A multivariate study of moss distributions in relation to environment in the Gulf of St. Lawrence region, Canada

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Abstract: Moss distribution patterns in the Gulf of St. Lawrence were investigated using multivariate analyses to determine the relationship of the patterns to environmental factors. Distance-based redundancy analysis was used to ordinate 29 operational geographical units (OGU) or sampling units based on their moss floras, and hierarchical cluster analysis in combination with indicator analysis was used to produce classifications of both species and sampling units. Climatic variables, in particular, warmth of the growing season, were the most important factors determining species distribution; this resulted in a north–south gradient through the study area. Oceanity was also shown to be important and manifested as an east–west gradient. Edaphic factors, in particular, amount of calcareous rock outcrop, had a secondary influence and modified the patterns established by climate. Ordination of OGUs showed the effects of environment to be more variable in the northern half of the Gulf of St. Lawrence, which may in part explain the higher species richness there. Seven OGU groups were recognized based on cluster analysis of floristic composition. Although indicator species were few, most groups were distinguished by unique sets of regionally rare species. Eleven species elements were identified based on species occurrence in OGUs. The elements constituted sets of overlapping distributions showing southern, northern, and eastern biases in the Gulf region. Multivariate analysis was shown to be effective tool for extracting moss–environment patterns, even at medium geographic scale.

Key words: Gulf of St. Lawrence, mosses, environment, richness, distribution, ordination, cluster analysis.

Résumé : L'auteur a étudié les patrons de distribution des mousses dans le golfe du St-Laurent en utilisant des analyses multivariées, afin de déterminer les relations entre ces patrons et les facteurs environnementaux. Il utilise une analyse de redondance basée sur la distance, pour l'ordination de 29 unités d'échantillonnage géographique (OGU) basée sur leurs flores muscinales, et l'analyse par regroupements hiérarchiques avec l'analyse d'indicateurs, pour en arriver à des classifications des espèces aussi bien que des unités d'échantillonnage. Les variables climatiques, et en particulier la chaleur au cours de la saison de croissance, constituent le facteur le plus important pour déterminer la distribution des espèces, et conduit à un gradient nord–sud pour l'ensemble de la région étudiée. On démontre également l'importance du climat maritime, qui se manifeste sous forme d'un gradient est–ouest. Les facteurs édaphiques, en particulier l'importance d'effleurements calcaires, exercent une influence secondaire et modifient les patrons établis par le climat. L'ordination des OGUs montre que les effets de l'environnement sont plus variables dans la moitié nordique du golfe du St. Laurent, ce qui pourrait expliquer en partie la plus grande richesse en espèces qu'on y trouve. On reconnaît sept groupes basés sur l'analyse par regroupements de la composition floristique. Bien qu'on identifie peu d'espèces indicatrices, la plupart des groupes se distinguent par un ensemble unique d'espèces rares régionales. On identifie onze éléments spécifiques basés sur la présence des espèces dans les OGUs. Ces éléments constituent des ensembles qui se recoupent et montrent des tendances méridionales, boréales ou orientales. On démontre ainsi que l'analyse multivariée constitue un moyen efficace pour déduire les patrons mousses–environnement, même à une échelle géographique intermédiaire.

Mots clés : golfe du St-Laurent, mousses, environnement, richesse, distribution, ordination, analyse par regroupement.

[Traduit par la Rédaction]

Introduction

The Gulf of St. Lawrence region (Fig. 1) is one of the most bryologically diverse in Canada, supporting more than half of Canada's moss flora. The region is relatively well known bryologically. The main contributions to the knowledge of the mosses in the Gulf are those of Belland (1987*a*, 1987*b*), which are comprehensive analyses of the distribution of the entire moss flora and of mosses with large-scale disjunct distributions. Other studies of moss distribution in various parts of the Gulf of St. Lawrence include Brassard (1983*a*, 1984*a*), Belland (1989), Belland and Favreau (1988), Belland and Brassard (1988), and Belland and Schofield (1994*a*, 1994*b*, 1994*c*). Brassard (1983*b*) provides a comprehensive list of floristic studies for Newfoundland.

Belland (1987*a*) documented 525 moss species from the Gulf of St. Lawrence region, a bryophyte richness that

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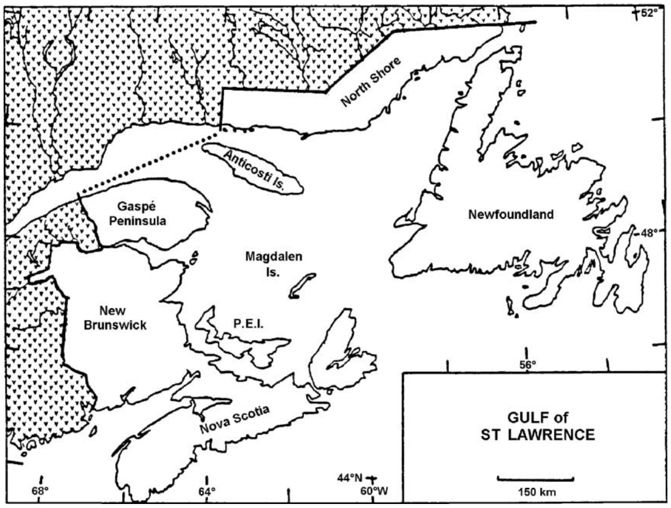
Fig. 1. The Gulf of St Lawrence, showing the extent of the study area and the major provinces and areas referred to in the text.



equals or surpasses many Canadian provinces of equivalent or larger size. The high moss richness has been attributed to a complex interaction of diverse physiography, geology, climate, and glacial history (Belland 1987*a*, 1987*b*) that has resulted in a high richness of distributional patterns within the region. However, the relative importance of these environmental factors and their influence on moss distributions have not been documented quantitatively.

Increasingly, the complex relationships of plants with the environment are being explored using multivariate techniques. While the application of these tools has largely been applied to ecological problems, several European studies have shown them to be useful for interpreting distributions at regional or larger scales (Proctor 1967; Hill 1991; Myklestad 1993; Myklestad and Birks 1993; Heikinnen et al. 1998; Vandenpoorten and Engels 2002; Korvenpää et al. 2003). Among the main advantages of these numerical analyses are objectivity, repeatability, ability to synthesize large volumes of data, and easy analysis of floras at different scales (Myklestad and Birks 1993; Heikkinen et al. 1998). Large-scale multivariate studies can lead to detection of environmental gradients and thus provide insight into the factors that influence distribution patterns. Multivariate floristic analyses can also classify species into groups characterized by similar distributions and delimit landscape or biogeoclimatic regions distinguished by groups of component species (Hill 1991; Retuerto and Carballeira 1991; Carey et al. 1995). Results from these studies provide baseline data on which further detailed phytogeographic and biodiversity studies can be founded.

Several bryological studies have utilized multivariate techniques in landscape scale studies (e.g., Gignac 1993; Gignac and Vitt 1990; Gignac et al. 1991; Jonsgard and Birks 1993; Belland and Vitt 1995). Typically these analyses have included only a small subset of the regional flora, and usually only those species restricted to specific habitats or those that were sampled using quadrats or relevés. Moreover, multivariate approaches have seldom been used to identify and describe the distribution patterns of entire moss floras at regional scales, especially in North America. Most such studies are European and include Proctor (1967), Carey et al. (1995), Hill (1991), Hill and Lozano (1994), Preston and Hill (1999), and Vanderpoorten and Engels (2002).

Two Gulf of St. Lawrence studies (Belland 1987*a*, 1987*b*) have made use of multivariate tools in their analysis. Belland (1987*a*) used numerical clustering methodology to define 11 distributional elements for the Gulf of St. Lawrence moss flora. The correlation of environmental factors with species distributional patterns, however, was largely qualitative and based mainly on field knowledge of individual species' ecology. Generalized climate, geological substrate, physiography, and several edaphic factors were all considered in this study. It was concluded that climate is the most important factor influencing species distributions in the Gulf of St. Lawrence region and that geological substrate and edaphic factors modify the basic patterns imposed by this factor. A later study (Belland 1989) used principal coordinate analysis to show gradients of floristic elements (e.g., boreal, temperate, etc.) in the same region. However, since floristic elements integrate many climatic variables, the precise nature (i.e., temperature, precipitation) of the floristic gradients was not identified.

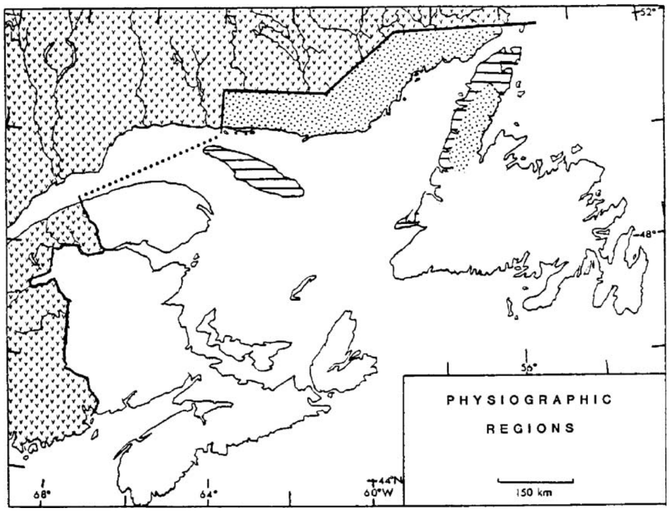
There are no studies that quantify the importance of climatic and edaphic variables in determining moss distributions in the Gulf of St. Lawrence region. This paper presents a multivariate floristic study of the moss flora to determine the importance of major climatic, physiographic, and geologic factors and their relation to moss distribution patterns in the region. It focuses on environmental factors cited in earlier works for the region. A new multivariate method, distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999), was used to extract species–environment relationships. The current paper builds on previous work (Belland 1987*a*, 1989) by providing both species and sample classifications using more rigorous numerical analyses than initially used by those studies.

Materials and methods

Physiography and climate

The Gulf of St. Lawrence region (Fig. 1) is situated on the east coast of Canada where it comprises the provinces bounding the Gulf of St. Lawrence. It includes the maritime provinces of Canada (Nova Scotia, New Brunswick, Prince Edward Island (PEI)), the islands of Newfoundland, Anticosti, and Magdalen, in addition to Gaspé Peninsula (Québec, east of the Matapédia River), the Québec North Shore, and southern Labrador along the northwestern shore of the Strait of Belle Isle. The region spans approximately 1250 km from south to north and 1200 km from east to west and includes a land area of nearly 317 000 km^2. Three physiographic regions are represented (Appalachian, Laurentian, and St. Lawrence Lowlands, Fig. 2), encompassing a diversity of landscapes: coastal plains, uplands, and highlands whose summits reach elevations exceeding 1200 m only 30 km from the coast. The Appalachian region comprises the largest area and includes both lowland and highland regions of Newfoundland, the Maritimes, and Gaspé Peninsula. Geologically, this physiographic region encompasses a wide spectrum of rock lithologies. Although the region is

Fig. 2. The physiographic regions of the Gulf of St. Lawrence. Stippled areas denote the Laurentian Region; horizontal lines denote the St. Lawrence Lowland; blank areas denote the Appalachian Region.



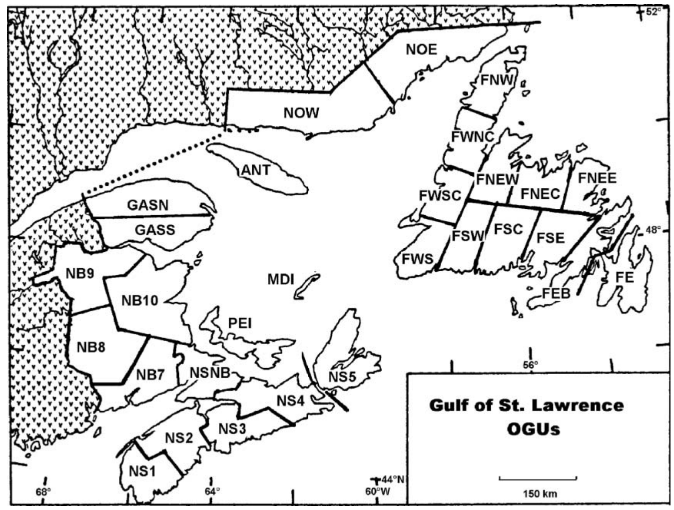
dominated by siliceous bedrock, ultramafic (e.g., serpentines), mafic (e.g., basalt), and metamorphic bedrock are well represented. The Laurentian physiographic region includes most of the Québec North Shore and southern Labrador, as well as the Long Range Mountains of western Newfoundland. This physiographic region is part of the Canadian Shield and is represented by highlands composed mainly of granite gneiss. The St. Lawrence Lowlands include Anticosti Island, the Mingan Archipelago (off the Québec North Shore), and the Coastal Plain of western Newfoundland. Low elevation and low relief characterize the St. Lawrence Lowlands; geologically they consist mainly of calcareous rocks. A detailed description of the physiography and geology is given in Belland (1987*a*).

The study area falls within the Boreal and Atlantic climatic regions (Hare and Thomas 1979). The Atlantic region includes the Maritimes and the island of Newfoundland. It has a continental climate, with mean annual temperatures between 0 and 8 °C and total precipitation ranging from 1100 to 1500 mm yearly. Gaspé Peninsula, Anticosti Island, as well as the Québec North Shore, belong to the Boreal climatic region. Cold winters and mean annual temperatures below 0 °C characterize this region. Precipitation is slightly less than that of the Atlantic region, ranging from 900 to 1000 mm annually.

Data

Only moss taxa with discrete distributions within the Gulf of St. Lawrence region were considered in this analysis. This included all taxa listed in Belland (1987*a*) with the exception of species that are widespread in the study area and thus do not show distinct distributional patterns. The resulting dataset consists of 322 of the total 532 species currently known from the region, including recent additions to the flora. Records for the Maritimes are mainly from Ireland (1982) supplemented with additional data from numerous sources (Bagnell and Clayden 1993; Bagnell et al. 1993; Belland 1984, 1992, 1993, 1995; Belland and Schofield

Fig. 3. The 29 operational geographic sampling units (OGU) in the Gulf of St. Lawrence region.



1988, 1994*a*, 1994*b*, 1994*c*). Data for Newfoundland was based primarily on herbarium vouchers (at NFLD, UBC, and CANM) in addition to published records in Tuomikoski et al. (1973). The moss flora of Gaspé Peninsula is known from Belland and Favreau (1988), while data for the Québec North Shore (especially the Mingan Archipelago) is from Belland et al. (1992). De Sloover's (1976) list is used for the Magdalen Islands.

The nomenclature follows Anderson et al. (1990) for mosses and Anderson (1990) for the peat moss genus *Sphagnum*.

The study area was divided into 29 operational geographical units (OGU) or sampling units for analysis (Fig. 3). For ease of data compilation, they were delimited, insofar as possible, using political units (e.g., counties, provincial boundaries) for the Maritimes and natural boundaries (e.g., Cabot Strait). With the exception of the Magdalen Islands (202 km^2) and PEI (5 660 km^2), the OGUs were large, varying in size from 7 450 (FWSC) to 21 391 km^2 (NB10).

Lists of species for each OGU were compiled into a presence–absence data matrix of species by OGU that composed the main dataset used for the multivariate analyses.

Eight environmental variables were initially included in the analysis: five climate variables and three physiographic and (or) geologic variables (Table 1). These variables were chosen based primarily on environmental factors that have been cited as botanically significant in determining plant distribution in the Gulf of St. Lawrence (Scoggan 1950; Rune 1954; Drury 1969; Damman 1965, 1976; Belland 1983, 1987*a*) and that were easily obtained or were available from published sources or maps. Several variables were included that are not explicitly mentioned as important in Gulf of St. Lawrence plant distributions, namely area of OGU, oceanity index, and maximum elevation of OGU. While there are many climatic variables that are easily obtained and could be included, earlier analyses showed that many were correlated, and this has also been observed in other studies (e.g., Myklestad and Birks 1993; Heikinnen et al. 1998). Moreover, for many of these variables, no data were

Table 1. Environmental variables used in the initial db-RDA analysis.

Variable	Abbreviation	Units/notes/references
Climatic variables		
Total annual rainfall	Rain	mm
Total annual snowfall	Snow	mm
Growing season warmth	GS	degree-days > 5 °C
Oceanic index	Oc	Kotilainen (1933)
Total precipitation	P_{tot}	mm
Physiographic variables		
Maximum elevation	Elev	metres above sea-level
Calcareous bedrock importance	Ca	1–5[a]
Area of OGU	Area	km^2

[a]Scoring of amount of calcareous bedrock is as follows: 1, calcareous bedrock is rare, present as occasional outcrops; 3, large areas of calcareous bedrock are present; 5, calcareous bedrock dominates the OGU.

available to show a biological relationship limiting species distribution.

Climatic data for each OGU was obtained from Environment Canada (1982*a*, 1982*b*). Mean values from two meteorological stations in each OGU were used for each climatic variable. No meteorological stations are available for the FSC OGU; therefore, climatic data for this unit are an average from the adjacent OGUs (FSE, FSW). Maximum elevation in each OGU was obtained by examining 1 : 250 000 topographic maps, and OGU areas were calculated using a large-scale map and a digitizer. Extent of calcareous bedrock in OGUs was scored based on geological information contained in Poole et al. (1970).

Multivariate analysis

Ordination

Distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999) was used to elucidate the relationship between environmental factors and species distribution. This is a new numerical tool that overcomes some of the limitations encountered with the popular and commonly used canonical correspondence analysis (CCA, ter Braak 1986), namely the influence of rare species and unequal samples sizes that are characteristic of floristic data sets such as the one used in this study. Distance-based RDA is considered the direct ordination counterpart of principal coordinates analysis (PCO) and uses sample scores resulting from a PCO as input data for a redundancy analysis (Lepš and Šmilauer 2003). In the present study, the PCO was run using the program PrCoord, included as part of the CANOCO software package (see below) with the distance matrix calculated using Hellinger's distance measure (Legendre and Gallagher 2001). The redundancy analysis was run using the CANOCO software package (Version 4.5, ter Braak and Šmilauer 2002). A minimal set of environmental variables that explains the species data almost as well as the full set was chosen using the forward selection option (Monte Carlo analysis) with program defaults (e.g., 499 unrestricted permutations). Only the minimal set of environmental variables was used in the final ordination, with scaling focussed on inter-sample distances. The original species–OGU data matrix was used as a supplemental data set to place species in the ordination space so their relationship to the OGUs could be visualized.

To determine the correlations of species with the db-RDA axis, Kendall's tau-B rank correlation coefficients were computed for each species between their OGU occurrence values and db-RDA axis scores.

Classification and indicator analysis

PC-ORD software (Version 4, McCune and Mefford 1999) was used for all classification and indicator analysis. Hierarchical clustering was employed to classify OGUs into groups based on similar species assemblages and also to classify species into groups based on their occurrence in OGUs. Both classifications used Jaccard's similarity index in conjunction with the flexible beta method (i.e., flexible clustering, McCune and Grace 2002) to produce OGU dendrograms. Clustering was run using the default value of $\beta = -0.25$ to avoid distortion (as recommended by McCune and Grace 2002). The group membership option was set to prune the dendrograms at 15 different classification levels during the clustering process for subsequent indicator analysis. Classifications were tested using multi-response permutation procedures (MRPP), a non-parametric procedure that tests the hypothesis of no significance between two or more a-priori groups. The test was run using the Jaccard distance measure in PC-ORD.

Indicator analysis (Dufrêne and Legendre 1997) was performed on each of the 15 classification levels for both species and OGU classifications to determine the optimal number of clusters to interpret and define indicator OGU or species that best characterize each cluster group. The optimal number of clusters interpreted in the OGU dendrograms was established by conducting a Monte Carlo test on the highest indicator values obtained for a species across groups during indicator analysis for each classification level. The ρ values for all species (OGU classification) or OGUs (species classification) were averaged for each classification level and the classification level with the lowest average ρ value was used for interpretation and further analysis (McCune and Grace 2002). For the OGU classification, species indicators for the resulting groups were narrowly defined to include only those species restricted to a single OGU group and whose ρ values were 0.05 or less as a result of 1000

Table 2. Summary of db-RDA of Gulf of St. Lawrence species distributions and environmental variables.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.158	0.097	0.050	0.036
Species–environment correlation	0.972	0.937	0.952	0.963
% variation explained for species data	15.8	25.5	30.5	34.1
% variation explained for species/environment relations	43.2	69.9	83.3	93.0

Note: Eigenvalues and percentage variance of species data accounted for by first four canonical axes are shown.

Table 3. db-RDA of Gulf of St. Lawrence species distributions and eight environmental variables.

	Interset correlation			Canonical coefficient		
Variable	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
GS	**–0.940****	–0.060	–0.059	(–0.301)	–0.043	0.091
Elev	0.357	–0.327	**–0.518****	(–0.080)	–0.006	(–0.136)
Ca	0.618**	**–0.652****	–0.074	0.040	(–0.209)	0.008
Oc	**0.367***	**0.784****	0.147	(0.130)	(–0.233)	0.324
P_{tot}	–0.024	0.716	**–0.488****	–0.095	–0.040	(–0.402)

Note: Canonical coefficients with t values greater than 2.1 in absolute value are given in parentheses. Boldface indicates variables having a combination of significant correlations and important coefficients (in parentheses) for an axis; these variables are considered to be the most important in defining the axis. *, statistical significance at $p < 0.05$; **, statistical significance at $p < 0.01$. Abbreviations for variables are found in Table 1.

Monte Carlo iterations on the highest indicator values for each species (McCune and Grace 2002).

The floristic classification of Belland (1987*a*) was used to compare the clusters resulting from the species classification. Four main floristic elements were used: boreal, temperate, arctic, and montane. These indicate latitudinal distribution of species as reflected by their occurrence in the major world vegetation biomes.

Results

Distance-based redundancy analysis

Species–environment correlations are high for the first four axes (Table 2), indicating that the variation extracted by the ordination was well explained by the environmental variables used in the analysis (ter Braak 1986; Lepš and Šmilauer 2003). The first two ordination axes describe the largest proportion of the variation, accounting for 25.5% of the total variation in the dataset. Addition of the third axis explained only an additional 5% of this variation (Table 2). While the proportion explained seems low, such values are typical of biological datasets (Gauch 1982) and reflect the inherent variability in this type of data.

Forward selection revealed five environmental variables that explained almost as much of the variation in the species data as all eight environment variables tested: warmth of growing season, maximum elevation, calcareous substrate, oceanity, and total precipitation. Based on a combination of significant interset correlations and significant canonical coefficients (Table 3), the first and most important axis was defined by warmth of the growing season, which shows both a very high negative correlation and a significant canonical coefficient value with this axis. Using similar criteria, the second axis was most highly correlated with amount of calcareous bedrock and oceanity index, with calcareous bedrock negatively correlated and oceanity positively correlated to axis scores. Although the latter variable also shows a significant correlation with the first axis, that correlation is considerably weaker than that with the second axis. Maximum elevation and total precipitation (P_{tot}) define the third axis with which they are both negatively correlated. There were no environmental variables used in this study that can be related to the fourth db-RDA axis.

The db-RDA ordination biplot of the first two axes shows three distinct groups of OGUs that are well separated in ordination space (Fig. 4) and reproduces the general geographical relationships of the OGUs in ordination space. The first axis separated the Maritimes (NS1, NS2, NS3, NS4, NS5, NSNB6, NB7, NB8, NB9, NSNB, PEI) and Magdalen Island (MDI) from OGUs located north of the St. Lawrence River and those of Gaspé Peninsula (GASN, GASS). The Maritimes and MDI clustered on the left side of the ordination where they were associated with the highest values of warmth of growing season. All other OGUs were positioned at the opposite (colder) end of axis 1. These "northern" OGUs were further separated into two groups along axis 2. The southern and easternmost OGUs of Newfoundland (FSE, FSC, FSW, FEB, FE) formed one group in the upper right quadrant of the ordination where they are associated with the highest values of oceanity index (indicated by the Oc vector on the ordination). The second group, in the lower right quadrant of the ordination, includes most of the remaining Newfoundland OGUs (FNEC, FWS, FNEW, FWNC, FWSC, FNW), the Québec North Shore (NOW), southern Labrador OGUs (NOE), and Gaspé Peninsula (GASN, GASS). These were all placed close to high values of exposed calcareous bedrock, indicated by the head of the Ca vector on the ordination. Northeastern Newfoundland

Fig. 4. db-RDA biplot ordination of axes 1 and 2 showing the vectors of significant environmental variables.

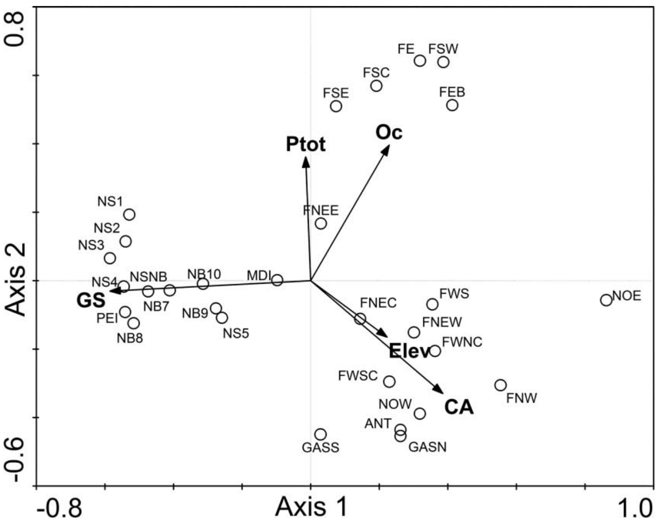
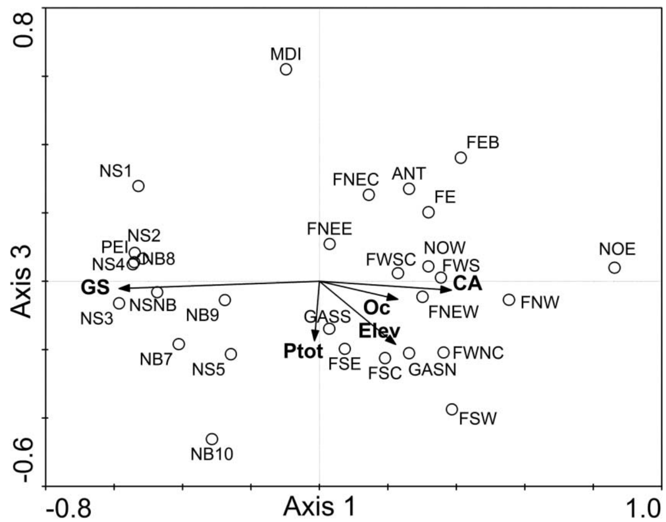


Fig. 5. db-RDA biplot ordination of axes 1 and 3 showing the vectors of significant environmental variables.



(FNEE) was isolated between the Maritime OGUs and the southern Newfoundland OGUs. It was characterized by more oceanic and cooler conditions than the Maritimes, but less so than the southern Newfoundland OGUs.

No distinct clusters could be defined along axis 3 (Fig. 5). However, numerous OGUs show weak association with the environmental variables defining the axis (Elev, P_{tot}). For instance, several OGUs from the Newfoundland west coast (FWNC, FSW) and from Gaspé (GASS, GASN) were positioned near the head of the maximum elevation vector (Elev). Also, the three OGUs of the Newfoundland South Coast (FSC, FSE, FSW) were positioned relatively close to the head of the maximum elevation vector (Elev) and also had high negative axis 3 scores, which has been shown previously to be correlated with total precipitation (Table 3). Two OGUs were outliers (MDI and NB1, Magdalen Islands and northern New Brunswick, respectively).

OGU hierarchical cluster and indicator species analysis

Hierarchical cluster analysis

Seven OGU groups resulted from hierarchical cluster analysis. The classification was supported by MRPP that shows the groups to be significantly different. The probability of obtaining a smaller or equal delta by chance was $p << 0.0001$. The chance corrected within-group agreement (A) was 0.1732, indicating that within groups heterogeneity was less than that expected by chance.

The OGU classification (Fig. 6) generally assigned geographically neighboring OGUs to the same group, indicating that OGUs included in these groups possess similar floras. The Southern Nova Scotia group formed a natural unit consisting of the three OGUs located in southernmost Nova Scotia (NS1, NS2, NS3). The Maritime group possessed the largest number of OGUs and consisted of the remaining OGUs in Nova Scotia (2 OGUs), all of New Brunswick (5 OGUs), and Prince Edward Island (1 OGU). The Gulf group was represented by seven OGUs bordering the Gulf of St. Lawrence and included Gaspé Peninsula (GASS, GASN), the Québec North Shore (NOW), southern Labrador (NOE), and three Newfoundland northwest coast OGUs (FWSC, FWNC, FNW). A smaller group (South Coast) consisted of the three contiguous OGUs of the Newfoundland south coast (FSW, FSE, FSC). The Newfoundland group included all the remaining OGUs from the northeastern (FNEE, FNEC, FNEW), eastern (FE, FEB), and southwestern parts of the Newfoundland (FWS). The latter is the only OGU that was not geographically contiguous with OGUs in the group to which it is assigned. Anticosti Island (ANT) and Magdalen Island (MDI) each formed “groups” composed of a single OGU.

When the OGU classification was overlain onto the db-RDA axis 1 – axis 2 ordination (Fig. 7), six of the groups occupied distinct, non-overlapping areas in ordination. The OGUs belonging to the Southern Nova Scotia group occurred in close proximity to one another and were slightly separated from the Maritime OGUs on the left side of the ordination. Both groups were associated with the highest values of warmth of growing season, which was revealed by their proximity to the head of the vector representing this climatic variable (GS).

The OGU groups located in the northern regions of the Gulf of St. Lawrence displayed a more complex pattern than those in the southern parts. They occurred exclusively on the right side of the ordination where they were associated with lower values of warmth of growing season. The OGUs of the Gulf group formed a natural cluster in the lower rightmost quadrant of the ordination. Anticosti Island was also positioned with this group, indicating a close relationship with it. Both groups were associated with high values of maximum elevations and amount of exposed calcareous bedrock. The Newfoundland South Coast group (FSW, FSC, FSE) was positioned in the upper right quadrant of the ordination where it was associated with high values of oceanity index.

Magdalen Island was isolated on the ordination and placed near the center of the biplot. Its central position reflects its geographical position in the study area, with warmth of growing season values that are intermediate between the Maritimes and more northern OGUs.

Fig. 6. Hierarchical tree showing the seven groups of OGUs resulting from hierarchical clustering analysis. 1, Southern Nova Scotia; 2, Maritimes; 3, Magdalen Island; 4, Anticosti Island; 5, Gulf; 6, Newfoundland; 7, South Coast.

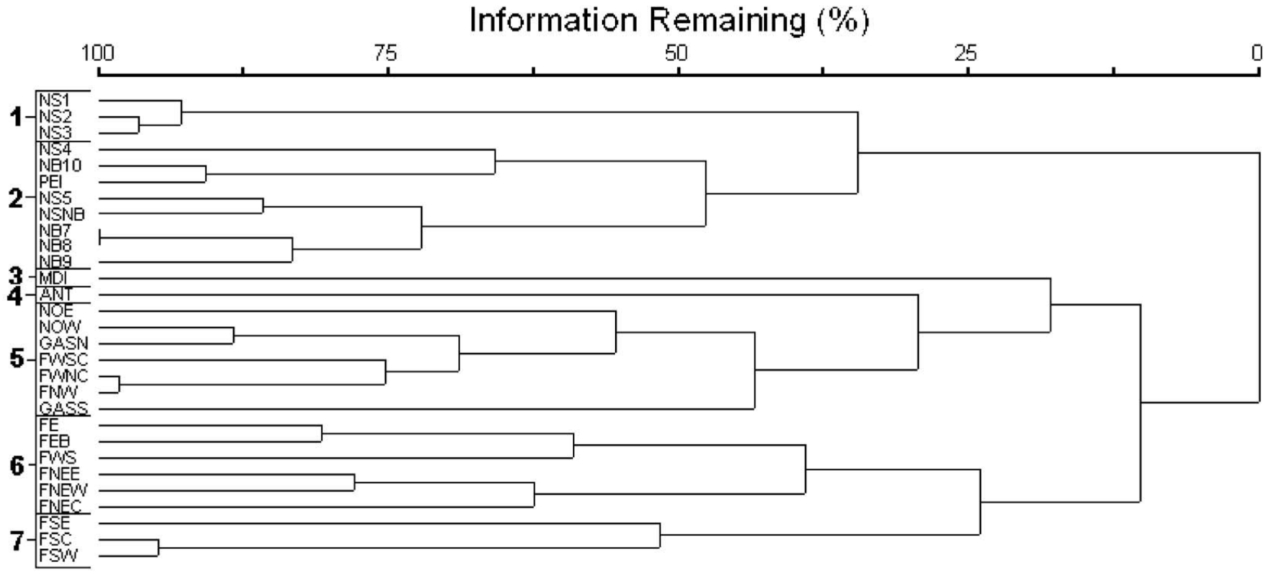


Fig. 7. db-RDA biplot ordination of the 29 Gulf of St. Lawrence OGUs. The ordination shows axes 1 and 2 with the OGU cluster overlain. ○, Southern Nova Scotia; ◇, Maritimes; ●, Magdalen Island; ■, Gulf; □, Newfoundland South Coast; ◆, Newfoundland; ▯, Anticosti Island.

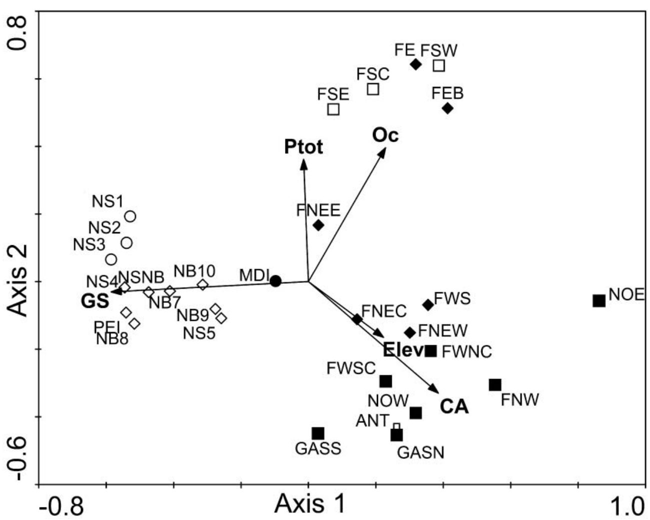
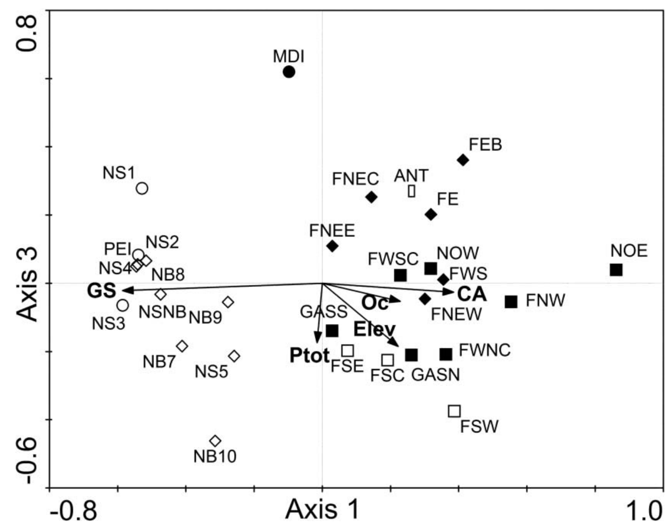


Fig. 8. db-RDA biplot ordination of 29 Gulf of St. Lawrence OGUs. The ordination shows axes 1 and 3 with the OGU cluster overlain. ○, Southern Nova Scotia; ◇, Maritimes; ●, Magdalen Island; ■, Gulf; □, Newfoundland South Coast; ◆, Newfoundland; ▯, Anticosti Island.



There was considerable overlap of OGU groups on the db-RDA biplot of axis 1 and axis 3 (Fig. 8). Although the Southern Nova Scotia and Maritime OGU groups were separated from the northern OGUs along axis 1, most groups showed intergradation along axis 3. For instance, the Southern Nova Scotia OGUs overlapped the OGUs of the Maritime group. Similarly, the OGUs of the Newfoundland group were intermixed with Gulf OGUs, and Anticosti Island was found among OGUs of the Newfoundland group.

Most of the OGU groups defined by the hierarchical classification, and based on species occurrence only, occupied non-overlapping areas on the axis 1 – axis 2 ordination (Fig. 7). The single exception was the Newfoundland group whose OGUs were divided between two quadrants on the right side of the ordination. OGUs from eastern Newfoundland (FE, FEB) were placed in the upper right quadrant of the ordination where they were associated with high values of oceanity index. The other three OGUs of this group (FNEC, FWS, FNEW) were positioned in the lower right quadrant adjacent to OGUs of the Gulf group. The latter are characterized by moderate elevations and moderate amounts of calcareous rock outcropping. Newfoundland northeast coast (FNEE), which also belongs to the Newfoundland group, was isolated between the South Coast and the Maritime groups (mentioned previously).

The environmental characteristics that differentiate the seven OGU groups can be discerned by examining the means and 95% confidence intervals of the five most impor-

Fig. 9. Mean and 95% confidence interval for warmth of growing season (as expressed by degree-days above 5 °C) for seven OGU groups in the Gulf of St. Lawrence region. ANT, Anticosti Island; Gulf, Gulf group; Maritime, Maritimes group; MDI, Magdalen Island group; Nfld, Newfoundland group; SCoast, Newfoundland South Coast; SNova, Southern Nova Scotia.

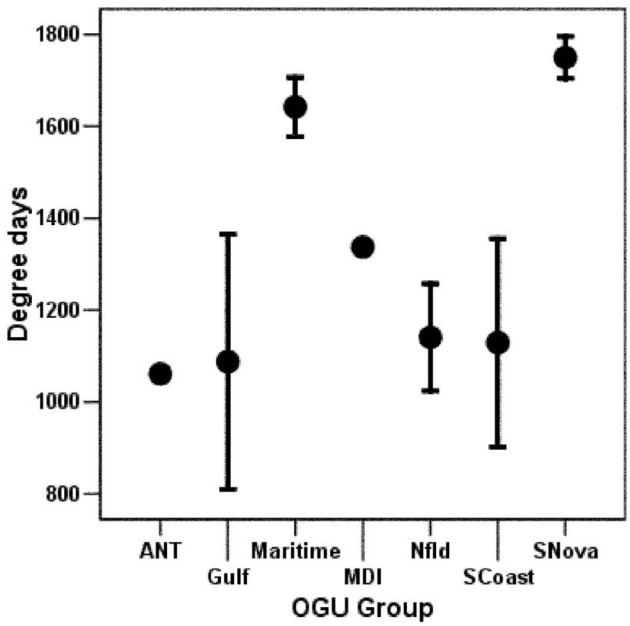


Fig. 10. Mean and 95% confidence intervals for oceanity index for seven OGU groups in the Gulf of St. Lawrence region. ANT, Anticosti Island; Gulf, Gulf group; Maritime, Maritimes group; MDI, Magdalen Island group; Nfld, Newfoundland group; SCoast, Newfoundland South Coast; SNova, Southern Nova Scotia.

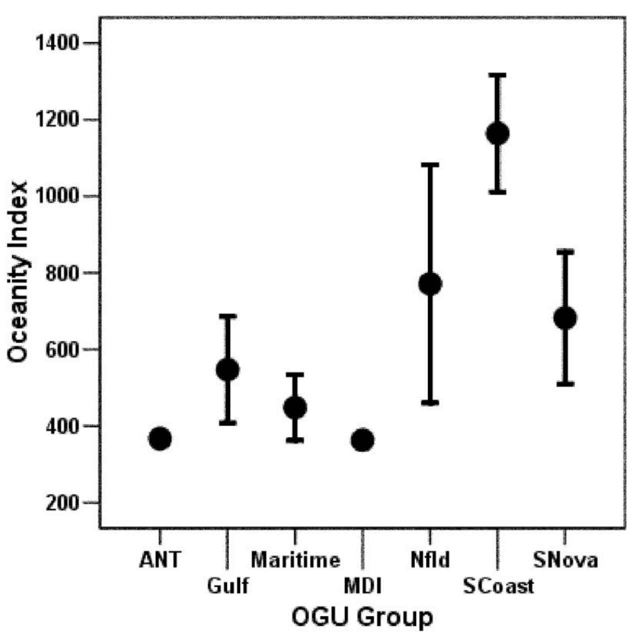


Fig. 11. Mean and 95% confidence intervals for amount of calcareous outcrop for seven OGU groups in the Gulf of St. Lawrence region. ANT, Anticosti Island; Gulf, Gulf group; Maritime, Maritimes group; MDI, Magdalen Island group; Nfld, Newfoundland group; SCoast, Newfoundland South Coast; SNova, Southern Nova Scotia.

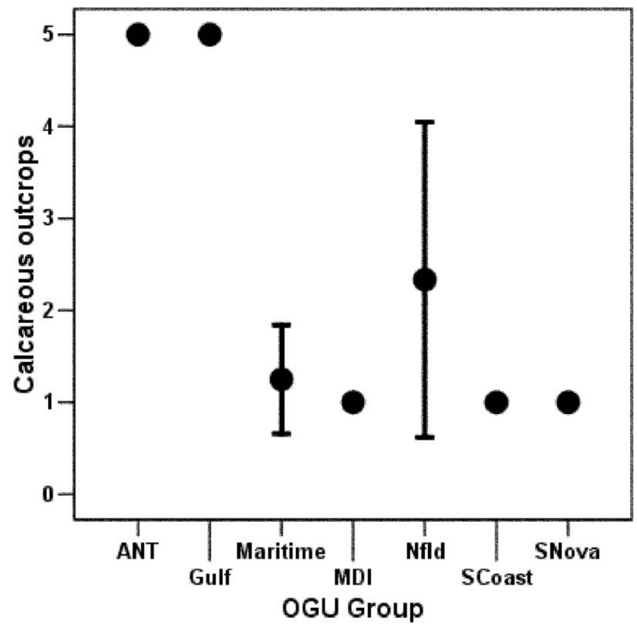
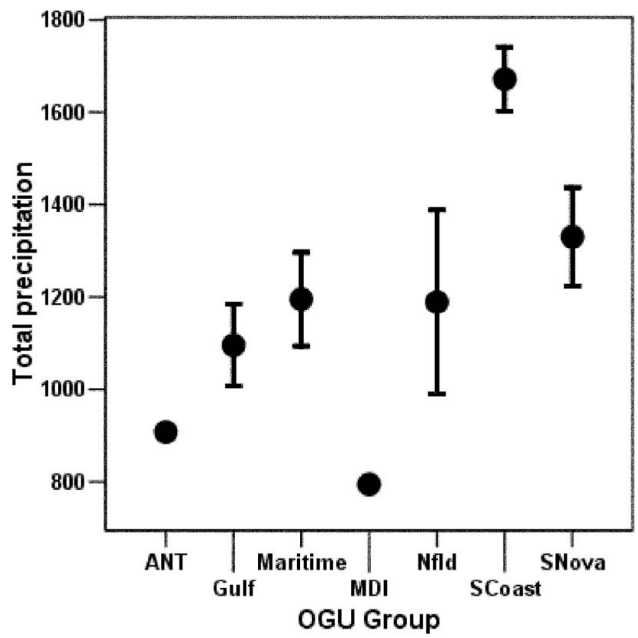


Fig. 12. Mean and 95% confidence intervals for total precipitation for seven OGU groups in the Gulf of St. Lawrence region. ANT, Anticosti Island; Gulf, Gulf group; Maritime, Maritimes group; MDI, Magdalen Island group; Nfld, Newfoundland group; SCoast, Newfoundland South Coast; SNova, Southern Nova Scotia.



tant environmental variables identified by the db-RDA ordination (Figs. 9–13). High mean values for warmth of growing season (Fig. 9) differentiated the Southern Nova Scotia and Maritimes groups from all other OGU groups. Both had small 95% confidence intervals for this variable and values that generally exceeded 1600. The Restricted Nova group had a slightly higher mean value than the Maritime group, although it did not differ significantly from the latter group.

Table 4. Floristic characteristics of mosses belonging to seven Gulf of St. Lawrence OGU groups.

	OGU Group						
Affinity	Gulf (239)	Southern Nova Scotia (119)	Maritimes (196)	Newfoundland (144)	South Coast (46)	Anticosti Island (32)	Magdalen Island (23)
Boreal	43.1	33.6	46.4	52.8	52.2	65.6	52.2
Temperate	20.9	62.2	39.3	25.7	21.7	15.6	39.1
Montane	15.9	0.0	5.1	8.3	15.2	0.0	0.0
Arctic-Alpine	17.6	0.8	5.6	8.3	4.3	18.8	4.3
Cosmopolitan	1.7	2.5	2.0	2.8	4.3	0.0	4.3
Unclassified or unknown	0.8	0.8	1.5	2.1	2.2	0.0	0.0
% of total in OGU	54.4	38.6	48.3	40.0	22.2	35.9	18.5

Note: Numbers are percentages of total species (in parentheses) of the OGU group.

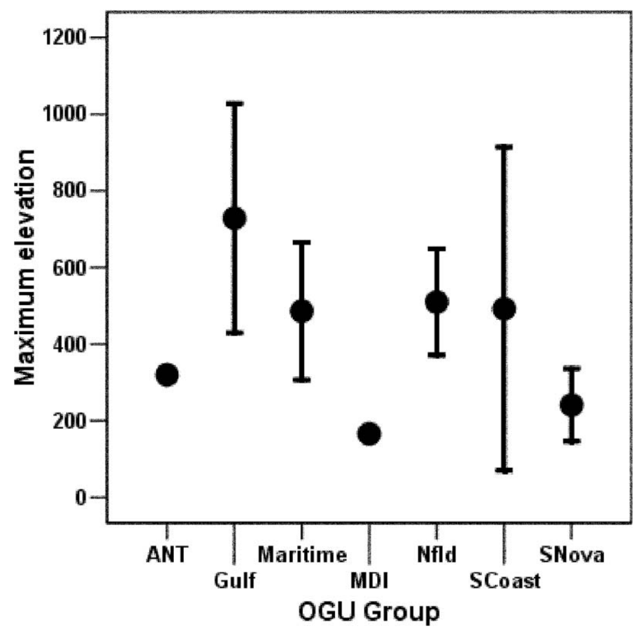
None of the OGU groups differed significantly from the other groups in oceanity index (Fig. 10). Although the Newfoundland South Coast group had the highest mean value of oceanity index, its confidence interval overlapped with that of the Newfoundland group. Banfield (1981) states that the Newfoundland South Coast and Avalon Peninsula (FE) show the greatest maritime influence of all regions of the island. Only the Southern Nova Scotia OGU group had oceanity index values comparable to those of the Newfoundland group, but the confidence intervals were smaller.

Amount of calcareous rock outcropping differentiated Anticosti Island and the Gulf group from all other groups (Fig. 11). Both had high mean values (i.e., 5) for this variable. Anticosti Island is composed entirely of calcareous bedrock, while the amount of calcareous bedrock varies for OGUs of the Gulf group. Nevertheless, large expanses of calcareous rock are exposed along the coasts of the Gaspé Peninsula, western Newfoundland (i.e., the coastal plain), along the Strait of Belle in coastal southern Labrador, and on the Québec North Shore, but especially in the Mingan Archipelago and adjacent shoreline. The Newfoundland group also has relatively high values of calcareous rock outcropping, but the amount is highly variable, as indicated by the wide confidence interval. Some OGUs of this group, in particular, southwest Newfoundland (FSW) have large areas of calcareous bedrock. However, most other OGUs of this group (e.g., the northeast coast (FNEE, FNEC, FNEW)) have very small, scattered calcareous outcrops.

High total precipitation characterized the Newfoundland South Coast. This OGU group surpassed the mean total precipitation of the next highest OGU group (Southern Nova Scotia) by more than 300 mm (Fig. 12). This OGU group also had the highest oceanity index. Anticosti Island and Magdalen Islands were the driest OGU groups in the region, with precipitation totals ranging from about 800 to 900 mm. All other OGU groups did not differ significantly in their total precipitation (Gulf, Maritime, Newfoundland, Southern Nova Scotia) and had intermediate totals between those of Anticosti Island and the Newfoundland South Coast.

Maximum elevation did not vary significantly among the OGU groups (Fig. 13). Considerable variation was observed within groups as reflected in the size of the confidence intervals. The Newfoundland South Coast had particularly wide variation, as did the Gulf OGU group. The latter has the highest mean maximum elevation, by virtue of possessing almost all of the Gulf of St. Lawrence areas with mountainous terrain. This included the Shickshock Mountains in Gaspé Peninsula and the Long Range Mountains that dominate the west coast of Newfoundland.

Fig. 13. Mean and 95% confidence intervals for maximum elevation for seven OGU groups in the Gulf of St. Lawrence region. ANT, Anticosti Island; Gulf, Gulf group; Maritime, Maritimes group; MDI, Magdalen Island group; Nfld, Newfoundland group; SCoast, Newfoundland South Coast; SNova, Southern Nova Scotia.



Floristic characteristics varied considerably between groups (Table 4). When considering only those species analyzed in this study, richness of OGU groups varied by a factor of 10, from 23 species in the Magdalen Islands to 239 in the Gulf group. Other species-poor OGU groups included Anticosti Island (32 species) and the Newfoundland South Coast (46 species). All other OGU groups had greater than 100 species, with the second richest group being the Maritimes (196 species), although this group had considerably fewer species than the richest group (Gulf group).

Boreal elements dominated the moss floras of most OGU groups (Table 4), comprising greater than 40% of the component floras. The highest proportion was in Anticosti Island (65%) and the lowest in Southern Nova Scotia (34%). Only

Table 5. Summary of OGU group indicator species analysis.

	Indicator value	Frequency	Floristic affinity	*p*
Southern Nova Scotia group				
Astomum muehlenbergianum	67	67	Temperate disjunct	0.018
Fontinalis sullivantii	67	67	Temperate endemic	0.02
Isopterygium tenerum	67	67	Temperate disjunct	0.02
Tortula papillosa	67	67	Temperate disjunct	0.018
Maritimes group				
Splachnum rubrum	50	50	Circumboreal	0.007
Gulf group				
Amblyodon dealbatus	86	86	Arctic–alpine	0.001
Aulacomnium turgidum	71	71	Arctic–alpine	0.005
Calliergon sarmentosum	71	71	Arctic–alpine	0.007
Calliergon trifarium	71	71	Arctic–alpine	0.008
Dicranum acutifolium	57	57	Arctic–alpine	0.004
Encalypta longicolla	57	57	Montane disjunct	0.007
Hypnum revolutum	57	57	Circumboreal	0.006
Kiaeria glacialis	57	57	Arctic–alpine	0.007
Lescuraea saxicola	57	57	Circummontane	0.006
Stegonia latifolia	57	57	Arctic–alpine	0.007
Tortula norvegica	57	57	Arctic–alpine	0.007
Newfoundland group				
Antitrichia curtipendula	33	33	Boreal disjunct	0.046
Grimmia torquata	67	67	Boreal disjunct	0.007
Pseudoscleropodium purum	33	33	Temperate disjunct	0.046
Sphagnum molle	67	67	Temperate disjunct	0.002

the Southern Nova Scotia group had an important component of temperate species (62%), although the Maritimes and Magdalen Islands also possessed significant percentages (approx. 40%). Arctic–alpine species were important only in northern OGU groups, but particularly the Gulf group and Anticosti Island, each with more than 17% of their floras belonging to the arctic–alpine element. Montane species were most important in the Gulf group where almost 16% of mosses were of this element. Surprisingly, the Newfoundland South Coast also possessed a high proportion of montane mosses. However, while these comprise 15% of the total flora, they include only seven species; the Maritime group, which possessed only 5% montane species, had a slightly greater number (eight species). Not unexpectedly, arctic–alpine and montane species comprise the smallest percentage of the Southern Nova Scotia group. Cosmopolitan species generally comprise only a small proportion of the OGU group floras.

Indicator species analysis

Indicator species were identified in four of the seven OGU groups and three groups had no indicators (Anticosti Island, Magdalen Islands, and South Coast) (Table 5). In none of the OGU groups did individual indicator species occur across all OGUs.

The Gulf group had the largest number of species indicators (11 species, Table 5). Arctic-alpine and montane species characterized these, and most were found in at least four of the seven Gulf OGUs (57%). *Amblyodon dealbatus* was the most widely distributed, known from six OGUs. One circumboreal species (*Hypnum revolutum*) was also identified, which occurred in four OGUs.

The Southern Nova Scotia and Newfoundland groups each possess four indicators (Table 5). Southern Nova Scotia group indicators were exclusively temperate mosses and all occurred in two of the three OGUs comprising the group. Temperate and boreal mosses were equally represented as indicators of the Newfoundland group. The width of their distributions varied somewhat, with two species (*Grimmia torquata*, *Sphagnum molle*) known from four of six OGUs in the group. The other two mosses have more restricted distributions occurring in only two OGUs (*Antitrichia curtipendula*, *Pseudoscleropodium purum*). *Pseudoscleropodium purum* is believed to be a species introduced to Newfoundland (Brassard 1983*c*), thus its restricted distribution to anthropogenic habitats explains its narrow distribution.

Only one indicator characterized the Maritimes group. *Splachnum rubrum* is a boreal species known from four locations (in four OGUs) scattered through the Maritimes.

Species hierarchical cluster analysis

Ten species clusters, or distributional elements, resulted from the hierarchical clustering of the 322 species used in this study. MRPP showed these elements to be significantly different. The probability of obtaining a smaller or equal delta by chance was $p \ll 0.0001$. The chance corrected within-group agreement (*A*) was 0. 2212, indicating that within group heterogeneity was less than expected by chance. The complete dendrogram and species lists are available from the author.

The distributional elements varied in size from 19 (group 5) to 51 species (group 9). Overall, the elements show distinct patterns based on the geographical patterns of richness

Table 6. Numbers of species in 10 Gulf of St. Lawrence species elements that are correlated to db-RDA ordination axes 1 and 2.

	Axis 1		Axis 2	
Element	No. of species with positive correlations	No. of species with negative correlations	No. of species with positive correlations	No. of species with negative correlations
Southern bias				
1	—	26	4	—
2	—	6	—	7
3	—	10	—	—
4	—	10	2	—
5	—	2	—	1
Northern bias				
6	24	—	—	23
Gulf bias				
7	7	—	—	10
8	8	—	—	2
9	16	—	—	12
Eastern bias				
10	7	—	8	—

and OGU indicator values (Figs. 14–23). The elements were divided into four groups of elements or “biases” (Table 6) based on the location of the highest OGU indicator values for the element.

Southern bias distributions

Southern bias elements were found primarily south of Cabot Strait and included elements 1, 2, 3, 4, and 5 (Figs. 14–18). These represent a series of increasingly larger species ranges from an area more or less restricted to the southernmost Gulf regions (elements 3, 4, and 5) to ranging widely across the Maritimes with northern range extensions to Gaspé Peninsula or southern parts of Newfoundland (elements 1, 2). Species with southern bias elements had mainly only negative correlations with axis 1 (Table 6), suggesting that most have distributions influenced mainly by warmth of growing season. Two of the elements, however, had lower percentages of species negatively correlated with axis 1, which implies that other factors were involved in their species distributions (elements 2, 5). Both also contained species that were negatively correlated with axis 2, indicating a correlation with calcareous bedrock, e.g., *Bryum uliginosum*, *Cirriphyllum piliferum*, *Cyrtomnium hymenophylloides*, *Hypnum pratense*, *Plagiomnium drummondii*, *Seligeria calcarea*, and *Tomenthypnum falcifolium*.

Element 1

Species in this element are distributed widely through the Maritimes, with many species extending their range into Newfoundland, Gaspé, the Quebec North Shore, or southern Labrador (e.g., *Buxbaumia aphylla, Isothecium stoloniferum*, *Platylomella lescurii*, *Pylaisiella selwynii*). OGU indicator values were high throughout most Maritime OGUs (except western New Brunswick), but dropped abruptly in Gaspé and Newfoundland where they were generally below 17 (Fig. 14). Richness was generally high in most Maritime OGUs (>27 species) but decreased to fewer than 15 species in the majority of OGUs located in the northern parts of the study area. Although one OGU in northeastern Newfoundland had a high indicator value, this OGU had a relatively low species richness in this element (19). Most species were widely dispersed and present in more than 10 OGUs (38 of 43 species). Species in this element were characterized by a diversity of ecologies, although all are lowland. Included are epiphytes (*Leucodon brachypus*, *Orthotrichum ohioense*), upland forest (*Aulacomnium androgynum*, *Fissidens cristatus*, *Rhytididadelphus loreus*), and peatland mosses (*Dicranum leioneuron*, *Sphagnum cuspidatum*, *Sphagnum flavicomans*, *Sphagnum torreyanum*). Temperate and boreal (92%) mosses dominated this element (Table 7).

Element 2

This element comprised a large group of mosses (43) whose distributions does not display a distinct geographical pattern. The element had high richness in northern Gaspé, western North Shore, northwestern New Brunswick, southern New Brunswick, Cape Breton, and southwestern Newfoundland (Fig. 15). Species in this element were generally absent from central and eastern Newfoundland, and southern Labrador. While high richness was evident in several OGUs, high indicator values were present only in Cape Breton Island and northwestern New Brunswick. Most species (23) were present in five to nine OGUs, but eight species were more widely distributed (=10 OGUs); three species were rare and occurred in only one OGU (*Bryum blindii*, *Grimmia laevigata, Grimmia pilifera*). All species occupied lowland habitats where they were found on cliffs (*Cyrtomnium hymenophylloides*, *Grimmia pilifera*, *Seligeria diversifolia*), in forest (*Brachythecium campestre*, *Cirriphyllum piliferum*), peatlands (*Sphagnum tenellum*, *Tomenthypnum falcifolium*), or were epiphytic (*Anomodon viticulosis*, *Platydictya confervoides*). The majority (91%) was boreal or temperate (Table 7). Montane and arctic/alpine affinities were each represented by only one species (*Cyrtomnium hymenophylloides* and *Hygrohypnum montanum*, respectively).

Fig. 14. Richness and indicator (in parentheses) values for species element 1 in 29 Gulf of the St. Lawrence OGUs.

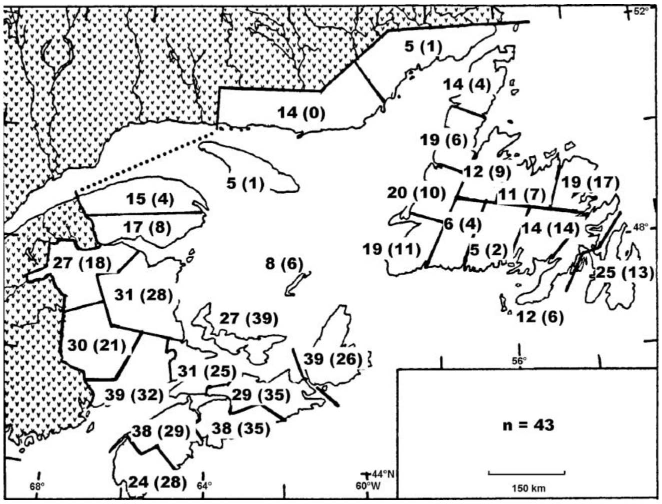


Fig. 15. Richness and indicator (in parentheses) values for species element 2 in 29 Gulf of the St. Lawrence OGUs.

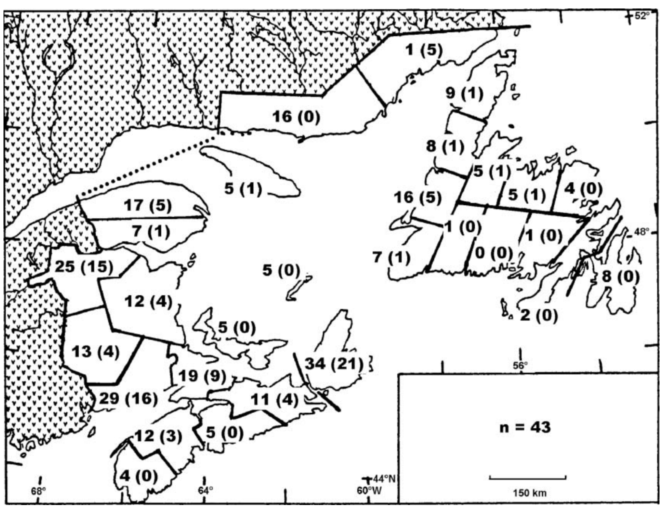


Fig. 16. Richness and indicator (in parentheses) values for species element 3 in 29 Gulf of the St. Lawrence OGUs.

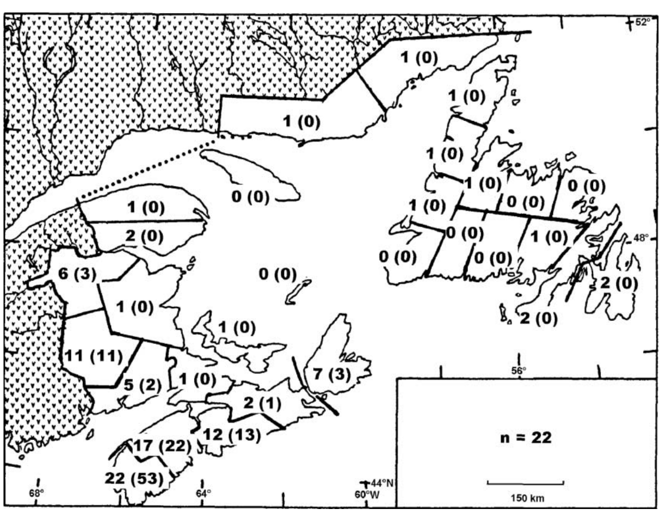


Fig. 17. Richness and indicator (in parentheses) values for species element 4 in 29 Gulf of the St. Lawrence OGUs.

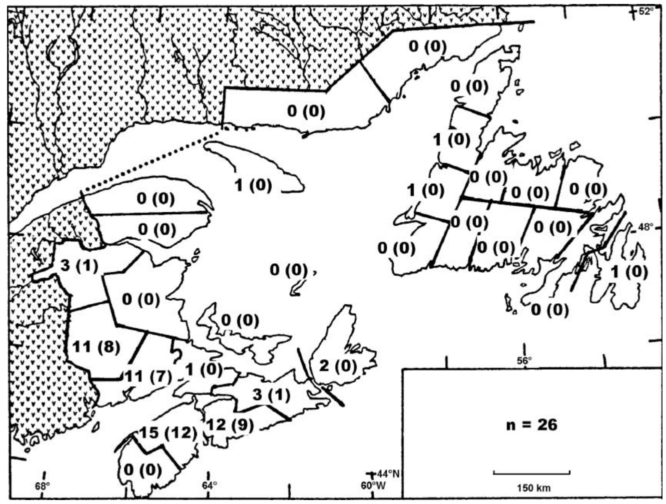


Fig. 18. Richness and indicator (in parentheses) values for species element 5 in 29 Gulf of the St. Lawrence OGUs.

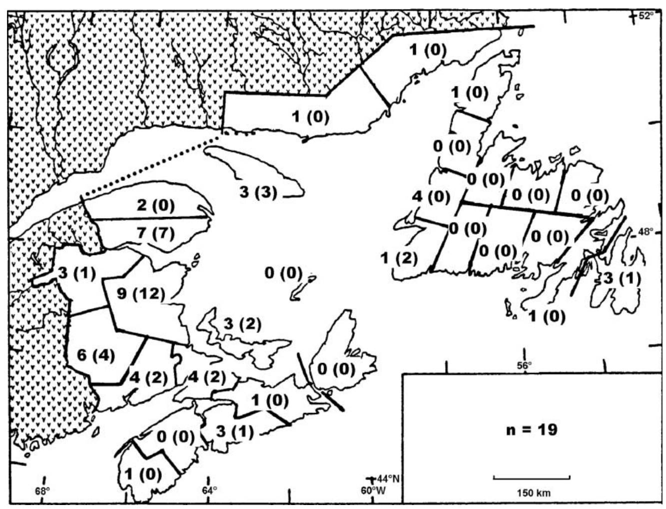


Fig. 19. Richness and indicator (in parentheses) values for species element 6 in 29 Gulf of the St. Lawrence OGUs.

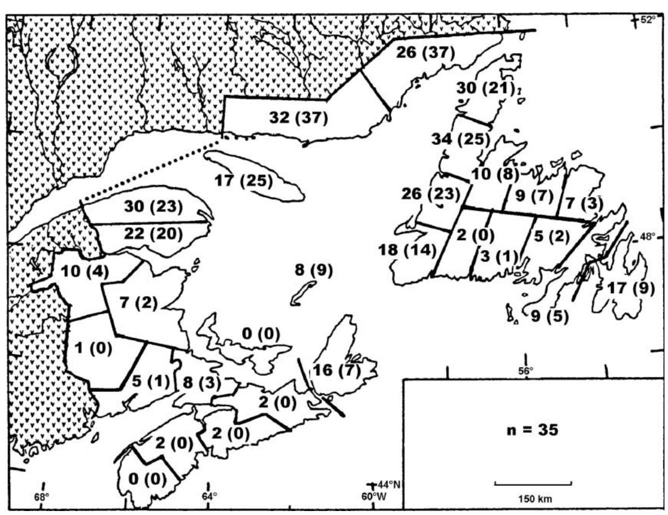


Fig. 20. Richness and indicator (in parentheses) values for species element 7 in 29 Gulf of the St. Lawrence OGUs.

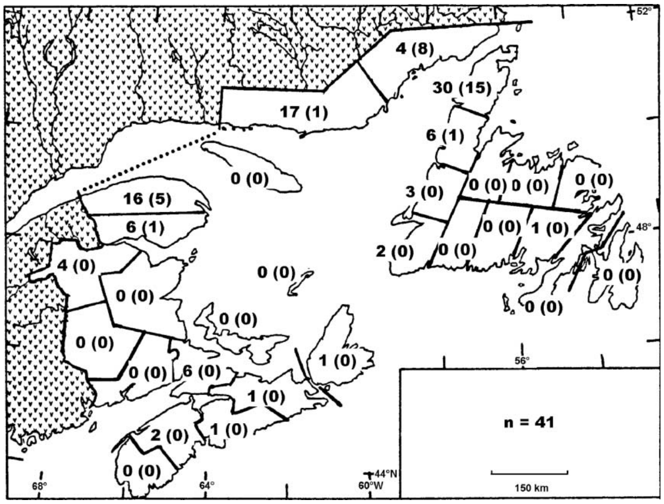


Fig. 21. Richness and indicator (in parentheses) values for species element 8 in 29 Gulf of the St. Lawrence OGUs.

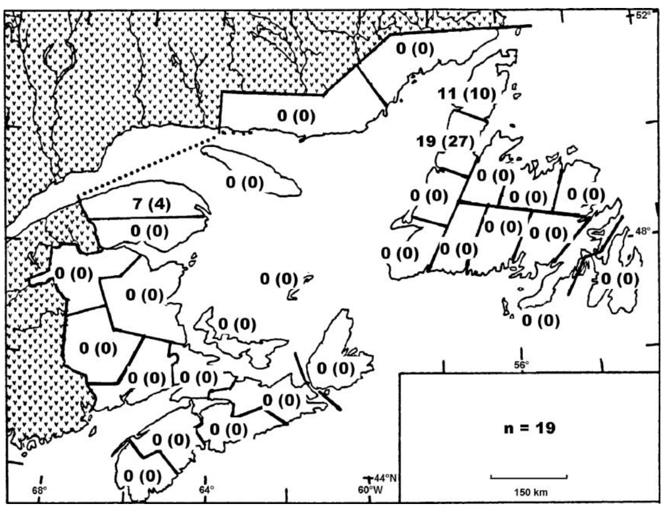


Fig. 22. Richness and indicator (in parentheses) values for species element 9 in 29 Gulf of the St. Lawrence OGUs.

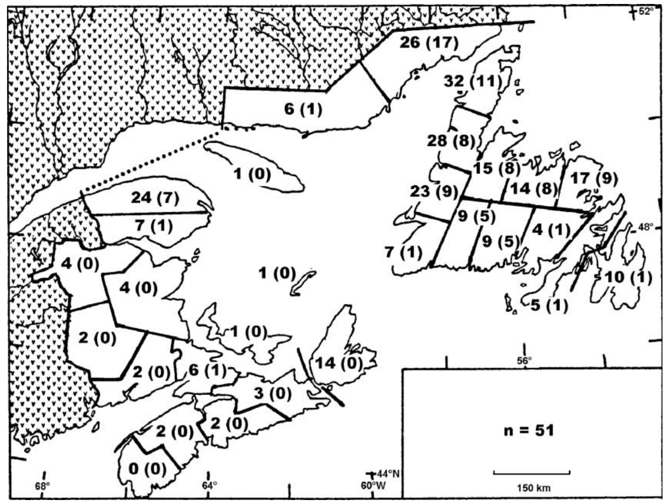
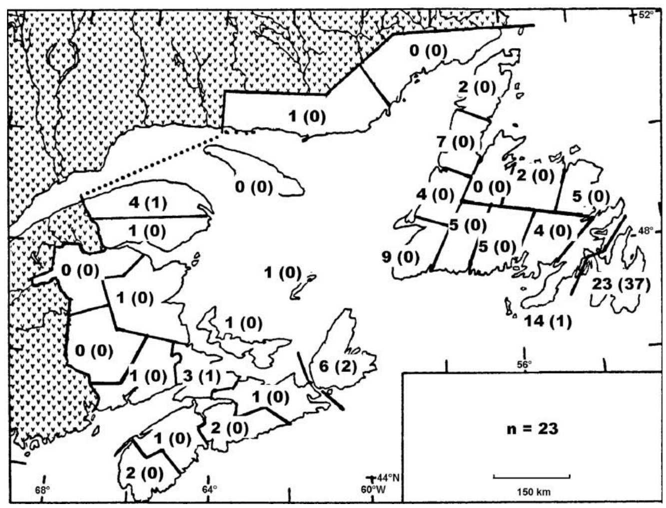


Fig. 23. Richness and indicator (in parentheses) values for species element 10 in 29 Gulf of the St. Lawrence OGUs.



Element 3

This element comprised 22 species that are centered in southern Nova Scotia, with species extending north into northwestern New Brunswick or Newfoundland. The element had its highest indicator values in southern Nova Scotia with moderate values in parts of southern New Brunswick (Fig. 16). Richness was highest in southernmost Nova Scotia (NS1) where all species in the element occurred, but decreased rapidly northward, with outliers occurring in Newfoundland (*Fontinalis flaccida*, *Sphagnum macrophyllum*, *Splachnum pennsylvanicum*). Several species had a small disjunction from south-central Nova Scotia (NS3) to Cape Breton Island (*Anomodon rugelii*, *Bryum radiculosum*, *Campylium radicale*, *Dichelyma capillaceum*, *Dicranum fulvum*, *Drummondia prorepens*, *Haplohymenium triste*). Species in this element varied widely in width of distribution, occurring in two to nine OGUs. The large majority of species (14) occurred in three to seven OGUs, but six species were found in one to two OGUs. Element 3 mosses were mainly lowland species that grow in deciduous or mixedwood forests (*Anomodon rugelii*, *Drummondia prorepens*, *Haplohymenium triste*, *Thelia hirtella*, *Zygodon conoideus*), on exposed rock outcrops (*Grimmia olnyei*), or associated with streams (*Fontinalis flaccida*, *F. sullivantii*). This element was strongly dominated by temperate mosses that include 91% of the species (Table 7).

Element 4

This element comprised a group of 26 mosses whose overall distributional pattern was similar to that of element 3. Mosses that are by and large restricted to the southernmost Maritimes characterized the element. Element 3 differed from element 3 by having fewer species reaching Cape Breton Island (NS5) or areas north of Cabot Strait. Northern outliers that occurred in Newfoundland included *Dichelyma falcata* and *Phycomitrium pyriforme*; *Ditrichum pallidum* was found on Anticosti Island. The highest indicator values and richness were found in southern Nova Scotia and New Brunswick (Fig. 17). Most species were narrowly distributed. Fifteen of the 26 species were restricted to one or two OGUs, and 24 occurred in fewer than five OGUs; only two

Table 7. Floristic affinities of mosses belonging to 10 Gulf of St. Lawrence distributional elements.

Element	Affinity Temperate	Boreal	Montane	Arctic
Southern bias				
1	48.8	44.2	0.0	0.0
2	41.9	48.8	2.3	2.3
3	90.9	4.5	0.0	0.0
4	96.2	3.8	0.0	0.0
5	47.4	42.1	10.5	0.0
Northern bias				
6	0.0	74.3	0.0	25.7
Gulf bias				
7	9.8	31.7	19.5	39.0
8	5.3	10.5	52.6	31.6
9	7.8	39.2	31.4	17.6
Eastern bias				
10	43.5	34.8	8.7	4.3

Note: Values are percentages of total species.

species (*Ditrichum pallidum*, *Physcomitrium pyriforme*) were more widely dispersed (5–6 OGUs). Most of the mosses belonging to this element are lowland species growing in habitats associated with deciduous forest (e.g., *Anomodon minor*, *Brachythecium digastrum*, *Bryohaplocladium virginianum*, *Entodon brevisetis*, *Eurynchium hians*, *Sematophyllum demissum*). Species in this element were almost exclusively of temperate affinity with 96% of the mosses belonging to this affinity (Table 7).

Element 5

This was the smallest element recognized, consisting of only 19 species. Mosses in this element occur mainly in the west-central part of the Gulf including central and southern New Brunswick, and southern Gaspé. Outliers were also found in eastern Newfoundland and western Newfoundland (*Cynodontium strumulosum*, *Gyroweisia tenuis*, *Oedipodium griffithianum*, *Pohlia lescuriana*). The highest indicator values were in NB10 and GASS with somewhat lower indicator values on Anticosti Island, southwestern Newfoundland, and southern New Brunswick (Fig. 18). Richness was highest in northeast New Brunswick (NB10), with lower richness in southern New Brunswick (NB7) and southern Gaspé (GASS). The majority of species in this group were rare (1–2 OGUs), although six species were somewhat more broadly distributed (4–10 OGUs). The most widely distributed species were *Pohlia lescuriana* and *Sphagnum riparium*, known from 9 to 10 OGUs, respectively. Species in this element included both forest and open habitat species that were restricted to mainly lowland or mid-elevations. Forest species included *Dicranum muehlenbeckii*, *Rauellia scita*, and *Platydictya minutissimum*. Cliff mosses were particularly well represented: *Campylostelium saxicolum*, *Cynodontium strumulosum*, *Grimmia anodon*, *Grimmia teretinervis*, *Gyroweisia tenuis*, *Oedipodium griffithianum*, *Seligeria brevifolia*. Temperate (48%) and boreal mosses (42%) dominated this element (Table 7). Two species (10%) represented the montane affinity (*Cynodontium strumulosum*, *Oedipodium griffithianum*). Both species are known only from Newfoundland.

Northern bias distributions

The northern bias included only one Gulf of St. Lawrence distributional element (element 6, Fig. 19). The northern bias element had a high percentage of species positively correlated with db-RDA axis 1 and many species negatively correlated to axis 2 (Table 6). The distributions of northern bias species were therefore presumed related to cool growing season temperatures and associated with the presence of calcareous bedrock.

Element 6

This element comprised 35 species whose distribution centers on the OGUs bordering the Gulf of St Lawrence, particularly the OGUs of western Newfoundland, Gaspé Peninsula, Québec North Shore, and southern Labrador (Fig. 19). These OGUs had the highest richness (>25 species) but moderately high richness was found also in Cape Breton Island (NS5), Anticosti Island (ANT), and Eastern Newfoundland (FE). The indicator values follow a pattern similar to that of the richness and the highest indicator values in Gaspé, Anticosti, North Shore, southern Labrador, and western Newfoundland. Although eastern Newfoundland had a moderate richness, this OGU had a low indicator value. Most species are widely distributed and occurred in more than 6 OGUs; more than half (19 species) were found in more than 10 OGUs. Only one species was “rare”: *Tortula muralis* was found in one OGU (FE), where it was presumed to have been introduced (Brassard and Weber 1977). Species included in this element grow mainly on limestone cliffs or in rich fens (e.g., *Cinclidium stygium*, *Desmatodon heimii*, *Brachythecium turgidum*, *Campylium halleri*, *Hypnum bambergeri*, *Meesia triquetra*, *Mnium thomsoniii*, *Scorpidium turgescens*, *Seligeria donniana*, *Seligeria tristichoides*). Several species not usually associated with calcareous bedrock were also included in this element (e.g., *Bartramia ithyphylla*, *Dicranoweisia crispula*, *Dicranum elongatum*, *Oncophorus virens*). Element 6 mosses are species of northern affinity, with the majority of boreal affinity (75%) and the remainder of arctic–alpine affinity (Table 7).

Gulf bias distributions

Elements with a Gulf bias included species that mainly occurred in OGUs adjacent to the Gulf of St. Lawrence and included elements 7, 8, and 9 (Figs. 20–22). All can be considered as subsets of the northern bias. As with southern bias groups, the groups included here can be viewed as a series of increasing larger ranges within the study area. Mosses in element 8 had the most restricted distributions where they occur on the Newfoundland Northern Peninsula and Gaspé. Species in element 7 displayed the widest distribution, occurring primarily in western Newfoundland, Gaspé Peninsula, North Shore, and southern Labrador with outliers in Nova Scotia and New Brunswick. As with the northern bias distributions, all three elements had species positively correlated to axis 1, as well as species negatively correlated to axis 2 (Table 6). However, the percentage of species correlated was somewhat lower and varies among groups. For all three elements, 17%–42% of the species within each group was positively correlated with axis 1. The proportion of species significantly correlated to axis 2 varied less widely, from only 10% represented in element 8 to 24% in elements 7 and 9. The species correlations to these axes indicate that the species distributions were related to both cool growing season temperatures and also to the presence of calcareous bedrock. However, the overall low proportions of mosses that were significantly correlated to the axes strongly suggest that other environmental factors are likely related to the distributions.

Element 7

Element 7 is a large group of 41 mosses with a center of distribution in northernmost Newfoundland, Québec North Shore, and northern Gaspé Peninsula (Fig. 20). The highest indicator values were in northernmost Newfoundland (FNW), with high values also obtained for the western North Shore (NOW) and northern Gaspé (GASN). Northernmost Newfoundland (FNW) also possessed the highest richness, with almost twice as many species as either northern Gaspé or western North Shore. Of the 41 mosses in this element, most (50%) were rare and known from only one OGU (e.g., *Brachythecium glaciale*, *Bryum wrightii*, *Hydrogrimmia mollis*, *Mielichhoferia macrocarpa*, *Tortella arctica*). This element was dominated by species typically associated with calcareous substrate (e.g., *Aloina rigida*, *Bryum wrightii*, *Calliergon trifarium*, *Funaria microstoma*, *Hypnum vaucheri*, *Tortella arctica*, *Stegonia latifolia*) although species that avoid calcareous habitats were also represented (e.g., *Dicranum angustum*, *Drepanocladus badius*, *Hydrogrimmia mollis*, *Hygrohypnum alpestre*). The majority of species (60%) are either arctic–alpine or montane; however, many (32%) belong to the boreal floristic affinity (Table 7).

Element 8

This element had the most restricted distributional pattern of all Gulf bias groups. It consisted of a small group of 19 species restricted to three OGUs in northwestern Newfoundland (FNW, FWNC) and northern Gaspé (GASN); all three OGUs had high indicator values (Fig. 21). One species occurred as an outlier in southern Newfoundland (*Campylopus schimperi*). The highest richness and indicator values were found in northwestern Newfoundland, but especially in the FWNC OGU where all 19 mosses of the element occurred. Northern Gaspé (GASN) had the lowest richness. This element was characterized by rare species; 16 were present in one to two OGUs and four of these occurred in only one OGU (*Encalypta alpina*, *Grimmia unicolor*, *Kiaeria falcata*, *Trematodon montanus*). Numerous mosses in this element occupy mainly upland–highland habitats, including high elevation exposed cliffs (*Campylopus schimperi*, *Myurella tenerrima*, *Orthothecium chryseum*, *Plagiobryum demissum*) and late snow beds (*Andreaea blyttii*, *Andreaea nivalis*, *Polytrichum sexangulare*, *Pohlia drummondii)*. The exposed nature of the habitats occupied was reflected in the affinities of the element: 84% of the mosses are either arctic–alpine or montane (Table 7).

Element 9

Element 9 was the largest element recognized and it comprised 51 species. It displayed a richness pattern similar to that of element 6 but its richness pattern differed in that it had relatively fewer species in three Gulf OGU all located in the northwestern portion of the study area: southern Gaspé Peninsula, Anticosti Island, and Québec North Shore. The highest indicator values were found in most parts of Newfoundland (except the southeast and extreme southwest), southern Labrador, and northern Gaspé (Fig. 22). OGUs with high richness were, however, concentrated in northwestern Newfoundland (FWSC, FWNC, FWN), southern Labrador (NOE), northern Gaspé (GASN), as well as Cape Breton (e.g., *Entodon concinnus*, *Kiaeria starkei*, *Orthotrichum alpestre*, *Plagiobryum zierii*, *Tortella fragilis*, *Ulota curvifolia*). Numerous outliers (e.g., *Fissidens viridulus*, *Hygrohypnum subeugyrium, Orthotrichum gymnostomum*) were found in more southerly OGUs (NS4, NB7). The majority of species in this group were moderately rare (24 species occurring in 1–4 OGUs), but most were found in 11 or fewer OGUs. Only two species (*Racomitrium lanuginosum*, *Tortella fragilis*) had a wide distribution, being found in 17 OGUs. Species in this element are mainly upland and highland species occupying cool–cold exposed habitats (e.g., *Arctoa fulvella*, *Dryptodon patens*, *Grimmia incurva, Grimmia tenerrima*, *Kiaeria blyttii*, *Lescuraea saxicola*, *Orthotrichum alpestre*). All major floristic affinities were represented (Table 7). Boreal mosses predominated (39%), but montane species were also important (31%). Temperate and arctic mosses together comprised about 25% of this element.

Eastern bias distributions

Gulf of St. Lawrence moss elements with an eastern bias included only element 10 (Fig. 23). Mosses in this bias had a positive correlation with both db-RDA axes 1 and 2 (Table 6). About one-third of mosses were correlated to either warmth of growing season (axis 1) or to oceanity index (axis 2).

Element 10

Although this element could be included in the northern bias group, it had a richness pattern with a distinctly eastern bias. The element was centered in eastern Newfoundland (FE and FEB) with species extending to western Newfoundland or Cape Breton Island (Fig. 23). Outliers occurred farther south (e.g., *Bryum salinum*, *Kindbergia praelonga*, *Sematophyllym marylandicum*) and also west to the Québec North Shore (e.g., *Dicranodontium denudatum*). Two-thirds of the species were restricted to Newfoundland (e.g., *Bryum aeneum*, *Campylopus atrovirens*, *Isothecium alopecuroides*, *Sphagnum balticum*). The highest indicator values were in eastern Newfoundland (FE, FEB). The highest richness was also in the latter areas, but especially in eastern Newfoundland (FE), where all 23 mosses in this element occurred. Richness decreased westward where the highest diversities were in Cape Breton Island and northern Gaspé. Ten species in this group were rare in the Gulf region, occurring in only one to two OGUs. Most other species were found in fewer than 11 OGUs, with only three species occurring in 10–11 OGUs. This element comprised species found in a wide array of habitats, most from lowland habitats including open (*Bryum salinum, Campylopus atrovirens*, *Homalothecium sericeum, Sphagnum balticum*), forested (*Sematophyllym marylandicum*, *Tetrodontium brownianum, Ulota* drummondii), or upland barrens (*Oligotrichum hercynicum*). Several of the species included in this element are considered oceanic or have oceanic tendencies (e.g., *Bryum miniatum*, *Campylopus atrovirens*, *Dicranodontium denudatum*, *Sphagnum balticum*, *Sphagnum molle*, *Ulota drummondii*). Three species are possible introductions to Newfoundland: *Orthotrichum stramineum* (Brassard 1984*b*), *Pseudoscleropodium purum* (Brassard 1983*c*), and *Tortula muralis* (Brassard and Weber 1977). This element was composed of mostly temperate species (44%), but it also had an important component of boreal species (35%) (Table 7). Montane and arctic species were also represented but comprised only 13% of the element.

Discussion and conclusions

The results of the db-RDA ordination show clearly that climatic variables are the most important factors influencing the distribution of mosses in the Gulf of St. Lawrence region. Warmth of the growing season, as expressed by degree-days, strongly defined the first axis of the ordination, which is generally considered the most important axis. This climatic variable had a well-defined gradient in the study area, with the highest values in the southern areas of the region and the lowest in the northernmost parts. The gradient was clearly reflected on the ordination because the warm southern Nova Scotia OGUs (NS1, NS2, NS3) are found on the leftmost side of axis 1 on the ordination and the coldest OGUs (FNW, NOE) are found at the opposite end.

Oceanity index was also identified as an important factor influencing moss distributions and defines the second axis. This environmental variable is a synthetic index that combines climatic parameters such as annual temperature, precipitation, and evapotranspiration to quantify the influence of the sea. Although some areas have distinct oceanic tendencies, the study area is generally considered to have a continental climate (Hare and Thomas 1979) because weather systems originate from continental areas. Consequently, oceanity displays a weak gradient in the region. The highest oceanity index values are on the Newfoundland south coast near the geographical center of the study area, although several OGUs in Nova Scotia also have relatively high values. Diminishing values are found both north and west of the Newfoundland south coast and New Brunswick areas.

Although climatic variables were the most important determinants of moss distributions in the Gulf, physiographic and geologic factors were also important. Amount of calcareous outcropping, in particular, has been presumed by many early workers to be important in the distribution of Gulf of St. Lawrence plants (Wynne-Edwards 1937; Griggs 1940; Scoggan 1950; Böcher 1951; Rune 1954; Drury 1969). Amount of calcareous rock outcropping and maximum elevation were both shown by db-RDA analysis to influence the distribution of Gulf of St. Lawrence mosses. Their effects were to modify the general distribution patterns established by climatic variables as indicated by their secondary importance in defining ordination axes 2 and 3. Neither variable shows distinct gradients within the Gulf region. Calcareous rock outcrops, for instance, are common only in the OGUs bordering the northern Gulf of St. Lawrence, especially in western Newfoundland, southern Labrador, North Shore (Québec), and Gaspé Peninsula. Similarly, OGUs with high elevations are found only in western Newfoundland and Gaspé Peninsula.

The effects of environmental factors on the moss flora varied across the Gulf of St. Lawrence. Although warmth of growing season appeared to be the only important influence on moss distribution in the southern parts of the study area (e.g., Maritimes), distribution patterns in the northern half of the Gulf region were affected by a complex mixture of both climatic and edaphic variables. While the Maritime OGUs and those located north of the Maritimes are dispersed along db-RDA axis 1, the latter also show well-defined OGU groups separated along axis 2. The wider dispersion of non-Maritime OGUs on the second ordination axes suggests that, as a group, these OGUs are overall more environmentally heterogeneous than the Maritime OGUs. This has not only resulted in more complex moss distribution patterns in that region, but also in an increase in richness in the region. It is well known that species diversity is highly correlated to environmental (i.e., habitat) diversity. Comparison of species richness between the Maritime and non-Maritime OGUs showed that non-Maritime OGUs had a higher total richness of species than that found in the Maritimes (Table 8). Total species richness for the Maritimes is 429 mosses, while for the non-Maritime OGUs, it is 16% higher or 482 species. This difference increased to 24% when only the species used in this study were considered, from 216 mosses for the Maritimes to 269 for the non-Maritime OGUs.

Differences in floristic affinities of the two areas (Table 8) further supports the difference in environmental heterogeneity. Although the Maritimes had 41% more temperate mosses than the non-Maritimes, the latter had nearly 4 times as many montane species and 3.5 times as many arctic species as the Maritimes. In eastern Canada, arctic and montane species generally occupy specialized or restricted habitats. Many authors, for instance, have attributed the limited distribution of a large number of "calcicolous" arctic–alpine species in the Gulf area to the limited occurrence of calcareous bedrock in this region (Wynne-Edwards 1937; Scoggan 1950; Rune 1954; Damman 1965, 1976; Drury 1969). Since calcareous bedrock is largely absent from the Maritimes, it follows that the diversity of arctic–alpine species should also be less. Of the 42 arctic mosses in the Gulf, 27 (64%) are found associated mainly with calcareous substrate, including *Amblyodon dealbatus*, *Barbula icmadophila*, **Brachythecium turgidum*, *Bryum wrightii*, *Calliergon trifarium*, *Cinclidium subrotundum*, **Cyrtomnium hymenophylloides*, *Desmatodon latifolius*, *Desmatodon leucostomus*, *Didymodon asperifolius, Encalypta alpina*, *Hypnum bambergeri*, *Hypnum procerrimum*, **Hypnum vaucheri*, *Myurella tenerrima*, *Orthothecium chryseum*, **Orthothecium strictum*, *Orthotrichum pylaisii*, *Plagiobryum demissum*, **Rhytidium rugosum*, *Scorpidium turgescens, Stegonia latifolia*, **Timmia austriaca*, **Timmia norvegica*, *Tortella arctica*, *Tortula norvegica*, and *Trichostomum arcticum*. Among the arctic–alpine mosses that are not associated with calcareous bedrock are *Aulacomnium turgidum*, **Bartramia ithyphylla*, *Calliergon sarmentosum*, *Conostomum tetragonum*, **Dicranoweisia crispula*, *Dicranum acutifolium*, *Dicranum angustum*, **Dicranum elongatum*, **Dicranum groenlandicum*, *Dicranum spadiceum*, *Drepanocladus badius*,

Table 8. Comparison of moss richness in Maritime and non-Maritime regions of the Gulf of St. Lawrence.

	No. of species	
Floristic affinity	Maritimes	Non-Maritimes
Cosmopolitan	4	4
Boreal	93	114
Temperate	95	67
Montane	10	39
Arctic–alpine	11	42
Unclassified or unknown	3	3
Total	216 (429)[a]	269 (482)[a]

[a]Numbers in parentheses are total numbers of species.

Kiaeria glacialis, *Splachnum vasculosum*, *Tayloria lingulata*, and *Tetraplodon pallidus*. Of the species listed above, only eleven were found in the Maritimes (indicated by an asterisk) where all were rare and known from fewer than five stations. These species are generally found in association with calcareous cliffs, while those not associated with this bedrock type occur in heath barrens or on siliceous cliffs.

A similar pattern exists for montane mosses. Their occurrence in the study area is dependent on habitats associated with the presence of highland terrain including alpine-like barrens, late snow-beds, high elevation streams, or cold, exposed cliffs (Belland 1983; Belland and Brassard 1988; Belland and Schofield 1994*a*). These habitats are generally rare or absent in the Maritimes and this is reflected in the relatively few (10) species with montane affinity found there: *Arctoa fulvella*, *Grimmia donniana*, *Grimmia incurva, Hygrohypnum montanum*, *Kiaeria blyttii*, *Kiaeria starkei*, *Lescuraea stenophylla*, *Oligotrichum hercynicum*, *Plagiobryum zierii*, and *Pseudoleskea patens*.

Hierarchical cluster analysis of the OGUs resulted in seven groups based on species composition only. While most of the groups were positioned together on the ordination, three OGUs from the Newfoundland group were placed proximally to the Gulf group on the ordination and separated from the other OGUs in their group. Since the db-RDA integrates the effects of environment during construction of the ordination, this result suggests that while the species compositions of the three OGUs were most similar to OGUs of the Newfoundland group, environmentally the OGUs belong with the Gulf group. Moreover, it suggests that species in the three OGUs were not responding to environment factors as expected. Carey et al. (1995) have shown that it is possible to develop an environmentally defined biogeographical zonation using direct (constrained) ordination and other multivariate tools. While this approach has advantages, information gained by performing and analyzing the species classification and OGU ordination separately might be lost. For example, it would be important to ask which species are not responding to the environment, or which species are indicators of the biogeographic zones.

Since few indicators were identified by indicator species analysis, it seems worthwhile here to consider other species that might serve to further characterize the OGU groups. Table 9 summarizes the occurrence of 108 “rare” species, defined as taxa that are restricted to one OGU group within the Gulf of St. Lawrence. What is surprising is that, although the width of occurrence of rare species varied somewhat across OGUs within groups, most rare species in all groups occurred in only one OGU (Table 9). This was true even for groups with relatively large numbers of OGUs (e.g., Gulf, Newfoundland). Such rare mosses were best represented in the Newfoundland group where they comprised 73% of the rare component and also in the Southern Nova Scotia group where they comprised 67% of the rare species. In both the Gulf and Maritime groups, rare species known from only 1 OGU comprised 43%–44% of the rare species.

The Southern Nova Scotia and Maritime groups were characterized by having a large proportion (80%) of rare mosses belonging to the temperate affinity (Table 10). The majority of these reached their eastern North American northern limits in the southern Maritimes. Examples from the Southern Nova Scotia group include *Astomum muehlenbergianum*, *Bryohaplocladium virginianum*, *Grimmia olneyi*, *Micromitrium austinii*, *Sematophyllum demissum*, and *Tortula papillosa*. Maritime group mosses reaching their northern limits in the study area were *Anomodon minor*, *Cyrto-hypnum minutulum*, *Entodon brevisetis*, *Grimmia pilifera*, *Rauellia scita*, and *Taxiphyllum deplanatum*.

The Gulf group was by far the most distinctive in terms of its rare species (Table 10). It possessed 25% more such species than all other groups combined and four times as many as any other OGU group. The group was characterized by species of primarily montane or arctic affinity that comprised 74% of rare species in this OGU group (Table 10). Most of these had restricted distributions in the Gulf and formed the core of species considered to have phytogeographic significance in the region. For instance, many are disjuncts to western North America or to the Arctic and are considered to have survived the last glacial epoch in Gulf of St. Lawrence refugia that were located near where the species occur today (Belland 1987*b*). Examples include *Andreaea nivalis*, *Barbula ferruginascens*, *Brachythecium glaciale*, *Coscinodon cribrosus*, *Desmatodon leucostomus*, *Encalypta longicolla*, *Funaria microstoma*, *Hydrogrimmia mollis*, *Bryum porsildii*, *Myurella tenerrima*, *Orthothecium chryseum*, *Plagiobryum demissum*, *Stegonia latifolia*, *Tayloria splachnoides*, *Trematodon montanus*, and *Trichostomum arcticum*.

Rare mosses of the Newfoundland group are either boreal or montane species (Table 10). Two of the temperate species are considered as introductions to the native flora: *Orthotrichum stramineum* (Brassard 1984*b*) and *Pseudoscleropodium purum* (Brassard 1983*c*). Boreal species included *Antitrichia curtipendula*, *Cynodontium jenneri*, *Grimmia torquata*, *Orthotrichum rupestre*, *Philonotis yezoana*. With the exception of *Grimmia torquata*, most were found at fewer than five locations in Newfoundland. Two species (*Gyroweisia tenuis*, *Isothecium alopecuroides*) were found at only one location.

Three OGU groups (MDI, ANT, and Newfoundland South Coast) did not have rare or indicator species. This may be explained by the small size of their floras, combined with a strong floristic dominance of these by regionally widespread distributional elements. Total sizes of these moss floras, including widespread species (Belland 1987*a*), range from 89 in Anticosti Island to 207 species on the Newfoundland

Table 9. Summary of rare species in seven Gulf of St. Lawrence OGU groups.

OGU group	No. of OGUs[a]	No of rare species	% of species
Southern Nova Scotia (3 OGUs)	1	10	67.0
	2	4	26.7
	3	1	6.7
Total	—	15	—
Maritimes (8 OGUs)	1	7	43.8
	2	5	31.3
	3	3	18.8
	4	1	6.3
Total	—	16	—
Gulf (7 OGUs)	1	27	43.5
	2	18	29.0
	3	5	8.1
	4	7	11.3
	5	3	4.8
	6	1	1.6
	7	1	1.6
Total	—	62	—
Newfoundland (6 OGUs)	1	11	73.3
	2	2	13.3
	3	2	13.3
Total	—	15	—
South Coast (3 OGUs)	0	0	0.0
Total	—	0	—
Anticosti Island (1 OGUs)	0	0	0.0
Total	—	0	—
Magdalen Island (1 OGUs)	0	0	0.0

[a]No. of OGUs in which the species was found.

Table 10. Floristic affinities in four Gulf of St. Lawrence OGU groups.

	OGU Group			
Affinity	Southern Nova Scotia	Maritimes	Gulf	Newfoundland
Boreal	1	4	10	6
Temperate	12	9	3	0
Montane	0	0	22	7
Arctic or arctic–alpine	0	0	24	0
Cosmopolitan	0	0	0	1
Total	15	16	62	15

Note: Values are numbers of rare species.

South Coast. However, the great majority of species (64%–81%) in all three groups belongs to the "widespread element" (Belland 1987*a*) and thus were not analysed in this study. Thus, the number of species that were included in the present analysis includes only 23 species from Magdalen Islands (MDI) to a maximum 46 from Newfoundland South Coast. By contrast, other OGU groups had considerably larger floras, ranging from 308 species (Southern Nova Scotia) to 448 species in the Gulf group and the number of species treated in this study is three (119, Southern Nova Scotia) to five times larger (237, Gulf). Only the Southern Nova Scotia group possessed a similarly high proportion of widespread species (61%), while the remaining three groups varied from 47% (Gulf) to 59% (Newfoundland group).

Although seven discrete OGU groups were identified by hierarchical clustering, this does not imply that distinctive floristic boundaries exist between the OGUs groups. While indicator species are most likely to characterize floristic regions, few (20) of these were identified in this study. Furthermore, of the four OGU groups with species indicators, three groups had four indicators or fewer. Moreover, further analysis using only "rare" showed that despite the large numbers of such species (108) their distributions within OGU groups were quite limited. If boundaries existed, it was expected that such restricted species would be more widely distributed within OGU groups, reaching their limits at or near the OGU group boundaries. Belland (1989) used a similar argument to refute floristic boundaries between Newfoundland, Labrador, and the Maritimes. Moreover, these results strongly suggest that the OGU groups are defined by their entire species component, including rare species, and not solely by the presence of single or several species of special significance (e.g., indicators, rare species).

Climate has long been known to be one of the most important factors controlling plant distribution at global and continental scales where it manifests as parallel vegetation belts or biomes (e.g., Cain 1944; Good 1947; Polunin 1960). The results presented here show that climatic factors are important determinants of moss distribution even at the medium geographical scales represented by the Gulf of St. Lawrence region. The results support the conclusions of Belland (1987*a*) who emphasized the primary importance of climatic factors and the secondary influence of edaphic factors such as geological substratum in this region. The recognition of climatic factors explains the richness patterns demonstrated by temperate and boreal elements (Belland 1987*a*, 1989), both of which show distinct gradients through the study area. Similar conclusions were presented for Gulf of St. Lawrence vascular plants by Damman (1965, 1976, 1983) and Hounsell and Smith (1968).

This is the first North American study to examine large-scale plant distributions using a constrained ordination. The multivariate analysis presented here has provided interpretable results showing the relationship of medium-scale moss distribution patterns to environmental variables. In Europe, Myklestad and Birks (1993) used canonical correspondence analysis to show that regional climate, but especially summer temperature, largely accounted for the distributional patterns of *Salix* in Europe. However, they caution that the climate factors that they identified are not necessarily the causative effect of the patterns observed because of possible auto-correlation with other factors or sets of factors that together may constitute complex gradients. Hill (1991) notes that auto-correlation may be more of a difficulty at small geographical scales than at larger geographic scales, with distributions being largely macroclimate related at the European scale. At the Gulf of St. Lawrence scale, which is rather smaller than the European scale, however, the north–south patterns of floristic affinity shown in Belland (1989) corroborate the climate patterns identified in this study with db-RDA. Since the affinities are based on the world latitudinal moss distribution (i.e., their relationship to major biomes, such as temperate, boreal, etc.), then they clearly reflect distribution along temperature gradients.

Compared with this study, most multivariate floristic studies have used OGUs of constant size and shape. Certainly, the use of smaller sampling units would extract more details of the species–environment relationships. The large size of some OGUs used in this study for instance, masked the influence of some variables. This was evident especially for OGUs that possess two or more distinct physiographic or geologic units. For instance, the OGUs of the Newfoundland Northern Peninsula (FNW, FWNC, FWSC) have both a large highland region comprised of siliceous bedrock and extensive calcareous coastal plains. Defining OGUs based on smaller OGUs, or on physiographic zones, would no doubt result in species groups with floras that show consistency in both substrate preference and floristic affinity. Use of smaller OGUs may also produce OGU groups with more indicators, reduce misclassification of OGUs, and enable more precise identification of the influence of climate variables that operate at a smaller scale, for example, snowfall and the development of late snow beds.

The main aim of phytogeography is to explain the distribution patterns of plants. Most studies begin by classifying species into groups with similar distributions and then analysing the groups by correlation with either historic or with physical factors. Until recently, much of this work was done manually by visual inspection and comparison; thus, species classification had a large element of inherent subjectivity. The advent of multivariate methodologies for classification and analysis has added objectivity and repeatability to studies. As with numerous previous plant distribution studies, the present work has shown that the multivariate techniques typically used only in ecological studies can also prove effective in moss floristic studies.

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