

Regional patterns and controlling factors in plant species composition and diversity in Canadian lowland coastal bogs and laggs

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SUMMARY

Inventories of natural assemblages of plant species are critical when planning ecological restoration of bogs. However, little is known about the regional variation in plant communities at the margins (laggs) of bogs, even though they are an integral element of raised bog ecosystems. Therefore, we investigated the regional patterns in the plant communities of bogs and laggs, and the factors that control them, for thirteen bogs in coastal British Columbia, Canada. Species richness was significantly higher in the bogs and laggs of the cooler, wetter Pacific Oceanic wetland region. Beta Diversity analyses showed that bogs in the Pacific Oceanic wetland region often shared species with their respective laggs, whereas half of the laggs in the warmer, drier Pacific Temperate wetland region had no species in common with the adjacent bogs and were thus more ecologically distinct from the bog. Primary climatic variables, such as mean annual precipitation, mean annual temperature and latitude, as well as climate-influenced variables, such as pH, peat depth, and Na⁺ concentrations were the main correlates of plant species composition in the studied bogs. Site-specific factors, particularly depth to water table, and fraction of inorganic material in peat samples, were as strongly related to lagg plant communities as climate, while hydrochemistry appeared to have less influence.

KEY WORDS: bog, ecotone, lagg, regional variation, vegetation

INTRODUCTION

Regional gradients in climate and proximity to the ocean shape variation in peatland plant communities and the controlling environmental factors that influence plant species composition, particularly the depth to water table, and peat and pore-water chemistry. Regional variation in peatland vegetation is well described for the Northern Hemisphere. For example, Ingram (1983) observed that fens are more common in areas with relatively low rainfall, that raised bogs form in climatically wetter locations, and that the wettest climate promotes the formation of blanket bogs. Riley (2011) found for wetlands in the Hudson Bay that differences in plant species composition and abundance were primarily correlated with depth to water table and pore-water pH. These characteristics varied across a series of adjacent ecoregions, whose boundaries were determined by climate, particularly mean annual precipitation, temperature, and relative humidity. Damman (1977) observed regional differences in plant communities of raised bogs in the Bay of Fundy in eastern Canada and the USA, and attributed

differences between inland and coastal bogs to the higher fog frequency and intermittent snow cover of coastal bogs compared to inland bogs. A similar oceanic-continental gradient in bog plant communities in Sweden appears to be related to relatively high base cation (particularly Mg²⁺) concentrations in precipitation, higher mean relative humidity and shorter dry periods in coastal areas (Rydin *et al.* 1999).

Plant species composition of bog margins (i.e. the lagg) might be expected to show regional variation as well. Several studies have characterised lagg vegetation (e.g. Hellquist & Crow 1999, Paradis *et al.* 2015, Howie & van Meerveld 2016), but few have examined regional patterns in lagg plant species composition and the factors that influence these patterns. In ombrotrophic bogs, water and inorganic nutrients are almost entirely supplied from the atmosphere (i.e. precipitation and dustfall), so regional variation in bog plant communities may be largely controlled by climate and precipitation chemistry. The lagg is generally characterised by a mixture of runoff water from the bog and the surrounding minerotrophic landscape so that the

minerotrophic water from areas outside the bog may also affect the hydrology and plant community composition in the lagg. For example, Damman (1977) showed for bogs in the Bay of Fundy that plant species composition at the bog margin was most strongly influenced by the topography and surrounding mineral soils, rather than climate.

Laggs are often important for the biological diversity (Risser 1995, Kutnar & Martinčič 2003, Korpela 2004, Mieczan *et al.* 2012) and hydrological functioning of bogs (Schouwenaars 1995, Schouten 2002, Langlois *et al.* 2015). Understanding lagg vegetation and the factors that influence it is thus essential for restoration and conservation. Key attributes include common lagg species and their preferred range in depth to water table, pH and cation concentrations, which are all critical for the development of restoration targets for disturbed laggs in support of their adjacent bogs. This type of inventory can also help determine whether a lagg is in a natural condition or has been changed by human activities, i.e. whether the lagg contains a plant assemblage expected for the region, or species that indicate disturbance.

In this work we aimed to determine whether or not there are regional patterns in bog and lagg plant communities in coastal British Columbia. We investigated the character and distribution of plant assemblages with respect to environmental factors, including climate and local gradients, such as depth to water table and the chemistry of near-surface pore water. Specifically, we tested the following hypotheses:

1. The biodiversity (species richness and diversity) of bog and lagg plant communities is related to climate.
2. Plant species composition in laggs is more strongly related to site-level environmental gradients (e.g. depth to water table, hydrochemistry) than it is to climate, while bog plant communities are more strongly related to climate.
3. Lagg plant communities are more distinct from adjacent bog plant communities in climates with drier summers because the wider seasonal variation in water level has a stronger effect on the vegetation in the lagg.

STUDY AREA

We studied thirteen little-disturbed bogs located within 20 km of the Pacific Ocean and less than 100 m elevation above sea level. The studied bogs are located on the coast of British Columbia within two

of the seven Canadian wetland regions: Pacific Oceanic and Pacific Temperate (Figure 1). These regions are based on broad climatic and vegetation zones, following a north–south temperature gradient and an east–west precipitation gradient (National Wetlands Working Group (NWWG 1988)). The Pacific Oceanic wetland region is divided into two subregions: North Coast and South Coast (Figure 1). The mean annual precipitation in the Pacific Oceanic wetland region, based on measurements from five long-term climate stations, ranges from 1261 to 3061 mm yr⁻¹ (mean = 2117 mm yr⁻¹), while the mean annual precipitation in the Pacific Temperate wetland region, based on measurements from three climate stations, ranges from 856 to 1206 mm yr⁻¹ (mean = 1044 mm yr⁻¹) (NWWG 1988). The Pacific Oceanic wetland region is cooler (average mean annual temperature: 8.2 °C) than the Pacific Temperate wetland region (average mean annual temperature: 9.6 °C).

The bogs were selected to provide a broad geographic sample for the coastal British Columbia region. Six bogs are in the North Coast subregion of the Pacific Oceanic wetland region: three are near Prince Rupert (Diana Lake, Oliver Lake, and Butze Rapids) and another three on Haida Gwaii (Tow Hill, Mayer Lake, and Drizzle Lake) (Figure 1). Three bogs are on Vancouver Island: one on the west coast (Shorepine Bog) within the South Coast subregion of the Pacific Oceanic wetland region and two on the east coast (Port McNeill and Campbell River) in the Pacific Temperate wetland region (Figure 1). Four bogs are in the Fraser Lowland region in the Pacific Temperate wetland region: Burns Bog, Surrey Bend, Langley Bog, and Blaney Bog (Figure 1). The Prince Rupert, Haida Gwaii, and Vancouver Island bogs were all near a roadway or trail, but the sites studied in these bogs were away from the roads/trails and are considered to be undisturbed based on visual observation of the sites. All four Fraser Lowland bogs contain areas that were disturbed decades ago by activities such as peat mining, utility and road construction, drainage, and conversion to agriculture. Study transects at the Fraser Lowland bogs were placed in remnant natural plant communities that were unlikely to have been affected in a significant way by the disturbance and are assumed to be representative of natural or near-natural conditions in terms of hydrology, chemistry, and plant community composition. Detailed site information and climate data for each study site can be found in Howie & van Meerveld (2013).

Four lagg plant communities have been described for the study area: *Spiraea* Thicket (shrub swamp characterised by *Spiraea douglasii*), *Carex* Fen (fen

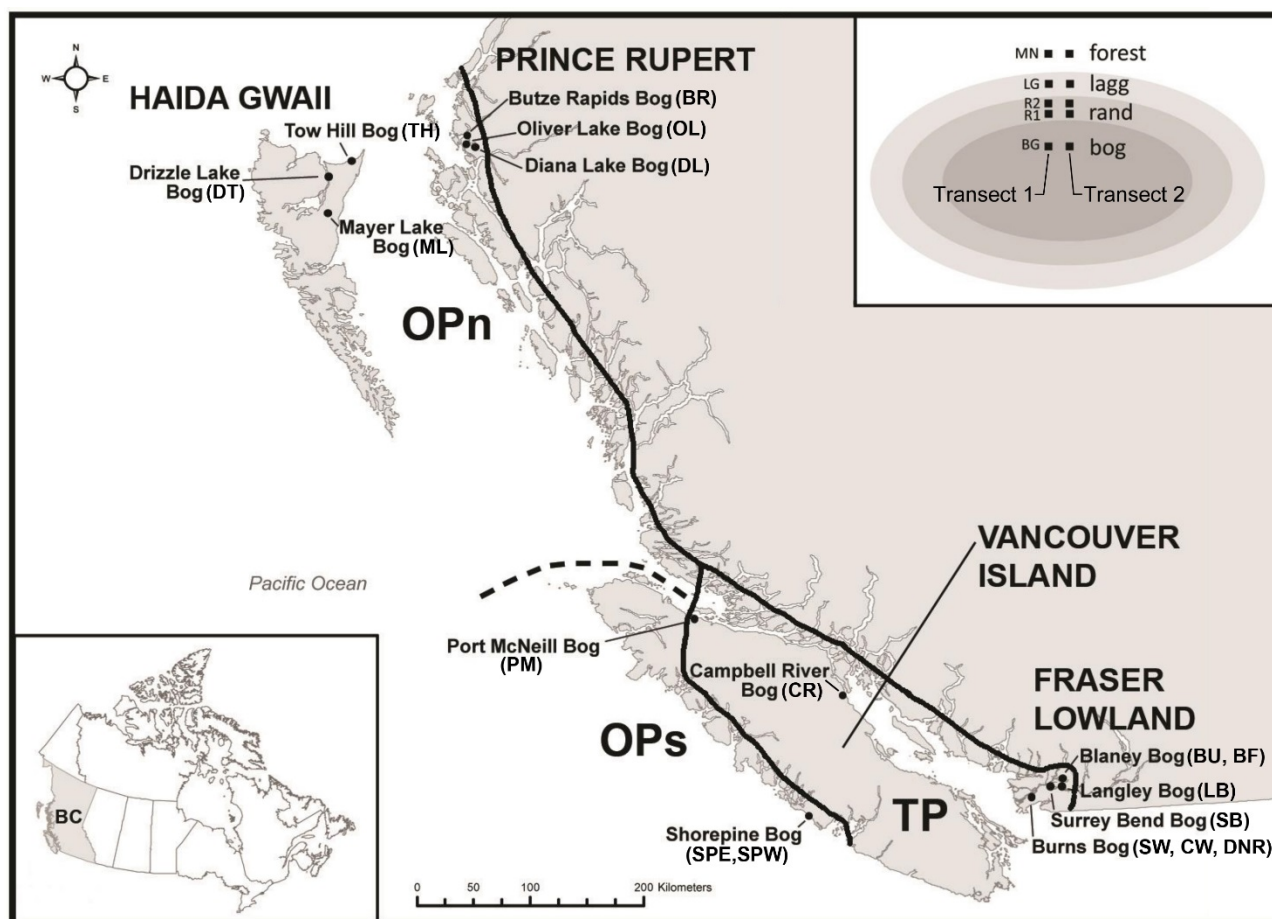


Figure 1. Locations of the research sites (black dots) and study regions in coastal British Columbia (BC). The thick black lines define the two coastal wetland regions and subregions: OPn = Pacific Oceanic, North Coast wetland subregion; OPs = Pacific Oceanic, South Coast wetland subregion; and TP = Pacific Temperate wetland region. Wetland region boundaries are from NWWG (1988). Lower inset: map of Canada; upper inset: generic study transect diagram, where closed symbols represent individual study plots on the transects. BG = bog, R1 and R2 = rand, LG = lagg, MN = minerotrophic ecosystem adjacent to lagg.

characterised by *Carex sitchensis* and *Myrica gale*), Peaty Forest (forested swamp characterised by *Thuja plicata*, *Picea sitchensis*, and *Tsuga heterophylla*), and Direct Transition (no distinct plant community between bog and forest) (Howie & van Meerveld 2016). The *Spiraea* Thicket and *Carex* Fen lagg plant communities are confined in topographic depressions at the bog margin, while the Peaty Forest and Direct Transition lagg plant communities are situated in topographically unconfined (relatively flat) zones at the bog margin. The *Spiraea* Thicket and Peaty Forest lagg plant communities are generally found in the Pacific Oceanic wetland region, while the *Carex* Fen and Direct Transition lagg plant communities are generally found in the Pacific Temperate wetland region (Howie & van Meerveld 2016).

METHODS

Field measurements

At each bog, a set of two parallel transects (Transect 1 and Transect 2) was laid out perpendicular to the bog margin in a location representative of the typical lagg condition (Figure 1 inset). Ten bogs contained one pair of study transects, two had two pairs (Shorepine Bog and Blaney Bog), and one bog had three pairs of transects (Burns Bog). Each transect consisted of five study plots (Figure 1 inset). The positions of the five plots were determined in the field based on the character of the dominant plant communities and were arranged such that one plot was located in the typical *Sphagnum*- and heath-dominated bog centre (BG), two plots were located in the transition from the

bog centre to bog margin, i.e. in the rand (one closer to the bog (R1) and one closer to the margin (R2)), the fourth plot was located in the lagg (LG), and a fifth plot was located in the forest on mineral soils adjacent to the bog (MN). The distance between the plots varied depending on the width of the lagg at each bog. LG plots were chosen in two ways: *i*) where the lagg plant community was distinct from the adjacent bog and forest, the centre of the lagg plant community was chosen for the LG plot; and *ii*) in situations where the bog blended into the forest without a distinct lagg plant community, the centre of the visually-obvious transition from bog to forest (as determined by tree height and species composition of the understorey) was chosen for the LG plot. The DNR and SW transects in Burns Bog each had two lagg plots to account for differences in plant species composition across relatively wide lags.

At each study plot, the cover of all vascular and bryophyte species was recorded in a 5 m × 5 m plot using the Braun-Blanquet scale of cover and abundance: “r” = solitary with small cover, “+” = few with small cover, “1” = numerous but < 5 % cover, “2” = 5–25 % cover, “3” = 25–50 %, “4” = 50–75 %, “5” = ≥ 75 % (Mueller-Dombois & Ellenberg 1974). One exception was for *Sphagnum* species: only the four *Sphagnum* species with the highest percent cover were recorded in each plot; *Sphagnum* cover in plots was generally dominated by only one or two *Sphagnum* species. Species nomenclature followed Klinkenberg (2015). Totals of 34, 32, 30, 38, and 34 vegetation plots were investigated in the BG, R1, R2, LG, and MN plots, respectively. The BG and LG plot data are the focus of this study because the objective was to search for regional patterns in bog and lagg plant communities; the rand (R1 and R2) plant community can be considered a drier variant of the adjacent bog plant community (Godwin & Conway 1939, Ingram 1983, Rydin *et al.* 1999), and the surrounding forest (MN) plant communities have been described in detail by others (e.g. Krajina 1965).

Shallow piezometers were installed in hollows at the five plots on each Transect 1. Depth of the piezometer base below the surface varied. We aimed to place the 40 cm slotted section as close as possible to the water table observed in the borehole, while still ensuring an adequate volume of water for sample collection. Mean depth of piezometer base below the water table was 0.53 m (standard deviation: 0.20 m). At each piezometer, in June/July of 2010 or 2011, a single depth to water table measurement was taken and a sample of near-surface pore water was collected for the analysis of pH, electrical conductivity and Ca²⁺, Mg²⁺, and Na⁺ concentrations. Cation concentrations were determined at the Pacific

Environmental Science Centre (North Vancouver, BC) by inductively coupled plasma spectrometry. Peat depth was determined at all piezometer sites by augering. For a detailed description of the depth to water table measurements and hydrochemical sampling methods, see Howie & van Meerveld (2013).

Data analyses

Ordination (multivariate) analyses were performed on the plant species cover and abundance data using PC-ORD (McCune & Mefford 2011). We used non-metric multidimensional scaling (NMS) to search for regional vegetative groups in the studied BG and LG plots, as well as indications of which environmental variables have the strongest effect on plant species composition. For this analysis we used Sørensen (Bray-Curtis) distance, a maximum of 200 runs, 100 iterations, and a stability criterion of 0.0005 because they were shown previously to be effective in the ordination of bog and lagg plant communities on Vancouver Island (Golinski 2004). The Sørensen distance (or percent dissimilarity) between vegetation plots *i* and *h* was calculated as:

$$D_{i,h} = \frac{\sum_{j=1}^p |a_{ij} - a_{hj}|}{\sum_{j=1}^p a_{ij} + \sum_{j=1}^p a_{hj}} \quad [1]$$

For ordination, correlation, and tests of significance, Braun-Blanquet cover values for plant species were converted to percent cover values using the mean of each class: “r” = 0.25 %, “+” = 0.5 %, “1” = 2.5 %, “2” = 15 %, “3” = 37.5 %, “4” = 62.5 %, “5” = 87.5 %.

The Sørensen Index (*SI*) was used to determine Beta Diversity of plant species composition between each BG vegetation plot and the other vegetation plots on the transect:

$$SI = \frac{2a}{(2a+b+c)} \quad [2]$$

where *b* is the number of species in one plot (e.g. BG), *c* is the number of species in another plot on the transect (e.g. LG), and *a* is the number of species in both plots. Beta Diversity was used because it is a well-known measure of diversity and allows for a comparison of the change in species diversity and composition between different ecosystems.

The following additional indices for the vegetation plots were calculated using PC-ORD (McCune & Mefford 2011): *i*) species richness (*S* = total number of species); *ii*) Shannon’s diversity index, *iii*) evenness, and *iv*) Simpson’s diversity index. The Shannon’s diversity index (*H'*), is calculated as:

$$H' = -\sum_{i=1}^S p_i \log p_i \quad [3]$$

where p_i is the importance probability for each species, relative to the total number of species for each vegetation plot. The evenness (E) is calculated as:

$$E = \frac{H'}{\ln(S)} \quad [4]$$

while Simpson's diversity index (D) is calculated as:

$$D = 1 - \sum_{i=1}^S p_i^2 \quad [5]$$

Species richness was used to determine whether there was a difference in the number of species in the BG and LG plots regionally (e.g. between the Pacific Oceanic and Pacific Temperate wetland regions). The Shannon and Simpson diversity indices were chosen because they account for both the abundance and evenness of the species in the plots; the Simpson diversity index emphasises common species (rare species have little effect on the measure of diversity),

whereas the Shannon diversity index also includes the species that are relatively rare (Hill 1973).

Since the data were generally not normally distributed, Mann-Whitney U-tests were used to determine whether the biodiversity measures, the depth to water table and hydrochemistry differed significantly between the Pacific Oceanic and Pacific Temperate wetland regions. A significance level of 0.05 was used for all analyses. Results are reported as significantly different only if the non-directional ("two-tailed") test was considered significant.

RESULTS

Distinctiveness of the lagg plant communities

All of the Pacific Oceanic wetland region LG plots had at least one species in common with their BG plots, while 10 out of 22 LG plots in the Pacific Temperate wetland region had no species in common with their BG plots (Figure 2). The median number of species shared by LG and BG plots varied as follows:

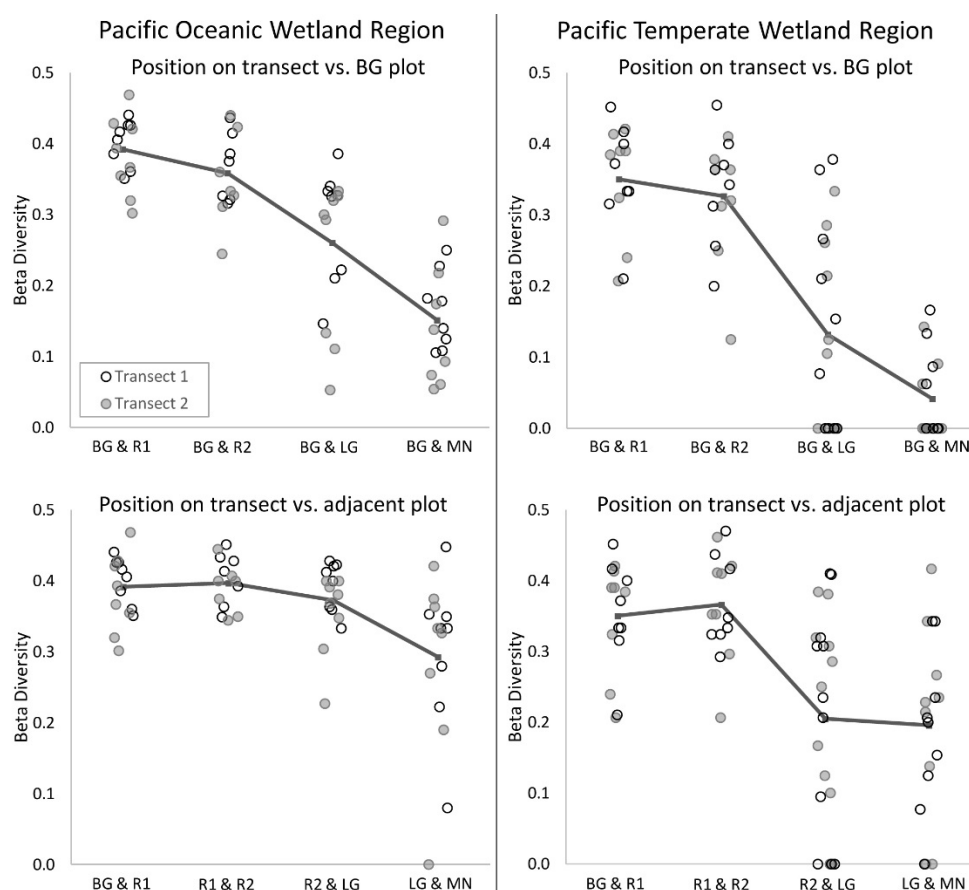


Figure 2. Sørensen Index of Beta Diversity comparing vegetation plots along the transects (R1, R2, LG, and MN) with the BG plot (upper row) and the adjacent plots on the transect (lower row). A value of zero indicates that paired plots had no species in common with each other. The symbols have been randomly offset along the x-axis for clarity. BG = bog, R1 and R2 = rand, LG = lagg, MN = minerotrophic ecosystem adjacent to lagg. Thick lines link mean values for the groups.

Prince Rupert: 5, Haida Gwaii: 7, Vancouver Island west: 8, Vancouver Island east: 4, and Fraser Lowland: 1. This suggests that the plant community composition of lags in the Pacific Temperate wetland region is more distinct from the adjacent bogs than in the Pacific Oceanic wetland region and that a more well-defined ecotone plant community develops in lags of the Pacific Temperate wetland region. A similar trend was found for the MN plots, which had at least one species in common with the BG plots in all of the Pacific Oceanic wetland region

plots, but shared no species with BG plots in 11 out of 18 transects in the Pacific Temperate wetland region (Figure 2).

Regional biodiversity of bogs and lags

The 168 vegetation plots contained 146 plant species, including 100 vascular plants and 46 bryophytes (Figures 3, 4). The BG, R1, R2, LG, and MN plots contained a total of 76, 81, 78, 89, and 95 species, respectively. Species richness in the BG and LG plots was significantly ($P < 0.05$) higher in the bogs of the

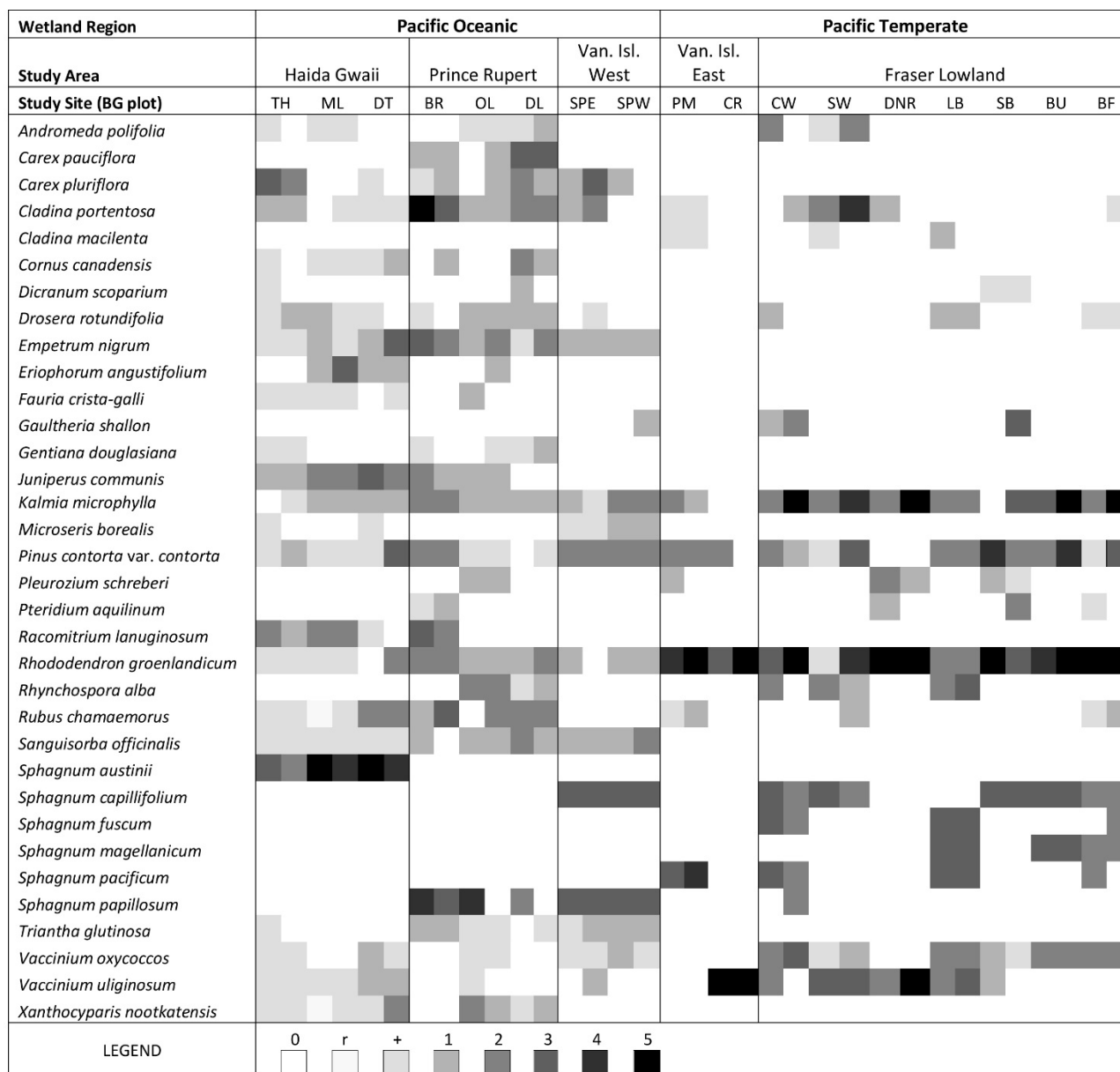


Figure 3. Species observed in at least three BG plots, with a minimum coverage ≥ 1 on the Braun-Blanquet scale in at least one plot. The squares are in pairs: the first for Transect 1, the second for Transect 2. Cover codes: “0” = absent, “r” = solitary with small cover, “+” = few with small cover, “1” = numerous but $< 5\%$ cover, “2” = $5\text{--}25\%$ cover, “3” = $25\text{--}50\%$, “4” = $50\text{--}75\%$, “5” = $\geq 75\%$ (Mueller-Dombois & Ellenberg 1974). See Figure 1 for site codes. The BG plots are ordered by wetland region and study area.

Pacific Oceanic wetland region than in the Pacific Temperate wetland region (Figure 5, Table 1). There was no significant difference in the evenness, median Shannon diversity index, or median Simpson diversity index for the BG plots in the two wetland regions (Table 1). Evenness was also not significantly different between the wetland regions for the LG plots. In contrast, the Shannon and Simpson diversity indices were both significantly higher for the LG plots in the Pacific Oceanic wetland region than for the LG plots in the Pacific Temperate wetland region (Table 1). These results agree with the species richness results, indicating that lagggs of the Pacific Temperate wetland region are less diverse than those of the Pacific Oceanic wetland region.

For the BG plots, the number of vascular plant species was significantly positively correlated with pH (Figure 5a) and the Na⁺ concentration in pore water (Figure 5d). Total species richness in BG plots also showed significant positive correlations with pH and Na⁺ concentration (Figures 5b, 5e), whereas species evenness in BG plots was significantly negatively correlated with pH and Na⁺ concentration (Figures 5c, 5f). There was no significant relationship between any of the diversity indices and Mg²⁺ or Ca²⁺ concentration. Differentiation between plots in the Pacific Oceanic and Pacific Temperate wetland regions was evident for the diversity indices and for pH (separation of open and closed symbols in Figure 5; Table 1). The median pH in BG and LG

Wetland Region	Pacific Oceanic										Pacific Temperate									
Study Area	Haida Gwaii						Van. Isl. West		Van. Isl. East		Fraser Lowland									
Study Site (LG plot)	TH	ML	DT	BR	OL	DL	SPE	SPW	PM	CR	CW	SW1	SW2	DNR1	DNR2	LB	SB	BU	BF	
<i>Calamagrostis nutkaensis</i>																				
<i>Carex pluriflora</i>																				
<i>Carex sitchensis</i>																				
<i>Cladina portentosa</i>																				
<i>Cornus canadensis</i>																				
<i>Empetrum nigrum</i>																				
<i>Fauria crista-galli</i>																				
<i>Gaultheria shallon</i>																				
<i>Isoetecium myosuroides</i>																				
<i>Kalmia microphylla</i>																				
<i>Lysichiton americanum</i>																				
<i>Maianthemum dilatatum</i>																				
<i>Menziesia ferruginea</i>																				
<i>Myrica gale</i>																				
<i>Picea sitchensis</i>																				
<i>Pinus contorta</i> var. <i>contorta</i>																				
<i>Pleurozium schreberi</i>																				
<i>Polytrichum strictum</i>																				
<i>Pteridium aquilinum</i>																				
<i>Rhamnus purshiana</i>																				
<i>Rhododendron groenlandicum</i>																				
<i>Rhytidiadelphus triquetrus</i>																				
<i>Rubus chamaemorus</i>																				
<i>Rubus ursinus</i>																				
<i>Sanguisorba officinalis</i>																				
<i>Sphagnum pacificum</i>																				
<i>Sphagnum papillosum</i>																				
<i>Spiraea douglasii</i>																				
<i>Thuja plicata</i>																				
<i>Tsuga heterophylla</i>																				
<i>Vaccinium oxycoccos</i>																				
<i>Vaccinium parvifolium</i>																				
<i>Vaccinium vitis-idaea</i>																				
<i>Xanthocyparis nootkatensis</i>																				
LEGEND	0	r	+	1	2	3	4	5												

Figure 4. Species observed in at least three LG plots with coverage ≥ 1 on the Braun-Blanquet scale in at least one plot. The squares are in pairs: the first for Transect 1, the second for Transect 2. Cover codes: Cover codes: “0” = absent, “r” = solitary with small cover, “+” = few with small cover, “1” = numerous but $< 5\%$ cover, “2” = 5–25 % cover, “3” = 25–50 %, “4” = 50–75 %, “5” = $\geq 75\%$ (Mueller-Dombois & Ellenberg 1974). See Figure 1 for site codes. The LG plots are ordered by wetland region and study area.

plots was significantly higher in the Pacific Oceanic wetland region than in the Pacific Temperate wetland region but Na^+ , Mg^{2+} , and Ca^{2+} concentrations did not differ significantly between the two coastal wetland regions (Table 1).

Influence of regional and local environmental gradients on plant species composition

Non-metric multidimensional scaling (NMS) analyses for the BG plots showed that bog plant communities can be grouped into the two coastal BC wetland regions, and the five study areas: Haida Gwaii, Prince Rupert, west coast of Vancouver Island, east coast of Vancouver Island, and the Fraser Lowland (Figure 6). The LG plots did not cluster as

clearly as the BG plots into the five study areas, but did separate according to the two wetland regions (open vs. closed symbols in Figure 6).

The NMS biplot in Figure 6a shows that climate variables (mean annual temperature and mean annual precipitation, which vary with latitude), and factors linked to climate (peat depth) and proximity to the ocean (pH and Na^+ concentrations), are the clearest predictors of species composition in the BG plots. The climate variables are important in the LG plots as well, but the longest biplot arrow in Figure 6b represents the local depth to water table. Other site-level factors (fraction of inorganic material at 50 cm depth and peat depth) also influence plant community composition in the LG plots (Figure 6b).

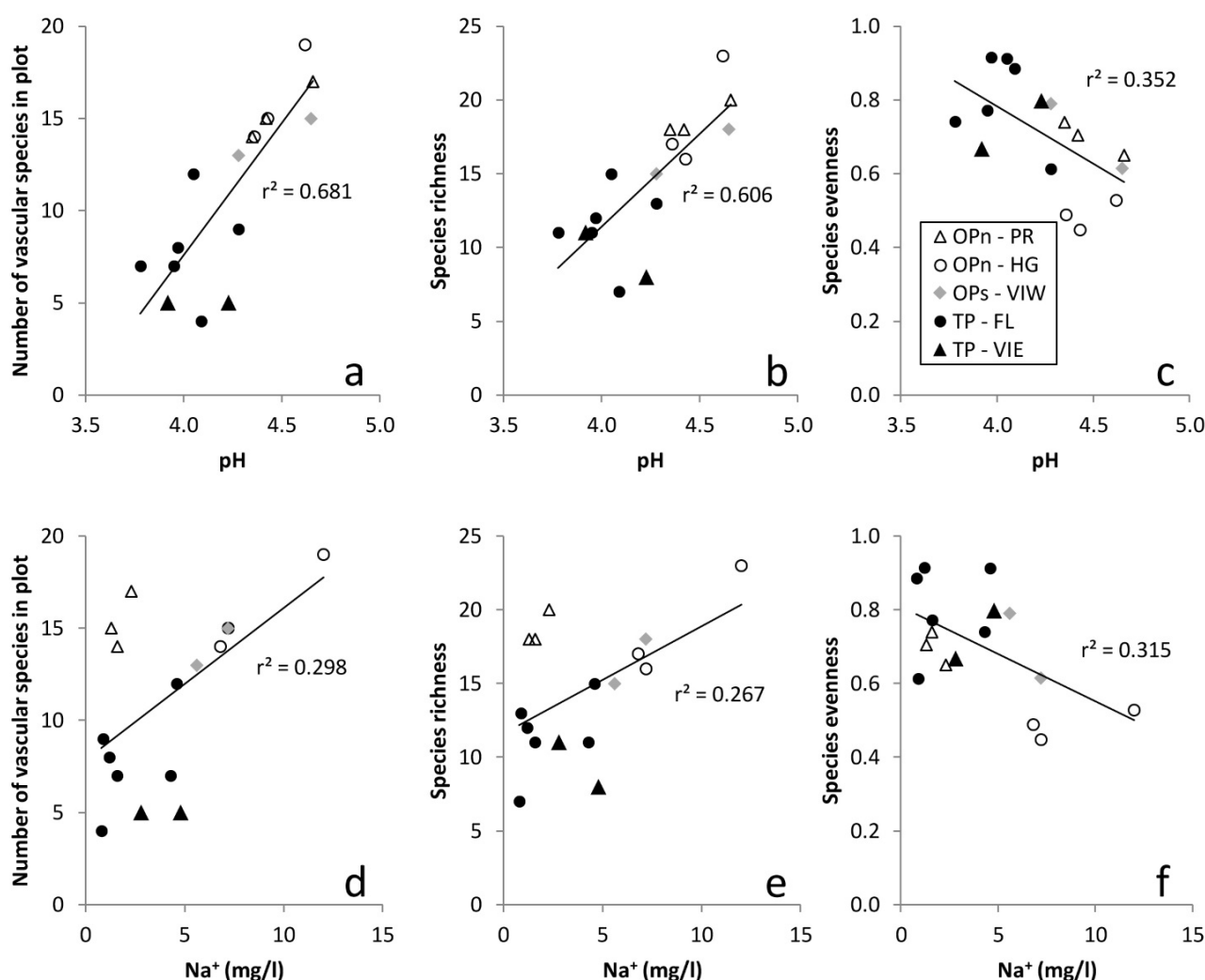


Figure 5. Significant linear regressions ($P < 0.05$) between the number of vascular plant species (left column), species richness (middle column) or species evenness (right column), and pH (top row) or Na^+ concentration in pore water (bottom row), in BG plots. OPn = Pacific Oceanic wetland region, North Coast subregion; OPs = Pacific Oceanic wetland region, South Coast subregion; TP = Pacific Temperate wetland region; PR = Prince Rupert; HG = Haida Gwaii; VIW = west coast of Vancouver Island; VIE = east coast of Vancouver Island; FL = Fraser Lowland.

Table 1. Median \pm mean absolute deviation of the environmental factors and plant species diversity indices for the BG (bog) and LG (lagg) plots. Pacific Oceanic (OP) and Pacific Temperate (TP) wetland regions are compared side by side; an asterisk (*) and bold text indicates a significant ($P < 0.05$) difference between the two wetland regions. For TP, $n = 8$ for depth to water table and hydrochemistry, and $n = 9$ for peat depth and the diversity indices.

	BG Plots		LG Plots	
	OP ($n = 8$)	TP ($n = 8$ or 9)	OP ($n = 8$)	TP ($n = 11$)
Depth to water table (cm)	18.5 \pm 4.8	14.0 \pm 7.5	25.8 \pm 11.9	23.0 \pm 15.9
pH	4.43* \pm 0.1	4.01* \pm 0.1	5.38 \pm 0.6	4.35 \pm 0.6
EC _{corr} ($\mu\text{S cm}^{-1}$)	47 \pm 25.8	39 \pm 27.8	77 \pm 25.1	60 \pm 48.0
Ca ²⁺ (mg L ⁻¹)	1.9 \pm 1.1	1.5 \pm 0.8	3.4 \pm 3.0	2.6 \pm 0.7
Mg ²⁺ (mg L ⁻¹)	0.9 \pm 0.4	0.7 \pm 0.3	1.0 \pm 0.5	0.8 \pm 0.4
Na ⁺ (mg L ⁻¹)	6.2 \pm 2.8	2.2 \pm 1.4	7.4 \pm 3.6	2.5 \pm 2.8
Peat depth (m)	1.8* \pm 1.0	3.6* \pm 1.7	0.8 \pm 0.4	1.0 \pm 1.6
Species richness	18.0* \pm 2.0	11.0* \pm 2.4	15.5* \pm 2.5	8.5* \pm 2.0
Species evenness	0.71 \pm 0.1	0.79 \pm 0.1	0.72 \pm 0.1	0.70 \pm 0.1
Shannon diversity	2.0 \pm 0.3	1.7 \pm 0.3	1.9* \pm 0.2	1.4* \pm 0.3
Simpson diversity	0.8 \pm 0.1	0.8 \pm 0.1	0.8* \pm 0.1	0.7* \pm 0.1

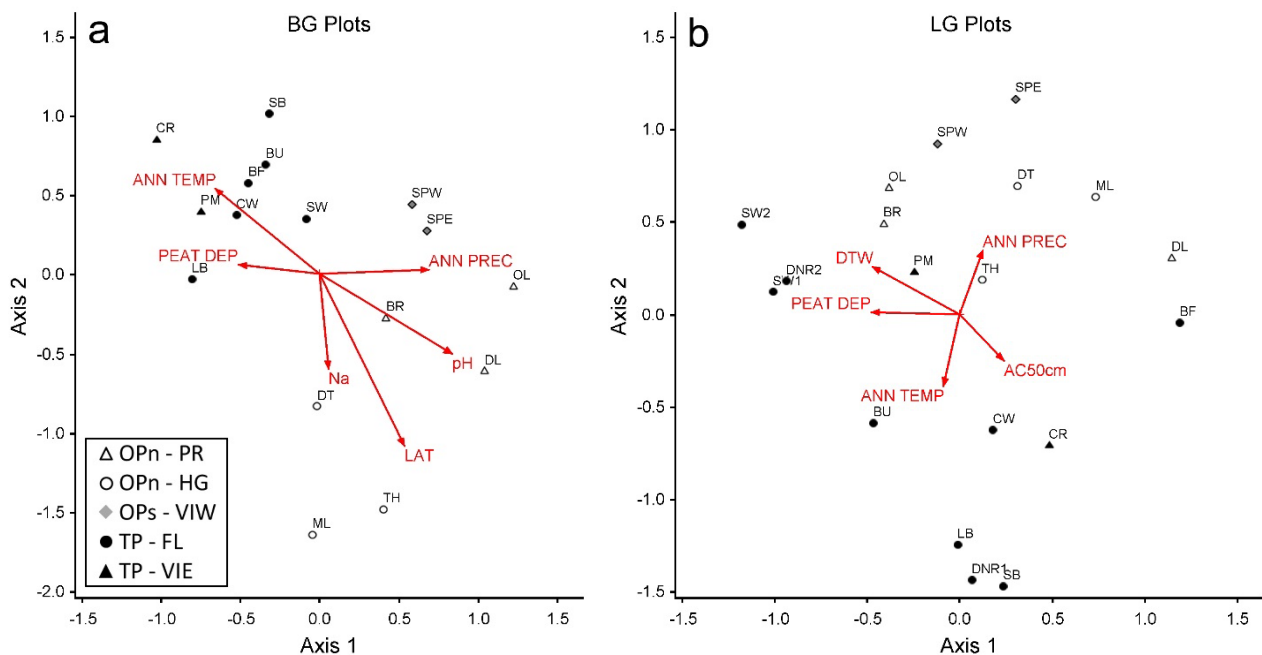


Figure 6. Non-metric multidimensional scaling (NMS) ordination and joint plot of plant species composition and abundance (average of the two paired plots) and environmental variables (for primary transect only) in BG plots and LG plots. The BG plot data for the DNR site is not included because hydrochemistry and water level data are missing. See Figure 1 for site codes. The vector arrow lengths are proportional to the strength of the correlation between the environmental variables and vegetation plot dissimilarities. Vector scaling: 100 %. Joint plot cutoff r^2 value: 0.200; variables with correlations below 0.200 are not displayed on the biplots. ANN TEMP is mean annual temperature, ANN PREC is mean annual precipitation, LAT is latitude, PEAT DEP is peat depth, Na is Na⁺ concentration, DTW is depth to water table, and AC50 is fraction of inorganic material at 50 cm below the soil surface.

DISCUSSION

Regional differences in species diversity of coastal bogs and lags

In many of our study sites, lags form a distinct ecotone between the bog and surrounding forest, similar to observations by Paradis *et al.* (2015) for lags in New Brunswick on the Atlantic coast. However, the Beta Diversity analysis showed that bogs of the Pacific Temperate wetland region have lagg plant communities that are more distinct from their respective central bog assemblages, while bogs in the Pacific Oceanic wetland region generally lack distinct lagg vegetation and share species with the bog and the surrounding wet forest. This may occur partly because Pacific Temperate lags contain fewer species and have lower diversity values. However, bogs in the Pacific Temperate wetland region are also more frequently confined topographically at the margins by an upland or a watercourse (Howie & van Meerveld 2016), which results in ponding of water and a water table at or above the surface in the lagg during the wet season. During the dry summer season when the adjacent bog cupola releases little or no water (Howie *et al.* 2009, Howie & van Meerveld 2012), the water table in the lagg often declines to a deeper position below the surface than in the bog proper, possibly due to the greater uptake of water by taller and more vigorous shrubs and trees. The greater water table fluctuations in the lagg (Howie & van Meerveld 2012), as well as the higher fraction of inorganic material in the lagg peat samples (Howie & van Meerveld 2013), promotes the establishment and predominance of swamp species such as *Spiraea douglasii*, which was not observed in the Pacific Oceanic sites. In the flat and low relief of the bogs in the Pacific Oceanic wetland region, the topographic change at the bog margin is often gradual, and thus the distinct lagg ecotone is often not present. However, sharp topographic depressions and distinct lagg plant ecotones do occur at the margins of some bogs in this wetland region as well (e.g. Diana Lake and Mayer Lake bogs). The high rainfall, cooler summers, and shorter dry periods in this region may result in a higher water table at the bog margin and contribute to the establishment and survival of bog species in the lagg and even in the adjacent forest.

Influence of regional and local variability in environmental conditions on plant species composition

Generally, species assemblages in the bog and lagg plots differed between the Pacific Oceanic (cooler, wetter climate) and Pacific Temperate (warmer, drier

climate) wetland regions (Figures 3, 4, 6). In a study of peatlands on Vancouver Island, Golinski (2004) similarly found that bog plant communities were different for the Pacific Oceanic and Pacific Temperate wetland regions, suggesting a regional control on species composition.

Based on the NMS biplots, both bog and lagg plant community composition and structure are linked to a combination of interrelated regional factors (e.g. latitude and climate) and local factors (e.g. depth to water table and hydrochemistry). Climatic variables, such as mean annual precipitation and mean annual temperature, as well as climate-related factors such as hydrochemistry and peat depth, had the strongest effect on the variability in plant species composition and abundance for the bog plots. Site-level factors such as early-summer depth to water table, peat depth, and fraction of inorganic material in peat samples were important factors for lagg species composition, but mean annual precipitation and mean annual temperature were also influencing factors. We expected the plant assemblage in the lagg to be more strongly influenced by site-level factors than plant assemblages in the adjacent bog because lags may receive runoff from adjacent mineral soils and because lagg peat often contains more inorganic material. For example, the fraction of inorganic material in peat samples from our study sites was 0–56 (mean: 6) and 0–73 (mean: 13) times higher in the lagg than in the bog at 10 and 50 cm depths, respectively (Howie & van Meerveld 2013). Depth to water table had indeed the longest biplot arrow in Figure 6b; peat depth and fraction of inorganic material in peat samples at 50 cm depth were also important factors. However, pH, Na⁺, Ca²⁺, Mg²⁺, EC_{corr}, and fraction of inorganic material in peat samples at 10 cm depth are not shown in Figure 6b because their correlations were below the joint plot cutoff r^2 value of 0.200. This suggests that these factors have less influence on plant species composition in the studied lags. Considering the relatively short lengths of the vectors in Figure 6, particularly for the LG plots, lagg plant community composition is probably also affected by factors that were not included in this study, such as concentrations of nitrogen, phosphorus and potassium, solute fluxes, light/shade, the difference in depth to water table between the wet and dry seasons, or the period that a site is inundated. Asada *et al.* (2003), for example, found that the position of the lowest water table and the length of time that the water table was below a certain depth had the strongest effect on plant species composition in Diana Lake Bog. Measurement of N, P, and

K concentrations and annual fluctuation of the water table in lags is therefore recommended.

Large-scale regional patterns in plant species composition and abundance are generally related to climate (Purves *et al.* 1992). For bogs, precipitation characteristics (i.e. annual rainfall, growing season rainfall, length of drought, and precipitation chemistry) are particularly important because bogs are ombrotrophic and thus highly dependent on precipitation for water and mineral nutrient inputs (Jeglum 1971, Ivanov 1981, Wheeler & Shaw 1995). Temperature is also an important factor because evapotranspiration lowers the water table during dry periods (Price *et al.* 2003, Waddington *et al.* 2009). The NMS biplots (Figure 6) support these assumptions. For example, pH and Na⁺ concentrations were predictors of plant species composition and abundance in BG plots and depth to water table was a predictor in LG plots (Figure 6). The reason is that plants may be broadly adapted to climatic attributes but they experience them through the characteristics of their local environment.

The significantly higher species richness in bogs and lags of the Pacific Oceanic wetland region (as well as significantly higher Shannon and Simpson diversity in the LG plots) may also be related to precipitation chemistry by way of its effect on peat and pore-water chemistry. It is well established that plant species diversity is correlated with mineral nutrient concentrations of peat (Jeglum 1971, Vitt & Chee 1990). For example, Riley (2011) found that sites with pH ≥ 4.9 displayed an abrupt increase in plant species richness compared to sites with pH < 4.8 . In this study, pore water pH was significantly higher and Na⁺ concentrations were (almost significantly) higher in bogs of the Pacific Oceanic wetland region. Both factors suggest a higher mineral nutrient availability in bogs of the Pacific Oceanic wetland region and may enable a greater variety of species than in Pacific Temperate wetland region bogs. Notably, concentrations of Mg²⁺ and Ca²⁺ were not significantly related to either bog or lagg species diversity, nor did they differ significantly between the two coastal wetland regions. The stronger correlations for Na⁺ are expected because Na⁺ concentrations are higher in coastal bogs owing to the oceanic influence, whereas continental bogs are more influenced by dustfall from cultivated areas, which would result in increased Ca²⁺ and Mg²⁺ concentrations (Gorham *et al.* 1985).

Species distribution in the region is also related to biogeography and historical factors such as the time since the last glaciation. For example, *Spiraea*

douglasii is mostly absent from Haida Gwaii (Ricklefs & Schluter 1993) and was not found in the BG and LG plots on Haida Gwaii. Such regional patterns of distribution clearly also influence the species richness and species dominance of plant communities.

Implications for conservation and management

Lags are important, not only because they play a role in supporting the water mound of a raised bog, but also because they increase the biological diversity of the raised bog ecosystem. This study shows that the combination of the bog and lagg plant communities differs throughout coastal British Columbia, making these ecosystems important islands of plant diversity within the forested matrix. Representative bogs for conservation must be chosen on a sub-regional level and should consider the bog-lagg vegetation combinations, not only the vegetation of the central bog, as a measure of diversity.

Our observations identify key natural restoration targets for lags in the different wetland regions and more specifically in different geographic sub-regions. Figures 3 and 4 provide a summary of target species assemblages for bog and lagg plant communities, respectively. Our results also identify the environmental gradients that are associated with the target plant communities (Table 1). More importantly, these results provide peatland managers with an indication of the most important environmental factors to consider for bog and lagg conservation/restoration.

Clearly, one prescription does not fit all situations and species that are key and dominant in one region may not be so in others, *Spiraea douglasii* being a good example. Measurements of peat depth, water table position, and pore water chemistry are needed prior to the development of a restoration plan and may inform the choice of species. These factors need to be measured at a relatively high spatial resolution, considering the specific gradients for each of the lagg plant assemblages. Should the associated factors not be suitable for any known lagg plant assemblage then actions to adjust them (such as raising the water table or reducing minerotrophic influences) will probably be required.

In general, knowledge of regional and local variability in coastal lowland bog and lagg plant communities is vital to the development of bog restoration plans and the delineation of conservation boundaries that include the lagg. This study also highlights the importance of conserving a representative diversity of bogs and lags in other regions of the world.

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