0.63
Sphagnum fuscum	1.31	1.72	-0.11	-1.32
Sphagnum girgensohnii	-1.13	1.50	-1.17	0.05
Sphagnum magellanicum	0.87	2.48	-0.64	-1.01
Sphagnum russowii	2.45	1.89	0.97	0.36
Tetraphis pelucidia	-1.41	2.17	-1.52	-0.30
Bazzania trilobata	-2.11	0.93	-0.90	-0.04
Lepedoza repens	-2.15	2.01	-1.30	0.17
Liverwort spp	-1.18	-1.34	-0.46	0.37
Ptilidium pulcherimum	-2.45	-0.38	-0.78	0.21

References

Andrés C, Ojeda F (2002) Effects of afforestation with pines on woody plant diversity of Mediterranean heathlands in southern Spain. Biodivers Conserv 11:1511-1520

Atlantic Canada Conservation Data Center (ACCDC) (2005a) Provincial Lists and Ranks. Available via http://www.accdc.com/products/lists/ Cited October 13, 2008

Atlantic Canada Conservation Data Center (ACCDC) (2005b) Glossary. Available via http://www.accdc.com/glossary/index.php#rank Cited October 13, 2008

Baird, C (1999) Environmental Chemistry. W.H. Freeman and Company, New York.

Bazzaz FA (1979) The physiological ecology of plant succession. Annu Rev Ecol Syst 10:351-371

Bradley RL, Titus BD, Fyles JW (1997) Nitrogen acquisition and competitive ability of *Kalmia angustifolia* L., Paper Birch (*Betula papyrifera* Marsh.) and Black Spruce (*Picea mariana* (Mill.) B.S.P.) seedlings grown on different humus forms. Plant Soil 195:209-220.

Breshears DD (2006) The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? Front Ecol Environ 4:96-104

Brodo E, Sharnoff SD, Sharnoff S (2001) Lichens of North America. Yale University Press, New Haven

Brooker RW, Osler GHR, Gollisch J (2008) Association of vegetation and soil mite assemblages with isolated Scots pine trees on a Scottish wet heath. Landscape Ecol 23:861-871

Burley ST (2009) Forest expansion into coastal barrens in Nova Scotia, Canada. MSc thesis, Saint Mary's University, Canada

Council Officers and Executive Committee (COEC) (1992) Handbook on Reference Material for Soil Analysis. Soil and Plant Analysis Council, Inc., Georgia, USA.

Crum, H (1983) Mosses of the Great Lakes Forest. 3rd ed. University of Michigan, Ann Arbor

Duarte LS, Machado RE, Hartz SM, Pillar V (2006) What saplings can tell us about forest expansion over natural grasslands. J Veg Sci 17:799-080

Dunwiddie PW, Zaremba RE, Harper K (1996) A classification of coastal heathlands and sandplain grasslands in Massachusetts. Rhodora 98:117-145

Ehrenfeld JG, Zhu W, Parsons WFJ (1995) Above- and below-ground characteristics of persistent forest openings in the New Jersey Pinelands. Bull Torrey Bot Club 122: 298-305

Faison EK, Foster DR, Oswald WW et al. (2006) Early Holocene openlands in southern New England. Ecology 87:2537-2547

Fraver S (1994) Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. Conserv Biol 8:822-832

Harper KA, Macdonald SE (2001) Structure and composition of riparian boreal forest: new methods for analyzing edge influence. Ecology 82:649-659

Harper KA, Macdonald SE (2002) The critical values program for assessing edge influence. Bull Ecol Soc Am 83: 61-62

Harris LD (1988) Edge effects and conservation of biotic diversity. Conserv Biol 2: 330-332

Hennenberg KJ, Goetze D, Minden V, et al. (2005) Size-class distribution of *Anogeissus leiocarpus* (Combretaceae) along forest-savanna ecotones in Northern Ivory Coast. J Trop Ecol 21:273-281

Latham ER, Thompson JE, Riley SA, et al. (1996) Pocono till barrens: shrub savannah persisting on soils favoring forests. Bull Torrey Bot Club 123:330-349

Linneman JS, Palmer MW (2006) The effect of *Juniperus virginiana* on plant species composition in an Oklahoma grassland. Community Ecol 7:235-244

Lloyd KM, McQueen AAM, Lee BJ, et al. (2000) Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. J Veg Sci 11: 903-910

Mallik AU (1995) Conversion of temperate forests into heaths: Role of ecosystem disturbance and Ericaceous plants. Environ Manage 19:675-684
Mallik AU (2003) Conifer regeneration problems in boreal and temperate forests with ericaceous understory. Crit Rev Plant Sci 22:341-366

Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures – implications for conservation. Biol Conserv 132:311-321

Mascarúa LE, Harper KA, Drapeau P (2006) Edge influence on forest structure in large forest remnants, cutblock separators, and riparian buffers in managed black spruce forests. Ecoscience 13:226-233

Maurice KR,Welch JM, Brown CP et al. (2004) Pocono mesic till barrens in retreat: topography, fire and forest contagion effects. Lanscape Ecol 19:603-620

McKinley DC, Blair JM (2008) Woody plant encroachment by *Juniperus virginiana* in a mesic native grassland promotes rapid carbon and nitrogen accrual. Ecosystems 11:454-468

Meades WJ (1983) The origin and successional status of anthropogenic dwarf shrub heath in Newfoundland. Advances in Space Research 2: 97-101

Neily P, McCurdy D, Stuart B et al. (2004) Coastal Forest Communities of the Nova Scotian Eastern Shore Ecodistrict. Nova Scotia Department of Natural Resources

Nova Scotia Museum of Natural History (1997) Natural History of Nova Scotia Volume I: Topics and Habitats. Nova Scotia Museum of Natural History, Nova Scotia.

Oberndorfer EC, Lundholm JT (2009) Species richness, abundance, rarity and environmental gradients in coastal barren vegetation. Biodivers Conserv 18:1523- 1553

Price JN, Morgan JW (2008) Woody plant encroachment reduces species richness of herb-rich woodlands in southern Australia. Austral Ecol 33:278-289

Rhoades CC, Miller SP, Skinner DL (2005) Forest vegetation and soil patterns across glade-forest ecotones in the Knobs region of Northeastern Kentucky, USA. Am Midl Nat 54:1-10

Roland AE, Smith EC (1963) The flora of Nova Scotia. Nova Scotian Institute of Science, Halifax, Nova Scotia.

Saldarriaga JG, West DC, Tharp ML et al. (1988) Long-term chronosequence of forest succession in the Upper Rio Negro of Columbia and Venezuela. J Ecol 76:938-958

Shachak M, Boeken B, Groner E, et al. (2008) Woody species as landscape modulators and their effect on biodiversity patterns. BioScience 58:209-221

Stark KE, Lundholm JT, Larson DW (2003) Relationships between seed banks and spatial heterogeneity of North American alvar vegetation. J Veg Sci 14:205-212

Stark KE, Lundholm JT, Larson DW (2004) Arrested development of soil on alvars of Ontario, Canada: implications for conservation and restoration. Nat Area J 24:95-100

Verhoeven KJF, Simonsen KL, McIntyre LM (2005) Implementing false discovery rate control: increasing your power. Oikos 108:643-647

Figure Legends

Figure 1. Locations of three coastal barrens study sites along the Atlantic coast of Nova Scotia, Canada.

Figure 2. Sampling design illustrating the placement of plots along a transect across a forest-barren ecotone. Transects were located at the edges of eighteen forest patches in three coastal barren study sites along the southeast coast of Nova Scotia.

Figure 3. DCA ordination diagrams with the first two axes showing the distribution of plant species composition along 18 transects across forest-barren transition zones: A) plot scores and B) species scores. Eigenvalues are 0.4880 and 0.4074 for axes 1 and 2, respectively. In A), F and B represent reference forest and barrens plots, respectively, while 1, 2 and 3 represent the transition zone (edge),. In B), species were classified according to their abundance in plot types: F: forest species; T: transition species; A: transition avoiders; U: ubiquitous; X: species found in less than 5 plots. See methods for details. Species scores are in Appendix 2.

Figure 4. CCA ordination with the first two axes showing the distribution of understory species composition relative to nine environmental variables along 18 transects across forest-barren transition zones at three study sites including Peggy's Cove, Taylor's Head, and Canso for A) vascular species except graminoids and ferns and B) nonvascular, fern and graminoid species. For clarity, species in less than 5 plots are indicated with a horizontal dash and tree species are indicated by a vertical dash. Abbreviations for other species are: A) An = *Aralia nudicalus*, Au = *Arctostaphylos uva-ursi*, Av = *Alnus viridis*, Cb = *Clintonia borealis*, Cc = *Cornus canadensis*, Ch = *Chamaedaphne calyculata*, Cm = *Corema conradii*, Ct = *Coptis trifolia*, En = *Empetrum nigrum*, Gb = *Gaylussacia baccata*, Gd = *Gaylussacia dumosa*, Gh = *Gaultheria hispidula*, Gp = *Gaultheria procumbens*, Iv = *Ilex verticillata*, Jc = *Juniperus communis*, Ka = *Kalmia angustifolia*, Kp = *Kalmia polifolia*, Lb = *Linnaea borealis*, Mc = *Maianthemum canadense*, Mg = *Myrica gale*, Mp = *Myrica pensylvanica*, Nm = *Nemopanthus mucronatus*, Oa = *Oclemena acuminata*, Pf = *Photinia floribunda*, Pp = *Prunus pensylvanica*, Rc = *Rhododendron canadense*, Rg = *Rhododendron groenlandicum*, Rt = *Rhus typhina*, Ru = *Rubus chamaemorus*, Sn = *Symphyotrichum novi-belgii*, Sp = *Sarracenia purpurea*, Tb = *Trientalis borealis*, Va = *Vaccinium angustifolium*, Vn = *Viburnum nudum*, Vo = *Vaccinium oxycoccos*, Vv = *Vaccinium vitis-idaea*; and B) Bt = *Bazzania trilobata*, Cb = *Cladonia boryi*, Cm = *Cladonia mitis*, Ct = *Carex trisperma*, Cx = *Cladonia maxima*, Cr = *Cladonia rangiferina*, Cu = *Cladonia uncialis*, Dp = *Dicranum polysetum*, Ds = *Dicranum scoparium*, Df = *Dicranum fuscesens*, Hs = *Hylocomium splendens*, Oc = *Osmunda cinnamomea*, Pa = *Pteridium aquilinum*, Pc = *Ptilium crista-castrenscens*, Ps = *Pleurozium schreberi*, Sc = *Sphagnum capillifolium*, Sf = *Sphagnum fuscum*, Sg = *Sphagnum girgensohnii*, Sm = *Sphagnum magellanicum*, Sr = *Scirpus cespitosus*. Some symbols were moved slightly to improve legibility See methods for details. Species scores are in Appendix 2

Table 1. Mean values ± 1 SE of abiotic variables and vegetation composition and structure sampled from 18 transects across the transition area between coastal barrens and forest patches (at three study sites). Significant differences from either the forest or barrens plots or both were determined using randomization tests to assess edge influence (see Methods for details). Multiple testing for the 192 tests was accounted for using the false discovery rate (Verhoeven et al. 2005).

			Distance from forest centre plot (m)		
	0 Forest	4 Edge	8 Edge	12 Edge	16 Barrens
Tree age (years)	60 ± 4*	46 ± 4***	29 ± 6***	25 ± 8***	6 ± 4**
Tree height (m)	4.9 ± 0.3*	3.6 ± 0.3***	2.3 ± 0.5***	1.4 ± 0.3***	0.2 ± 0.2**
Vegetation height (m)	4.5 ± 0.6*	2.8 ± 0.7*	1.2 ± 0.2***	0.9 ± 0.1***	0.4 ± 0.0**
Canopy cover (%)	65 ± 5*	50 ± 6*	9 ± 5***	10 ± 4***	0 ± 0**
Soil depth (cm)	48 ± 8	47 ± 6	39 ± 6	34 ± 7	35 ± 6
Soil development^1	2.2 ± 0.06	2.1 ± 0.06	1.9 ± 0.06	1.5 ± 0.06	1.6 ± 0.06
% Organic^2	11.5 ± 0.3	9.1± 0.2	5.8 ± 0.2	12.1 ± 0.3	12.5 ± 0.3
% N	0.41 ± 0.05	0.37 ± 0.04	0.28 ± 0.04	0.36 ± 0.04	0.28 ± 0.04
P (ppm)	78.8 ± 0.5	88.6 ± 0.7	47.2 ± 0.6	80.3 ± 0.8	81.9 ± 0.8
K (ppm)	70.9 ± 0.5	55.8 ± 0.4	68.9 ± 0.6	68.6 ± 0.6	87.6 ± 0.5
Ca (ppm)	183.8 ± 1.0	181.0 ± 1.0	192.4 ± 1.3	260.6 ± 1.3	288.7 ± 1.1
Mg (ppm)	145.9 ± 1.0	180.7 ± 1.3	142.3 ± 1.0	251.1 ± 1.2	197.8 ± 0.9
Na (ppm)	71.8 ± 0.4	88.3 ± 0.6	68.8 ± 0.6	82.8 ± 0.5	74.8 ± 0.4
S (ppm)	64.3 ± 0.5	87.3 ± 0.5*	57.0 ± 0.6	65.4 ± 0.5	51.2 ± 0.3
Fe (ppm)	214.6 ± 0.8	214.3 ± 1.1	164.9 ± 1.0	213.6 ± 1.0	209.6 ± 0.8
Mn (ppm)	2.63 ± 0.13	1.80 ± 0.08	1.67 ± 0.08	1.21 ± 0.05	1.63 ± 0.08
Cu (ppm)	0.10 ± 0.00	0.10 ± 0.00	0.19 ± 0.05	0.10 ± 0.00	0.10 ± 0.00
Zn (ppm)	2.02 ± 0.07	1.76 ± 0.06	2.54 ± 0.14	2.49 ± 0.09	2.66 ± 0.10
B (ppm)	0.13 ± 0.02	0.12 ± 0.02	0.12 ± 0.02	0.13 ± 0.02	0.15 ± 0.02
CEC	11.1 ± 0.2	11.2 ± 0.2	10.7 ± 0.2	12.5 ± 0.2	11.0 ± 0.1
Richness (# species)	12 ± 1	10 ± 1*	11 ± 1*	13 ± 0	13 ± 1
DCA site score axis 1	-0.97*	-0.69*	0.08***	0.25***	0.96**
DCA site scores axis 2	0.54*	0.31*	-0.18**	-0.18**	-0.52**

* Significantly different from the barrens.

** Significantly different from the forest.

*** Significantly different from both the barrens and the forest.

[1] See methods for explanation.

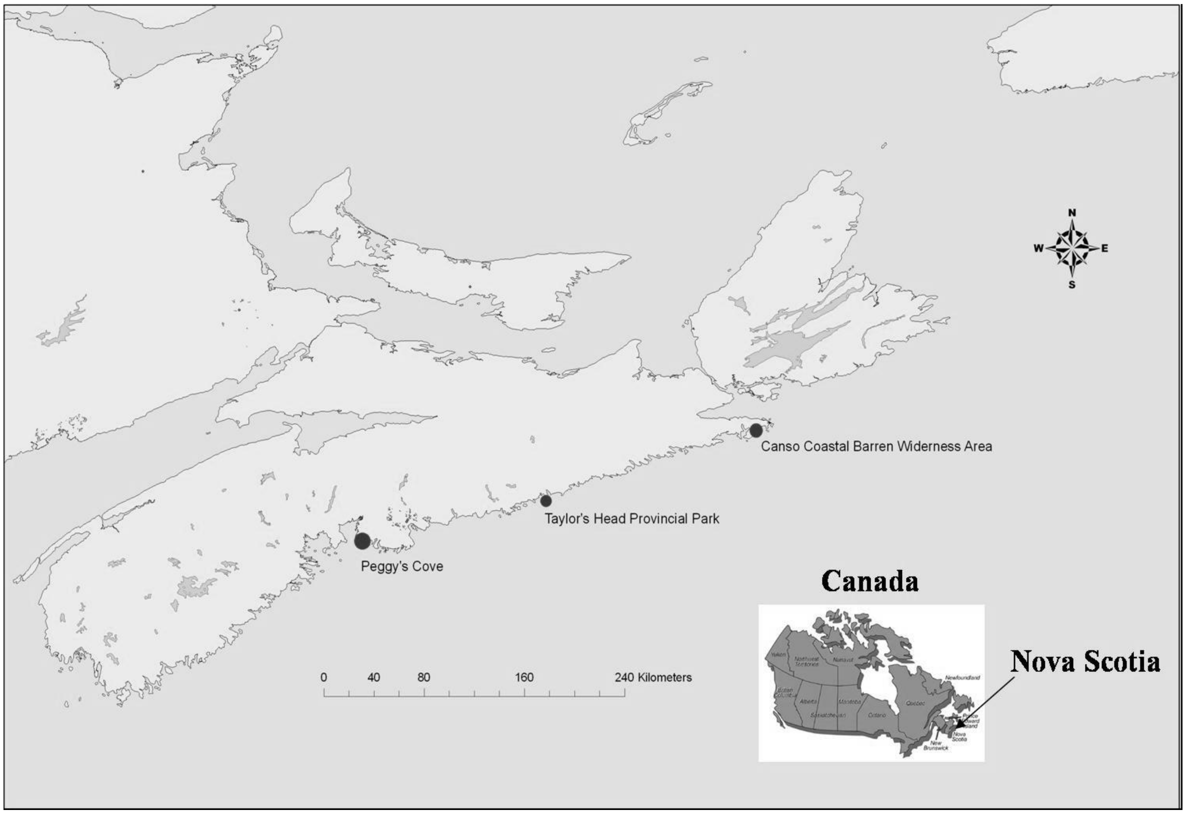
[2] Maximum depth of soil collected for analyses corresponds to soil depth recorded for each plot.

Table 2. List of species classified according to their pattern of abundance across the forest-barren transition. Barrens and forest species showed increasing and decreasing patterns respectively, transition species and avoiders had peaks and troughs in abundance in the transition, and ubiquitous species exhibited no strong pattern across the transition. Rare species found in less than five plots are not included. See Appendix 1 for average values in plots across the transition.

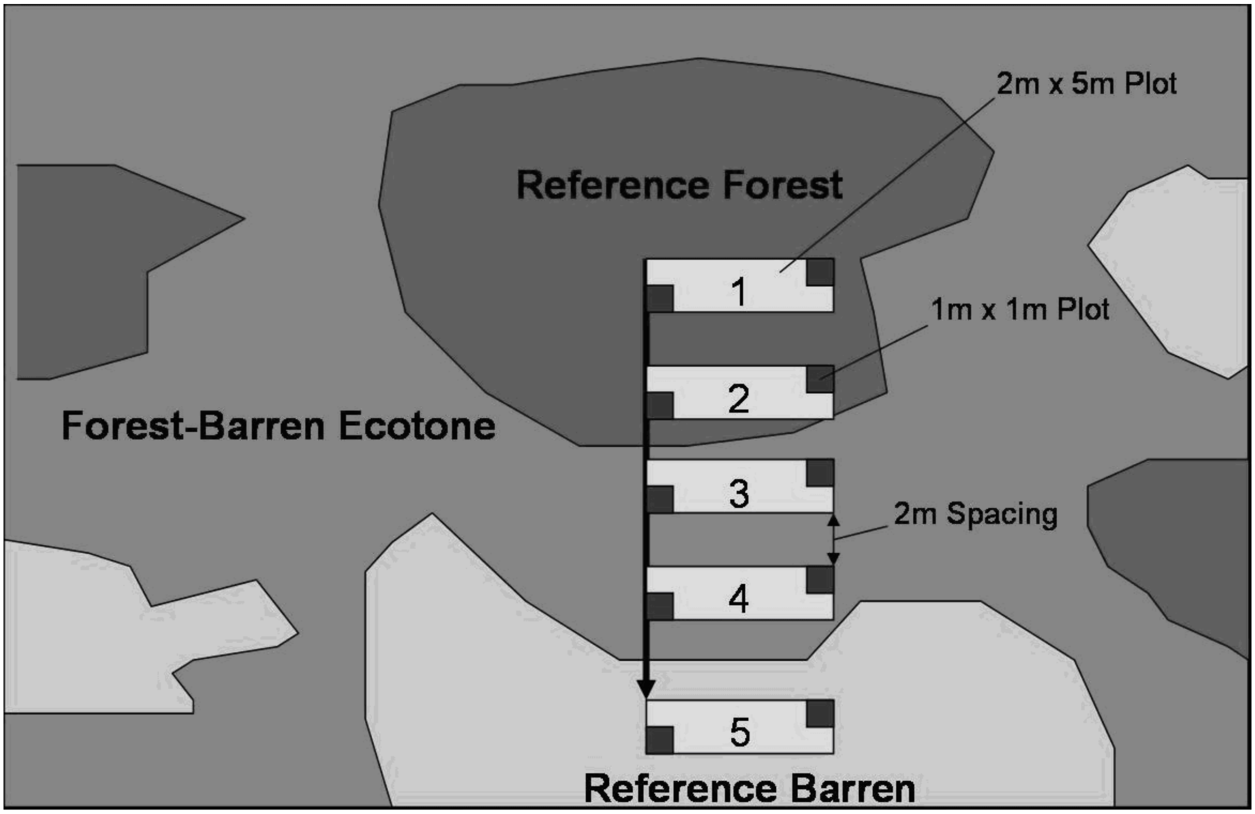
	Barrens species	Forest species	Transition species	Transition avoiders	Ubiquitous
Vascular plants	*Arctostaphylos uva-ursi* *Photinia floribunda** *Aster nova-belgii** *Chamaedaphne calyculata* *Coptis trifolia* *Corema conradii** *Eleocharis sp.* *Empetrum nigrum** *Gaultheria procumbens** *Gaylussacia baccata** *Gaylussacia dumosa* *Juniperus communis** *Kalmia polifolia* *Myrica gale* *Pteridium aquilinum* *Rubus chamaemorus* *Vaccinium oxycoccos*	*Aster acuminatus* *Gaultheria hispidula* *Linnaea borealis* *Osmunda cinnamomea* *Picea glauca* *Picea mariana* *Picea rubens** *Rhus typhina*	*Abies balsamea** *Alnus viridis* *Aralia nudicalus* *Ilex verticillata* *Kalmia angustifolia* *Ledum groenlandicum* *Myrica pensylvanica** *Nemopanthus mucronatus* *Prunus pensylvanica* *Rhododendron canadense* *Sarracenia purpurea* *Vaccinium angustifolium** *Viburnum nudum var. cassinoides**	*Carex trisperma* *Cornus canadensis*	*Clintonia borealis* *Maianthemum canadense* *Trientalis borealis* *Vaccinium vitis-idaea*
Lichens	*Cladonia boryi* *Cladonia mitis* *Cladonia rangiferina** *Cladonia uncialis*	*Cladonia maxima*			
Mosses, liverworts		*Bazzania trilobata** *Dicranum fuscesens* *Dicranum polysetum* *Dicranum scoparium** *Pleurozium schreberi** *Ptilium crista-castrenscens**	*Hylocomium splendens** *Sphagnum fuscum*	*Sphagnum capillifolium* *Sphagnum gergensonii* *Sphagnum magellanicum*	

*At least one distance significantly different from either the coastal barrens, forest or both (Appendix 1)

Figure 1.


N
W
E
S
Canso Coastal Barren Widerness Area
Taylor's Head Provincial Park
Peggy's Cove
0
40
80
160
240 Kilometers
Canada
Nova Scotia
Yukon
Northwest Territories
Nunavut
British Columbia
Alberta
Saskatchewan
Manitoba
Ontario
Quebec
Newfoundland
Prince Edward Island
Nova Scotia
New Brunswick

588 Figure 2.



589

Figure 3.

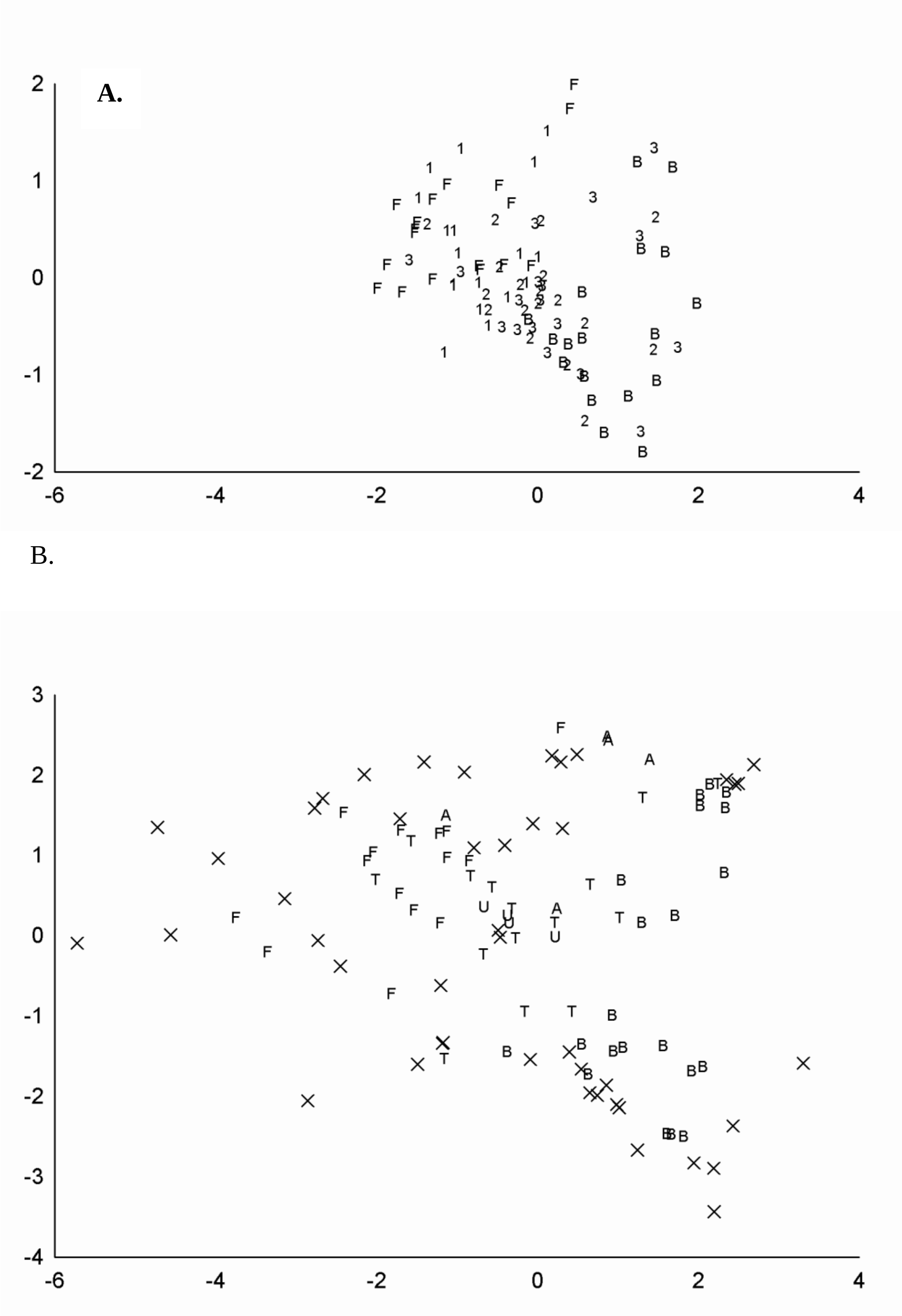
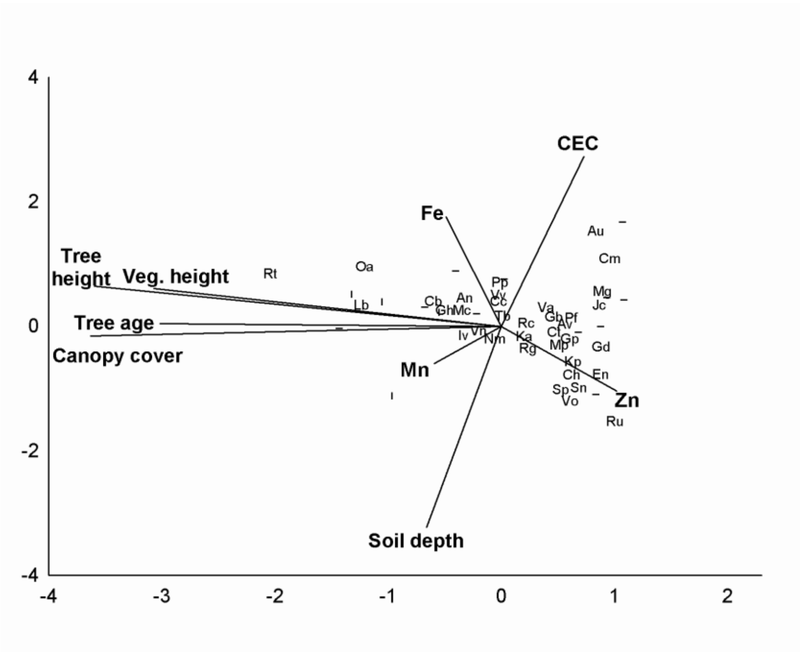
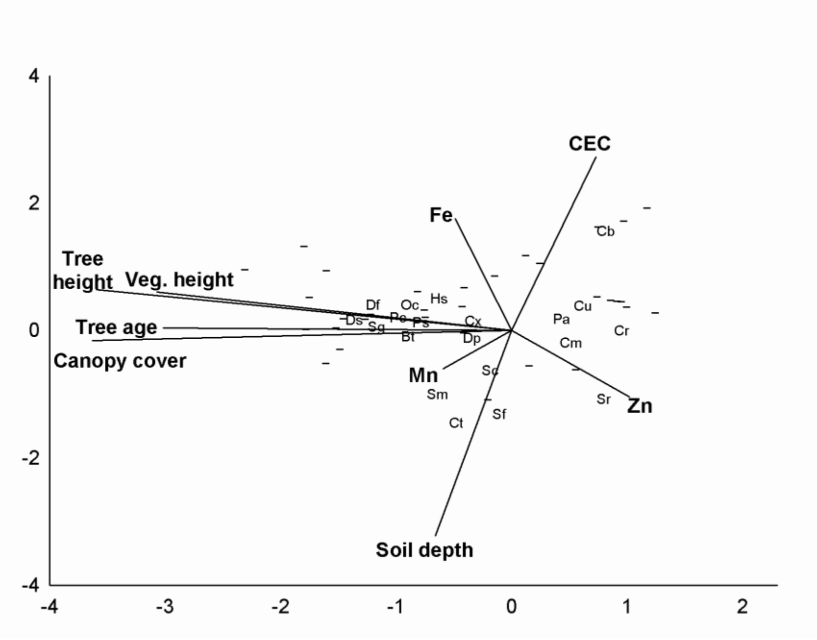


Figure 4.

A.


CEC
Fe
Tree height
Veg. height
Tree age
Canopy cover
Mn
Zn
Soil depth
Rt
Oa
Lb
Cb
Gh
Mc
An
Pp
Vy
Cc
Tb
Vn
Iv
Nm
Rc
Ka
Rg
Va
Gb
Pf
Av
Cf
Gp
Mp
Au
Cm
Mg
Jc
Gd
Kp
Ch
En
Sp
Sn
Vo
Ru
4
2
0
-2
-4
-4
-3
-2
-1
0
1
2

B.


CEC
Fe
Tree height
Veg. height
Tree age
Canopy cover
Mn
Zn
Soil depth
Cb
Hs
Df
Oc
Ds
Pe
Ps
Sg
Bt
Cx
Dp
Cu
Pa
Cr
Cm
Sc
Sm
Sf
Ct
Sr
4
2
0
-2
-4
-4
-3
-2
-1
0
1
2