

Plant community and diversity change due to localized permafrost dynamics in bogs of western Canada

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Abstract: Localized permafrost formation and melt at the southern limit of permafrost has a large effect on boreal bog plant community structure and diversity in continental western Canada (Alberta, Saskatchewan, and Manitoba). Non-metric multidimensional scaling ordinations show that non-permafrost-affected bogs, areas currently underlain by permafrost (frost mounds), and areas of permafrost degradation (internal lawns) have distinct plant communities. Bryophytes respond more strongly than vascular plants to lengthened environmental gradients in the bogs studied. Seventy-two vascular plant and bryophyte species were found, with mean alpha diversity (species richness) similar in bogs and internal lawns (22.6 and 22.1) and lowest on frost mounds (15.6). Beta diversity (species turnover between landforms) is greater for bryophytes (4.22) than vascular plants (2.54). Comparisons within internal lawns show highly variable height above water table, community composition, and species diversity in wet communities and reduced variability as peat accumulates and converges on dry surfaces dominated by *Sphagnum fuscum* (Schimp.) Klinggr. Overall, localized permafrost dynamics increase bog plant diversity by 47% by introduction of unique dry, shaded (frost mound) and wet, open (internal lawn) conditions absent from non-permafrost-affected bogs, making localized permafrost bogs one of the most bryologically diverse peatland types in western Canada.

Key words: peatlands, bryophytes, plant communities, non-metric multidimensional scaling ordination, permafrost, climate change.

Résumé : La formation de permafrost et de fonte, à la limite sud du permafrost, exerce une grande influence sur la structure et la diversité des communautés végétales des tourbières boréales de l'ouest continental canadien (Alberta, Saskatchewan et Manitoba). Des ordinations non métriques multidimensionnelles par échelons montrent que les tourbières non affectées par le permafrost, les sites à permafrost courant (palses) et les surfaces avec permafrost en dégradation (pelouses intérieures) portent des communautés végétales distinctes. Dans les tourbières étudiées, les bryophytes réagissent plus fortement que les plantes vasculaires aux gradients environnementaux accrus. On retrouve 72 espèces de plantes vasculaires et bryophytes, avec une alpha diversité moyenne (richesse en espèces) semblable dans les tourbières et les pelouses intérieures (22,6 et 22,1) et plus faible au dessus des palses (15,6). La bêta diversité (renouvellement en espèces selon le relief) est plus prononcée chez les bryophytes (4,22) que chez les plantes vasculaires (2,54). Une comparaison des pelouses intérieures montre une grande variabilité de la profondeur de la nappe phréatique, de la composition des communautés et de la diversité en espèces dans les habitats humides, ainsi qu'une variabilité réduite à mesure que s'accumule la tourbe, en convergeant vers des surfaces plus sèches dominées par le *Sphagnum fuscum* (Schimp.) Klinggr. En général, la dynamique d'un permafrost localisé augmente la diversité en espèces végétales de tourbière d'environ 46%, par l'introduction de conditions sèches, ombragées (palses) et humides, ouvertes (pelouses intérieures) uniques, qui sont absentes des tourbières non-affectées par le permafrost, faisant des tourbières à permafrost localisé un des types de site tourbeux le plus diversifié en bryophytes, de l'ouest canadien.

Mots clés : tourbières, bryophytes, communautés végétales, ordination non-métrique multidimensionnelle par échelons, permafrost, changement climatique.

[Traduit par la Rédaction]

Introduction

Permafrost is an important part of Canada's north, as Continuous and Discontinuous Permafrost Zones cover about half the country's land area (Heginbottom 1995). Permafrost is a ground temperature phenomenon, defined as earth mate-

rials that remain below 0°C for two or more years (Harris et al. 1988). As such, it is sensitive to environmental changes that affect ground temperature at the microclimate through regional-climate scales (Williams and Smith 1989), especially at the climatic limits of its occurrence. Thus, factors such as disturbance (that affects the local microclimatic conditions) and long-term regional climatic change determine whether it is aggrading, degrading, or is in equilibrium with its environment.

In the Discontinuous Permafrost Zone, permafrost occurs most commonly in treed boreal and subarctic peatlands. Permafrost landforms in peatlands have long been divided into two

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types based on morphology (Brown 1968): large expansive peat plateaus (completely underlain by permafrost), and small restricted landforms of isolated permafrost (treed frost mounds) in largely unfrozen peatlands (localized permafrost peatlands). The distribution of these two morphologies follows climate (Vitt et al. 1994; Halsey et al. 1997; Beilman et al. 2001), and localized permafrost peatlands occur at the southern limit of permafrost in continental western Canada (Alberta, Saskatchewan, and Manitoba). Permafrost at its climatic limit has value as a climate change indicator (Washburn 1980; Sollid and Sørbel 1998), and localized permafrost expansion in the southern boreal forest has been argued to have reached its maximum during the Little Ice Age (Vitt et al. 1994; Halsey et al. 1995). Localized permafrost in peatlands is degrading throughout its range (Vitt et al. 1994, 2000), creating areas of collapse called internal lawns. Permafrost has disappeared from some of these peatlands, mostly in the south of the localized permafrost peatland region (Beilman et al. 2001). Ongoing permafrost degradation has many potential, but largely unknown, ecological effects (Woo et al. 1992; Gorham 1994) and important ramifications for plant community structure and diversity.

Peatland plant communities have been moderately well studied in western Canada, and general plant communities were described in early studies (Lewis and Dowding 1926; Lewis et al. 1928; Moss 1953). More recent work has focussed on patterns of vegetation relative to environmental gradients across a range of different peatland types (Jeglum 1973; Kenkel 1987; Vitt and Chee 1990; Bubier et al. 1995), as well as within peatland types for fens (poor fens, Vitt et al. 1975; extreme-rich fens, Slack et al. 1980; moderate-rich fens, Chee and Vitt 1989), bogs (Belland and Vitt 1995), and peat plateaus (Horton et al. 1979; Camill 1999a). However, localized permafrost peatlands have not been investigated in detail (with the exception of a single frost mound (treed palsa) described by Zoltai and Tarnocai (1971)). To more fully understand the impact of past permafrost dynamics and ongoing degradation, investigation into ecological changes in localized permafrost bogs is needed.

This study describes patterns of plant community change in western Canadian continental bogs affected by localized permafrost dynamics. Specifically, I address two questions: (i) how do plant communities and diversity in localized permafrost bogs respond to permafrost formation and melt as determined through comparison of plant communities between continental bog, frost mounds, and internal lawns; and (ii) how do plant communities vary within internal lawns, and how do community and diversity patterns relate to peatland development following permafrost melt?

Study region and peatland sites

Localized permafrost peatlands occur in a wide belt across boreal continental western Canada and cover 17 505 km² (Beilman et al. 2001). This area largely falls within Zoltai et al.'s (1988) Continental High Boreal Wetland Region and is characterized by low precipitation (relative to coastal boreal wetland regions) and cold winters, where localized permafrost peatlands are a characteristic wetland type (referred to as palsa bogs by Zoltai et al. (1988)). To determine the effects of permafrost dynamics on vascular plant and bryophyte vegetation, three localized permafrost bogs were

selected for study in each of Alberta, Saskatchewan, and Manitoba from aerial photography of the whole region. These were chosen to have distinct frost mounds and internal lawns, reasonable accessibility, and to span the longitude of the region. These bogs occur where localized permafrost landforms are the dominant permafrost feature (peat plateaus occur only rarely nearby), in the south of the localized permafrost peatland region (Fig. 1). Regional climate and the degree of degradation are comparable for all three peatlands (Table 1).

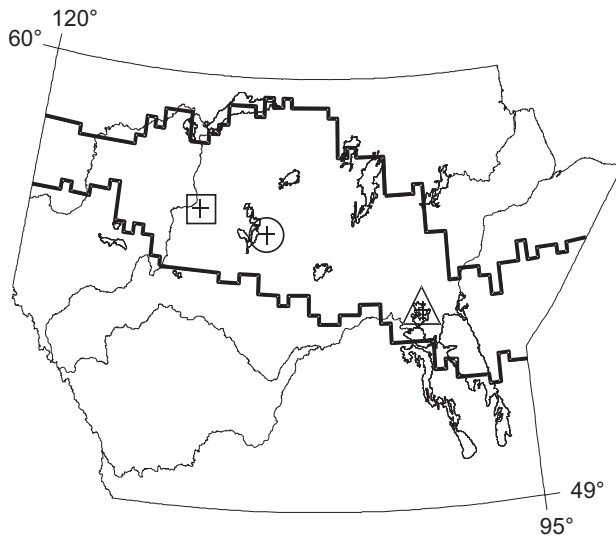
Materials and methods

Plant community surveys

Three distinct landforms were surveyed: continental bog (the background peatland matrix in which localized permafrost landforms occur), frost mounds, and internal lawns (Fig. 2). The vegetation of 10 landforms of each type was assessed in each peatland (with the exception of frost mounds at the Patuanak, Sask., peatland, where only 9 were found) for a total of 89 landform surveys. Bog vegetation was evaluated by locating random coordinate points from a grid overlain onto large-scale aerial photographs of each peatland. Frost mounds and internal lawns were randomly selected from the total accessible population of landforms in each peatland. For treed bog and frost mound surveys with relatively homogeneous vegetation, a 5 × 5 m plot was placed within a representative area of vegetation. Percent cover of all vascular plant and bryophyte species, and all lichens that had >1% cover, was estimated visually within each plot. Cover data were supplemented by a search for new species within a 25-m radius until no new species were found. Species that occurred outside the plots were assigned a cover value of 0.05% for abundance analyses. Internal lawns have the most variable vegetation and surface wetness conditions of the three landform types because of the effects of time-transgressive degradation, as well as variable degrees of collapse following melt (Beilman 2001), and could not be sampled accurately using 5 × 5 m plots. Instead, abundance values were estimated for each entire landform. Estimates of abundance were facilitated by the open, largely treeless nature of internal lawns. Internal lawn edges represent a transition between affected and unaffected bog, as pre-existing localized permafrost lenses thin out at their margins (Zoltai 1972). Therefore, a 1-m margin around the inside border of each internal lawn was excluded from surveys to ensure only vegetation affected by permafrost melt was included. Water samples from pools or excavated shallow pits in each bog and internal lawn plot were collected in acid-washed polyethylene bottles. Samples were refrigerated and the pH and conductivity (corrected for pH following Sjörs (1950)) of each sample were determined in the laboratory.

To determine the spatial variability in vegetation resulting from post-melt peatland development, an additional five internal lawns were chosen randomly in each peatland for finer scale survey. Internal lawns are typically oblong or irregular in shape (Fig. 2), and degrade along "melting fronts" following the initiation of melt, creating a newly collapsed area and an older area. To capture the range of conditions along this temporal or wetness gradient, a central transect was placed along the longest axis of each internal lawn. This transect was divided into 10 equal lengths, and a 2-m diameter round quadrat was randomly placed within each length (10 quadrats per internal lawn, 50 quadrats per peatland, 150 quadrats total). Within each quadrat, cover values of all vascular plants and bryophytes, and lichens that had >1% cover, were visually estimated. Height of the peat surface above the water table and microrelief were measured within each quadrat. Microrelief was estimated by measuring the height between the highest hummock top and the lowest hollow bottom within each quadrat.

Fig. 1. Continental western Canada with the outline of the localized permafrost peatland region (Beilman et al. 2001) and location of study sites: Anzac, Alberta (square), Patuanak, Saskatchewan (circle), and Moose Lake, Manitoba (triangle).



In all surveys, vascular plants and bryophytes were identified to species. True mosses and *Sphagnum* are treated separately, and “mosses” refer to non-*Sphagnum* mosses hereafter. Species names follow Moss (1983) for vascular plants, Ireland et al. (1987) for mosses and *Sphagnum*, Stotler and Crandall-Stotler (1977) for hepatics, and Esslinger and Egan (1995) for lichens.

Data analysis

Non-metric multidimensional scaling (NMDS) was used to compare plant communities from bog, frost mound, and internal lawn surveys. NMDS is a nonparametric dimension reduction technique that works without assumption of linear or unimodal response and escapes many of the distortions of eigenvector techniques (Kenkel and Orlóci 1986; Minchin 1987; Legendre and Legendre 1998). Sorensen (Bray–Curtis) distance was used as a general measure of ecological similarity (Faith et al. 1987) for all NMDS ordinations. To explore thoroughly the effects of permafrost dynamics on total bog vegetation as well as on the vascular plant and bryophyte components, four analyses were run using different data subsets: (i) abundance data for total vegetation including coverages for lichen species that had >1% cover (*Cladina mitis* (Sandst.) Hustich, *Cladina rangiferina* (L.) Nyl., *Cladina stellaris* (Opiz) Brodo) and coverages of bare peat; (ii) vascular plant and bryophyte presence–absence; (iii) vascular plant presence–absence; and (iv) bryophyte presence–absence. Differences in pH and conductivity between bog and internal lawn surface waters were determined by Mann–Whitney *U* tests (Zar 1999). Summary statistics and tests for pH were conducted on hydrogen ion concentrations and reported as pH.

To decrease the effect of the few *Sphagnum* species that dominated each of the small quadrats (and thereby increase the sensitivity of analyses to patterns in less common species), abundance values in the quadrat data set were square-root transformed. The 150 internal lawn quadrats were then classified using Sorensen distance between quadrats and flexible beta clustering ($\beta = -0.25$) (Legendre and Legendre 1998). Groups were named by their dominant vegetation (*Sphagnum* species). Abundance data from these quadrats were ordinated by NMDS. All multivariate analyses were implemented in PC-ORD (McCune and Mefford 1999).

Alpha, beta, and gamma diversity were assessed following the diversity concepts of Whittaker (1972). Alpha diversity was calculated as the mean number of species (richness) in bogs, frost

mounds, or internal lawns from the landform survey data or the mean number of species in each vegetation group for the internal lawn quadrat data. Beta diversity was calculated for both the landform survey and quadrat data as the ratio of total number of species in each data set to the mean richness across all sample units (all 89 landform surveys, or all 150 quadrats). Gamma diversity was defined as the total species richness from all surveys in all three peatlands and represents the landscape diversity of localized permafrost bogs. The equality of mean alpha diversity values between internal lawn quadrat groups was determined by Kruskal–Wallis *H* tests.

Results

Community–floristic ordinations, vegetation patterns, and water chemistry

Ordination of abundance data for the total vegetation (including lichen and bare peat cover) did not have a substantially lower stress value for solutions beyond two dimensions: final two-dimensional stress was 7.6. Landform groups are clearly separated, with bogs intermediate on the diagram, and frost mounds and internal lawns clearly separated at the ends of the first NMDS axis (Fig. 3A). Among-peatland differences are greatest in the frost mound and internal lawn vegetation, which is evident in the higher degree of closeness and clumping of localized permafrost landform data points from the same peatland compared with the more freely intergrading bog vegetation on the diagram. Broad vegetation patterns among landforms are shown by plotting tree cover values (*Picea mariana* (Mill.) BSP) and ground cover values (ground cover by *Sphagnum* spp., feathermosses (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp. in BSG, and *Ptilium crista-castrensis* (Hedw.) De Not.) and lichens) onto the ordination space (Figs. 3B–3E). Landform types differed markedly in tree cover (Fig. 3B) and were nearly always bryophyte-dominated in ground cover (ranging from *Sphagnum* to feathermoss dominance). Bog vegetation (unaffected by permafrost) was characterized by open *Picea mariana* and was always *Sphagnum* dominated. Frost mounds had *Picea* cover greater than that of bogs (more than double on average (Fig. 3B) often resulting in closed canopies) and had ground cover dominated by feathermosses (except for seven frost mounds in the Moose Lake peatland that were dominated by lichens of the genus *Cladina*; Figs. 3C and 3E). Internal lawn tree cover was less than 1% on average and did not exceed 3%. Sparse tree cover present was from stray collapse survivors or newly established spruce on older, drier surfaces. Groundcover in internal lawns was strongly dominated by *Sphagnum* (Fig. 3D), with much reduced cover by other mosses and a nearly complete exclusion of lichens (Fig. 3E). Two thirds of the internal lawns had *Sphagnum fuscum* (Schimp.) Klinggr. cover greater than 50%, and mean cover of *Sphagnum fuscum* in all internal lawns was 63.4%.

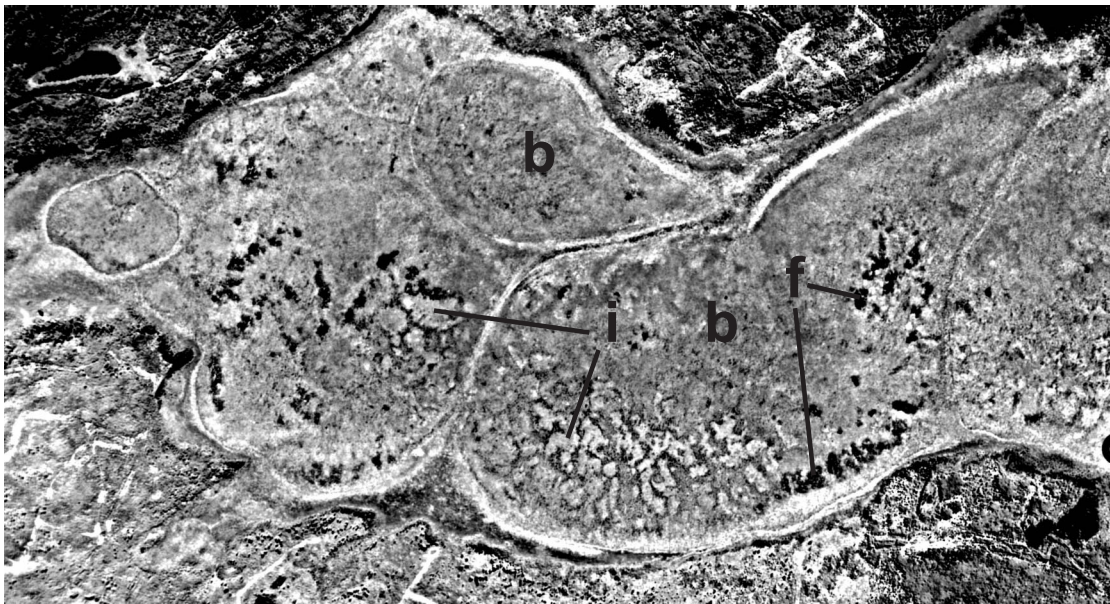
Surface water pH in bogs (mean 3.65) and internal lawns (mean 4.02) ranged between 3.08 and 4.49 and was significantly different ($P < 0.001$) between the two landforms. Surface water corrected conductivity (bog mean 15.0 $\mu\text{S}/\text{cm}$; internal lawn mean 52.2 $\mu\text{S}/\text{cm}$) was also significantly higher after permafrost collapse ($P < 0.001$). The pH and conductivity are shown plotted within the vegetation ordination space in Fig. 4.

Table 1. Climate and physiography of three localized permafrost bogs studied.

		Anzac Bog, Alberta	Patuanak Bog, Saskatchewan	Moose Lake Bog, Manitoba
Climate	Mean annual temperature (°C)	-0.4	-1.0	-1.2
	Mean annual precipitation (mm)	472	444	496
Peatland	Bog form*	Flat bog	Plateau bog (islands)	Plateau bog (islands)
	Total permafrost landform cover (ha)	11.084	9.424	17.411
	Mean permafrost landform size (ha)	0.198	0.248	0.295
	Extent of degradation (%)	60.3	65.5	53.2

Note: Permafrost landform (frost mound and internal lawn) areas were calculated by mapping small-scale aerial photography taken between 1987 and 1995 and digitizing in ArcInfo. Climate data is taken from 1951–1980 climate normals (Environment Canada 1982) from the nearest permanent climate station to each peatland, except for mean annual temperature at Patuanak that follows interpolated mean annual temperatures corrected for elevation from Vitt et al. (1994) because of the lack of available nearby temperature data.

*After Zoltai et al. (1988).

Fig. 2. Aerial photograph of the Moose Lake, Manitoba, localized permafrost bog. Treed frost mounds (f) and internal lawns (i) occur within the continental bog (b) matrix.

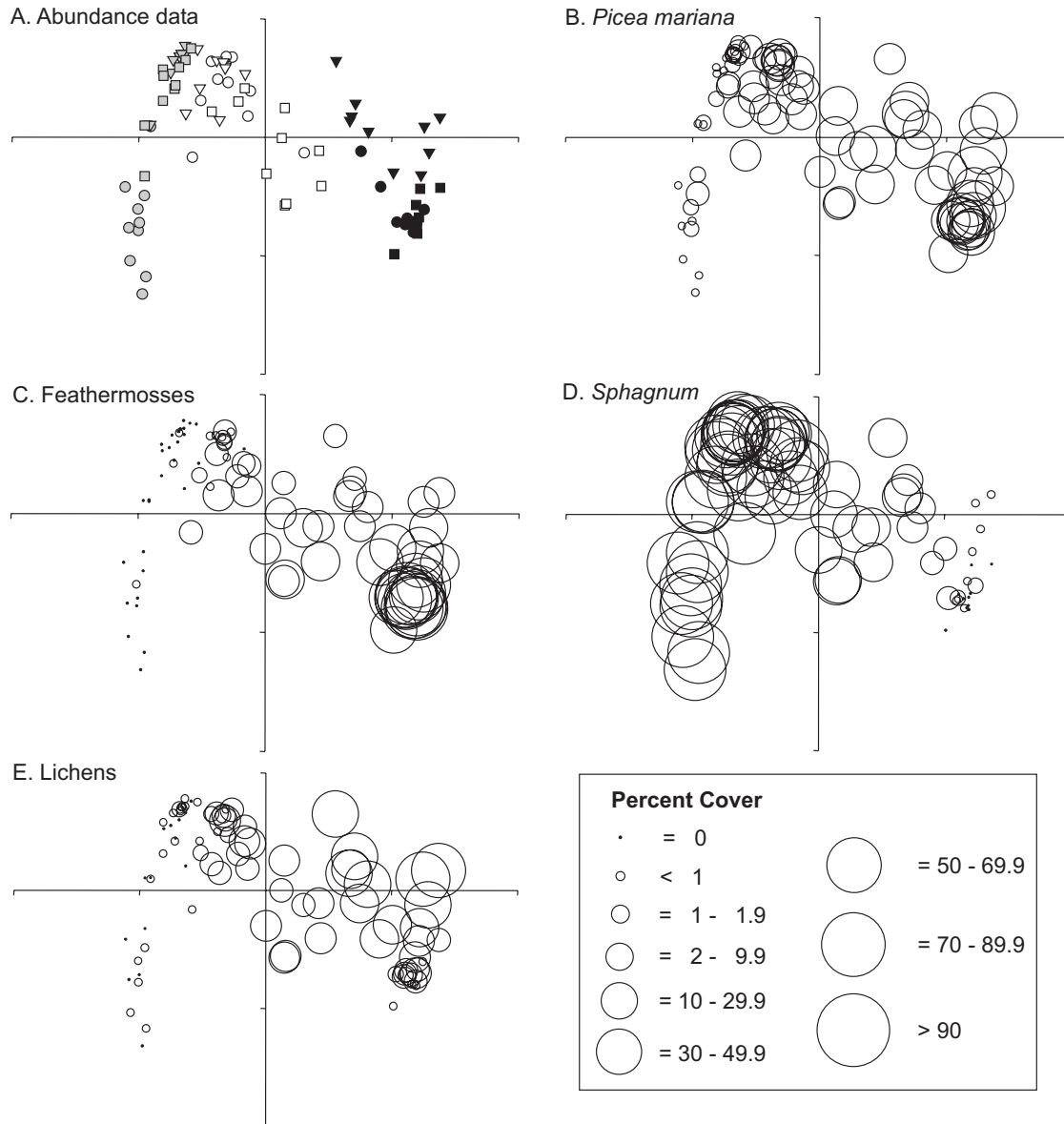
Ordination of landform survey data based only on the presence–absence of species using both vascular plant and bryophyte species also shows distinct separation of frost mounds from internal lawns, although some overlap occurs between bogs and internal lawns (Fig. 5A). Among-peatland differences (within landform types) are not as clearly expressed in the floristic data as in the abundance data (compare Figs. 3A and 5A), and landform types from the different peatland sites overlap more freely when only presence–absence is used. Separate floristic analyses of the vascular plant and bryophyte vegetation components by NMDS show that much of the landform separation and general pattern in the total vegetation data comes from the bryophyte component of the data (Fig. 5C) and less from the vascular plant component (Fig. 5B). Vascular plant species ordination had a final stress of 16.59, and bryophyte species had a final stress of 22.06; both had the best solution in two dimensions. Both ordinations show a distinct position of frost mounds from bogs and internal lawns in the ordination space. However, the vascular plant analysis shows strong floristic overlap of *Sphagnum*-dominated bogs and internal lawns.

Diversity

Seventy-two vascular plant and bryophyte species were en-

countered in the three localized permafrost bogs (Table 2; list provided in Appendix). Comparison of species diversity among landforms reveals that mean alpha diversity is similar in bogs and internal lawns and lower in frost mounds (decrease of 31% from bog; Table 3). This decrease due to permafrost aggradation is due to reduction in the number of vascular plant, *Sphagnum*, and hepatic species, as moss diversity increased and was highest in frost mounds. Vascular plant diversity is nearly double in internal lawns relative to frost mounds because of presence of common bog species in addition to *Betula pumila* L., *Scheuchzeria palustris* L., and species of *Carex*, plants common in poor fens (Vitt et al. 1975) and absent from bog surveys. Internal lawn vascular plant diversity was higher than that of the bog matrix. *Sphagnum* diversity was much higher in internal lawns compared with frost mounds and also exceeded that of the bog surveys because of the introduction of species that were either rare or absent from the bogs (*Sphagnum jensenii* H. Lindb., *Sphagnum obtusum* Warnst., and *Sphagnum lindbergii* Schimp. ex Lindb.). Hepatic diversity was highest in *Sphagnum*-dominated bogs and internal lawns, although cover values were greatest in frost mounds because of the presence of large mats of *Myliia anomala* (Hook.) Gray. Moss diversity was lowest in internal lawns (Table 3). Beta diversity was greatest

Fig. 3. (A) Non-metric multidimensional scaling (NMDS) ordination of total species abundance data from bog (open symbols), frost mound (solid symbols), and internal lawn (shaded symbols) landform surveys from three peatlands; Anzac, Alberta (squares); Patuanak, Saskatchewan (circles); and Moose Lake, Manitoba (triangles). Tree cover by *Picea mariana* (B) and ground cover by feathermosses (C), *Sphagnum* spp. (D), and lichen (E) in each survey are shown on the ordination space.



for true mosses and hepatics, with lower values for *Sphagnum* and lowest values for vascular plants (Table 3).

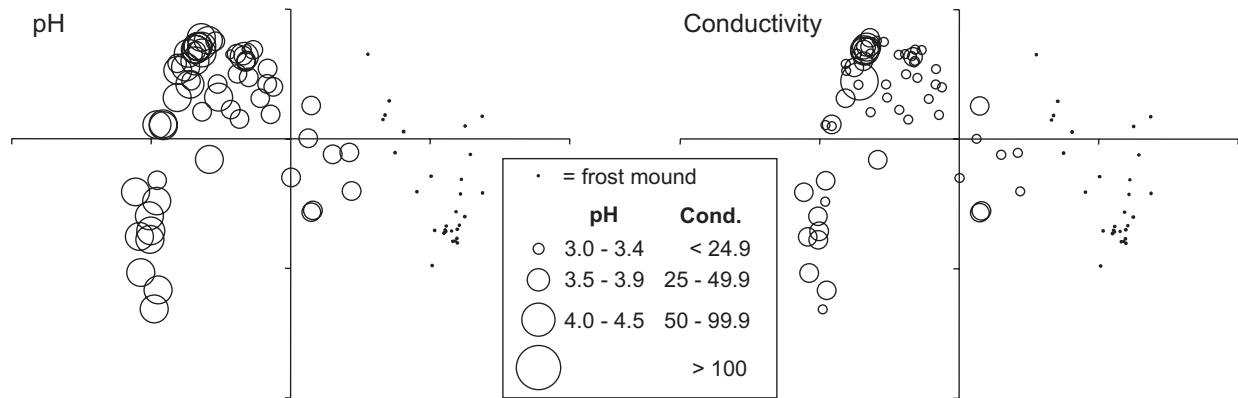
Internal lawn plant communities

Quadrats within internal lawns were divided into six groups by cluster analysis (Fig. 6) and named for their dominant (*Sphagnum*) species. Nearly two-thirds of the quadrats were strongly *Sphagnum fuscum* dominated (greater than 90% cover, on average). Another 20 quadrats included *Sphagnum fuscum* as a dominant species (>50%), but also included high cover of *Sphagnum magellanicum* Brid., *Sphagnum russowii* Warnst., and *Sphagnum angustifolium* (C. Jens ex Russ.) (named mixed *Sphagnum fuscum*). Twenty quadrats

were dominated by *Sphagnum angustifolium*, although these also included up to 20% coverage by *Sphagnum riparium* Ångstr. Six quadrats were *Sphagnum riparium* dominated, three quadrats were *Sphagnum russowii* dominated, and a single quadrat had 98% *Sphagnum jensenii* cover. The NMDS ordination of the internal lawn quadrats supports the groups from the cluster analysis (Fig. 7) and had a final two-dimensional stress of 13.8. The 98 *Sphagnum fuscum* quadrats are closely clustered on the right side of the diagram, whereas the remaining quadrats show greater compositional variability on the left of the diagram.

Ordering internal lawn plant community groups by increasing height above water table shows that microrelief had its

Fig. 4. Surface water pH and corrected conductivity from bog and internal lawn surveys plotted on total abundance data NMDS space. Dots are frost mounds (frozen peat with no surface water).



greatest value in the mixed *Sphagnum fuscum* group and was slightly less in the *Sphagnum fuscum* group (Fig. 8). Mean alpha diversity of all vascular plant and bryophyte species does not significantly change between groups ($P = 0.60$). When separated into vascular plant and bryophyte components, opposite trends in species richness are evident; vascular plant richness slightly increases with height above water table ($P < 0.001$), while bryophyte richness slightly decreases, although the decrease is not significant ($P = 0.20$). Variability in height above water table and mean alpha diversity (total, vascular plant, and bryophyte) decreases along the vegetation sequence (Fig. 8).

Discussion

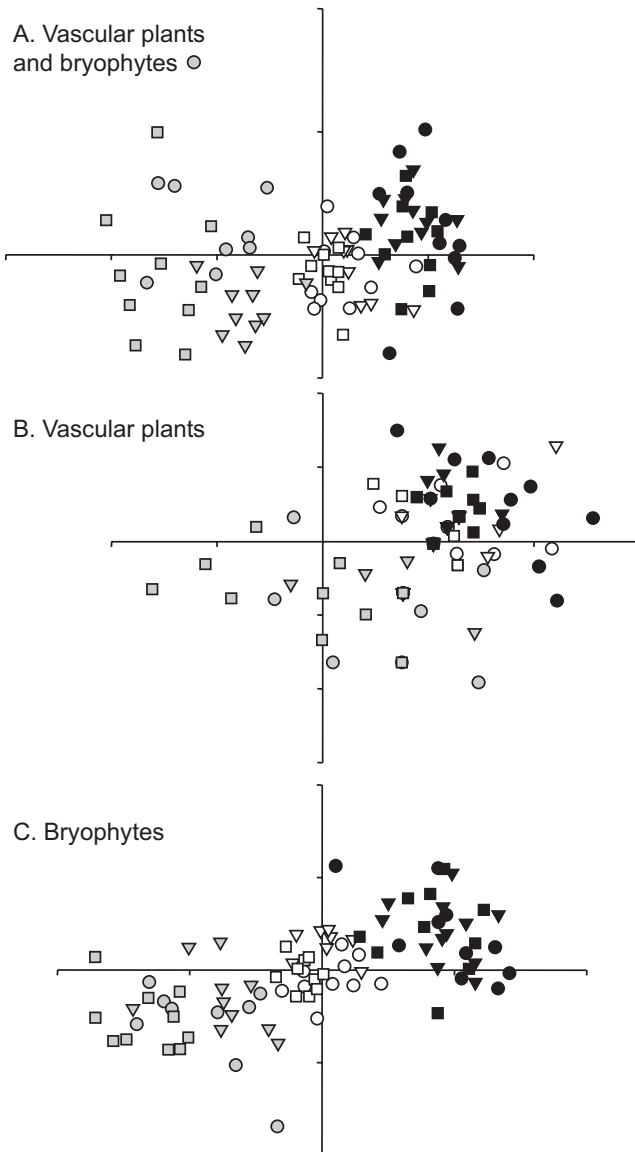
Gradient analyses across North American peatland types show that peatland vegetation patterns are strongly affected by surface water chemistry and wetness gradients (Kenkel 1987; Glaser et al. 1990; Vitt and Chee 1990; Jeglum and He 1995). In the continental bogs of western Canada, water chemistry gradients are truncated (relative to rich fens) and other environmental factors such as shade and dryness have a greater effect on vegetation (Belland and Vitt 1995). In contrast to permafrost that occurs in dry Continuous Zone bedrock or Discontinuous Zone upland soils, the abundance of water in saturated subsurface peat leads to the elevation of permafrost-underlain surfaces above water tables resulting from the volumetric expansion and buoyancy of ice (Zoltai 1972). Soil conditions on frost mounds become free from water table influence, and depth to permafrost (active layer) is typically about 60 cm but can be over 100 cm (Zoltai and Tarnocai 1971; Zoltai 1972). *Picea mariana* growing in peat responds strongly to decreased water tables (Dang and Lieffers 1989; Lieffers and MacDonald 1990), and increased tree vigor results in a more shaded ground cover (Fig 3B). Degradation of localized permafrost results in collapse of the frost mound surface to below that of the surrounding bog, creating open conditions that are clearly evident on aerial photographs when trees are drowned (Vitt et al. 1994). Localized permafrost aggradation and degradation at the southern limit of permafrost thus has a great influence on peatland vegetation, as frost mounds and internal lawns form the driest-shadiest and wettest – most open conditions, respectively, that occur in Canadian continental bogs.

Community–floristic ordinations and vegetation patterns

The clear separation of landform types on the total vegetation abundance data ordinations (Fig. 3A) shows that the landform groups are well supported by the vegetation data and that localized permafrost aggradation and degradation result in landforms with distinct plant communities. Separation is complete between frost mounds and internal lawns on both total species abundance and floristic ordination diagrams (Figs. 3A and 5A) clearly representing the non-wetland conditions that can be created by permafrost aggradation, and the unique, wet conditions created by permafrost melt. The position of frost mounds are most distinct in the ordinations because of their unique vegetation and low diversity. Change in tree cover between landforms is impressive (Fig. 3B) and of importance in its effect on peatland habitat (*P. mariana* is the only source of large physiognomic structure in bogs), the influence on understory vegetation (Zoltai and Tarnocai 1971; Belland and Vitt 1995; Camill 1999a), and potential changes in net primary production and aboveground biomass due to increased tree vigor. The dense tree cover, feathermoss–lichen groundcover, and isolation from peatland water tables make frost mound plant communities more similar to boreal upland black spruce ecosystems than wetlands (cf. LaRoi and Stringer 1976). Permafrost degradation in boreal peatlands can proceed quickly once initiated (Thie 1974; Engelfield 1994); thus, the large community change that occurs when permafrost degrades (evident in distance and separation between frost mound and internal lawn points in Fig. 3A and 5A) is very fast. Since linear collapse rates are faster in warmer regional climates (Camill and Clarke 1998), these large community changes may occur even more rapidly with increases in mean annual temperature predicted for the region over the next century (Boer et al. 2000).

Plant community change in boreal forest ecosystems (at temporal scales from decades to centuries) is strongly affected by disturbance from fire (Johnson 1992; Payette 1992). Although fire also occurs frequently in boreal peatlands (Wein 1983; Zoltai et al. 1998), macrofossil evidence shows that bogs recover quickly from fire with tree cover and *Sphagnum* groundcover returning quickly to pre-fire conditions (Kuhry 1994). Permafrost degradation, on the other hand, results in longer, more pronounced changes in the macrofossil record (Zoltai 1993; Camill 1999b; Beilman

Fig. 5. NMDS ordinations of presence–absence data for vascular plants and bryophytes (A), vascular plants only (B), and bryophytes only (C) from continental bog (open symbols), frost mound (solid symbols) and internal lawn (shaded symbols) surveys. Symbol shapes indicate surveys from Anzac, Alberta (squares); Patuanak, Saskatchewan (circles); and Moose Lake, Manitoba (triangles).



2001). Frost mound collapse after permafrost melt is likely the greatest disturbance that occurs in boreal and subarctic ombrogenous peatlands. This likely is greatest when melt is initiated by fire that results in combustion and loss of surface peat (and therefore greater depth of collapse relative to water table upon melt). The magnitude of this disturbance is evident in the significant increases in pH and conductivity between bogs and internal lawns. This suggests that internal lawns in bogs can collapse to the degree that they become geogenous (are influenced by minerotrophic ground water) and are in fact small areas of poor fen. This is further supported by the occurrence of *Sphagnum jensenii* and *Cladopodiella fluitans* (Nees.) Joerg. in wet internal lawns, species

that Vitt and Belland (1995) recommend as poor fen indicators. It is likely that minerotrophic conditions, when they do occur, are limited to newly melted landforms and that ombrogenous conditions return after a given amount of peat accumulates.

Among-peatland differences are clearly evident in the abundance data and less distinct in the floristic data and show that differences between peatlands are more strongly expressed in changes in the cover of species that occur in all three peatlands, rather than in the addition or removal of species between peatlands. Among-peatland differences in frost mound plant communities are related to the degree of environmental change caused by permafrost aggradation. For example, Zoltai and Tarnocai (1971) found that the densest and tallest tree growth was associated with the thickest permafrost on a frost mound. Differences in the magnitude of permafrost aggradation among peatlands is determined by past conditions, including site-specific hydrology and plant communities (that affected surface thermal balances when permafrost formed), and regional climate patterns during the Little Ice Age (that may have been substantially different from present patterns). Differences in internal lawn vegetation among peatlands are closely related to the permafrost conditions expressed in the frost mound vegetation data and the amount of time passed since degradation (increased time for peat accumulation and succession). Since permafrost aggradation also affects the composition of the peat (Zoltai 1993) and the rate at which it vertically accumulates relative to undisturbed peat accumulation in the surrounding peatland (Robinson and Moore 2000; Turetsky et al. 2000), differences in permafrost conditions determine the degree of landform collapse when permafrost melts. Among-peatland differences in frost mound and internal lawn plant communities are attributable to differing permafrost conditions, as well as asynchronous degradation.

Continental bogs are floristically simple and relatively consistent ecosystems, with the lowest bryophyte diversity of all peatland types in continental western Canada (Vitt et al. 1995) and low vascular plant diversity compared with coastal bogs (Glaser 1992). Bryophyte diversity in continental bogs is strongly associated with microhabitat heterogeneity (Vitt et al. 1995). Frost mounds lack the dryness gradient present along the peatland hummock–hollow sequence, evident in the decreased mean alpha diversity values for frost mounds compared with bogs. However, the abundance of shaded, cool forest floor and tree base microhabitats results in increased forest floor moss diversity on frost mounds (species of *Ceratodon*, *Dicranum*, and feathermosses (*Ptilium* and *Hylocomium*) that are more uncommon in bogs). Internal lawn mean alpha diversity (particularly *Sphagnum* diversity) is greater than that of frost mounds because of the presence of the peatland dryness gradient. In internal lawns, this gradient is lengthened because of the presence of very wet, nearly aquatic conditions in newly (or more substantially) collapsed areas and the presence of carpet vegetation. Mean moss diversity, however, is very low in internal lawns (Table 3). Since the availability of microhabitats in peatlands is strongly affected by the presence of trees (of the nine peatland microhabitats named by Vitt et al. (1995), four are associated with tree bases), moss diversity will likely rebound following tree establishment and growth.

Table 2. Gamma or landscape diversity (total number of species) from three localized permafrost bogs in western Canada by plant group and landform type.

	Bog	Frost mound	Internal lawn	All landforms
Vascular plants	11	13	19	20
Bryophytes	38	32	37	52
Mosses	16	19	14	25
<i>Sphagnum</i>	9	4	10	11
Hepatics	13	9	13	16
Total	49	45	56	72

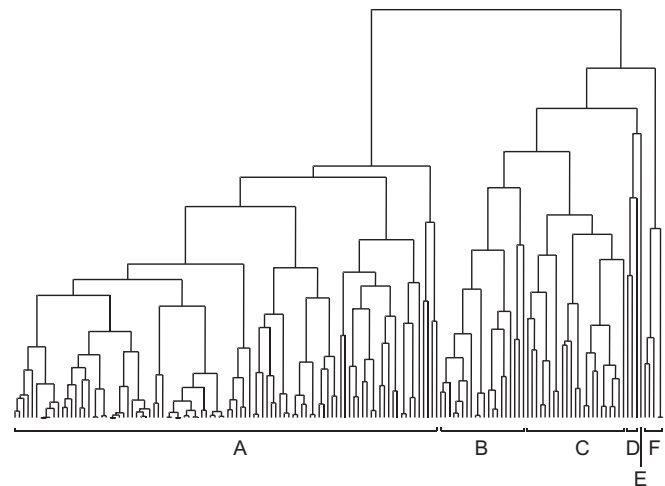
Table 3. Summary of mean alpha diversity (number of species) and beta diversity (species turnover) from bog, frost mound, and internal lawn surveys.

	Bog	Frost mound	Internal lawn	All landforms	Beta diversity
Vascular plants	8.3	5.4	9.8	7.9	2.54
Bryophytes	14.3	10.2	12.3	12.8	4.22
Mosses	5.3	6.3	2.6	4.7	5.51
<i>Sphagnum</i>	4.1	1.1	5.9	3.8	2.93
Hepatics	4.9	2.8	3.8	3.8	4.44
Total	22.6	15.6	22.1	20.2	3.66

Internal lawn plant communities

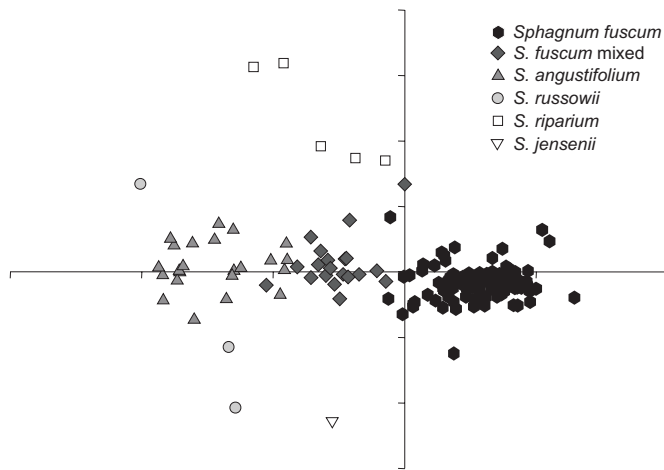
Peat accumulation rates following permafrost melt in internal lawns exceed those in non-permafrost-affected bogs (Turetsky et al. 2000), a phenomenon also observed in more northern collapse scars within peat plateaus (Camill 1999b). Resultant accelerated changes in internal lawn surface height above water table drives post-melt plant community succession quickly (Zoltai 1993; Camill 1999b; Beilman 2001). The strong groups recognized by cluster analysis reflect both the *Sphagnum*-dominated nature of internal lawn vegetation in bogs, as well as the well-defined niche space of *Sphagnum* along the wetness gradient (Horton et al. 1979; Vitt and Slack 1984). The large number of quadrats dominated by dry-adapted *Sphagnum fuscum* is indicative of accelerated temporal change in internal lawns as peat quickly accumulates (also supported by the abundance of *Sphagnum fuscum* in internal lawns in the landform surveys). Organization of these groups by their mean height above water table reflects the developmental series from wet to dry taking place in internal lawns following permafrost collapse. These mean height above water table values (Fig. 8) are supported by those reported from autecological studies of *Sphagnum* species' tolerances and optima relative to peatland water tables (Gignac et al. 1991). Microrelief increases along this series, as newly collapsed surfaces have even microtopography resulting from very wet conditions and the occurrence of wet-adapted sphagna occurring in carpets (*Sphagnum jensenii*) and lawns (*Sphagnum riparium* and *Sphagnum angustifolium*). Further peatland development and establishment of hummock-forming species at higher levels above the water table brings increased microtopography. The slight decrease in microrelief when vegetation becomes strongly dominated by *Sphagnum fuscum* represents the loss of hollow microhabitat within the area captured by quadrats.

Most diversity change across the sequence is captured in the beta diversity (species turnover) values, as total mean alpha diversity does not change significantly. Beta diversity is greatest in bryophytes regardless of nonsignificant mean al-

Fig. 6. Dendrogram of the flexible beta ($\beta = 0.25$) cluster analysis (Sorensen distance) of 150 internal lawn quadrats following square-root transformation of abundance data. The six strongest groups are shown and correspond to dominance by *Sphagnum fuscum* (A), mixed *Sphagnum fuscum* (B), *Sphagnum angustifolium* (C), *Sphagnum russowii* (D), *Sphagnum jensenii* (E), and *Sphagnum riparium* (F).

pha diversity changes, largely resulting from the localized sensitivity of bryophytes to microhabitat wetness compared with rooting vascular plants. Thus, the greatest diversity in any internal lawn occurs when this dryness gradient is maximized, i.e., melt sites that have both recently degraded and older, drier surfaces. This time-transgressive pattern of permafrost melt within individual internal lawns is common across the study region and is most evident in features with recently degraded surfaces. The period of high variability in mean alpha plant diversity and dryness following permafrost melt and initial peatland development is followed by reduced variability as surfaces converge on *Sphagnum fuscum* dominated vegetation. The eventual establishment of trees in

Fig. 7. NMDS ordination of 150 internal lawn quadrats (abundance data). Quadrat groups follow cluster analysis results in Fig. 6.



internal lawns will re-introduce associated microhabitat conditions and likely increase moss diversity towards bog values (Table 3).

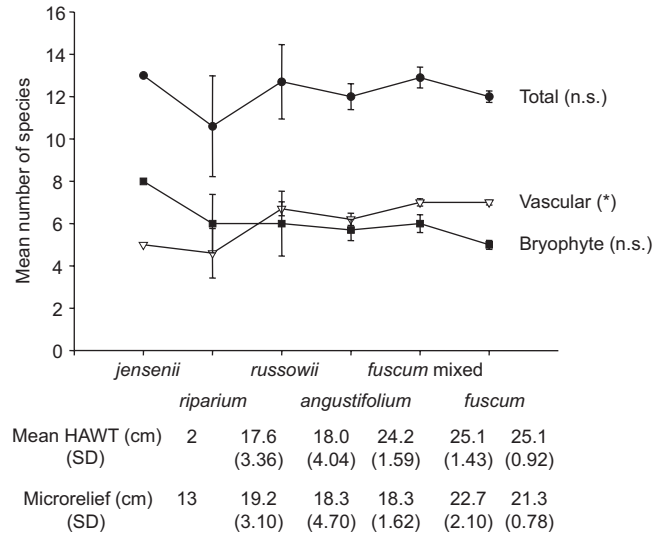
Landscape diversity

The mean alpha diversity of frost mounds and internal lawns is lower than or equivalent to that of the bog matrix that surrounds them. However, the total number of species increases by 47% when additional species present in frost mounds and internal lawns are added to the list of species found only in the bog surveys (Table 2). Vitt et al. (1995) summarized bryophyte gamma diversity by peatland type and noted that bryophyte species richness is 19% higher in peat plateaus (with collapse scars) than in bogs. The total bryophyte gamma diversity of the three localized permafrost bogs surveyed in this study (52 species; Table 2) is more comparable with diversity in peat plateaus (44 species, Vitt et al. 1995) than continental bogs (38 species; Table 2; 37 species, Vitt et al. 1995). Permafrost dynamics, whether they result in frost mounds and internal lawns or peat plateaus and collapse scars, increase species diversity in similar ways, by the creation of habitat conditions absent from bogs. The bryophyte gamma diversity of localized permafrost bogs is as high as pooled gamma diversity from both continental bogs and peat plateaus, and second only to extreme-rich fens (Vitt et al. 1995). Thus, localized permafrost bogs are previously undescribed centres of bryophyte diversity in the mosaic of peatland types in the expansive peatlands of western Canada.

Localized permafrost in fens

Localized permafrost occurs in both bogs and fens across the region (Vitt et al. 1994). Permafrost aggradation likely leads to similar vegetation whether it occurs in bogs or fens because of the isolation of surfaces from the surrounding peatland regardless of that peatland’s hydrological status. Considerable similarity exists between the frost mound vegetation described here and that of a frost mound located in a rich fen described by Zoltai and Tarnocai (1971), especially in dominant ground layer cryptogams. Permafrost degradation, however, creates internal lawns strongly affected by the hydrology of the surrounding peatland matrix, and internal lawns in localized permafrost fens are likely very different

Fig. 8. Patterns of mean alpha diversity (number of species) and microrelief among vegetation groups from 150 internal lawn quadrats, shown in increasing order of height above water table (HAWT). Error bars are SDs. The *Sphagnum jensenii* group has only one quadrat. Nonsignificant (n.s.) and significant (*, $P < 0.001$) results from Kruskal–Wallis H tests are indicated.



than that shown here for bogs. Unique microhabitats are probably not created in fens to the degree they are in bogs following localized permafrost melt because of movement of minerotrophic surface waters through fens and the presence of pool microhabitats in the surrounding fen matrix (regardless of their position on the poor – rich fen gradient). Therefore, while community change is probably equally dramatic in fens when localized permafrost forms and melts, the gamma diversity of localized permafrost fens may be more similar to other fen types. Localized permafrost fens cover a large amount of western Canada (Beilman et al. 2001) and have not been studied comprehensively, representing a large gap in our understanding of how western peatlands respond to climate and permafrost conditions.

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Appendix

Table A1. List of vascular plant and bryophyte species.

Vascular plants	True mosses	<i>Sphagnum</i>	Hepatics
<i>Andromeda polifolia</i>	<i>Amblystegium serpens</i>	<i>Sphagnum angustifolium</i>	<i>Anastrophyllum michauxii</i>
<i>Betula papyrifera</i>	<i>Aulacomnium palustre</i>	<i>Sphagnum balticum</i>	<i>Calypogeia muelleriana</i>
<i>Betula pumila</i>	<i>Brachythecium starkei</i>	<i>Sphagnum fuscum</i>	<i>Calypogeia sphagnicola</i>
<i>Carex aquatilis</i>	<i>Calliergon stramineum</i>	<i>Sphagnum jensenii</i>	<i>Cephalozia bicuspidata</i>
<i>Carex canescens</i>	<i>Ceratodon purpureus</i>	<i>Sphagnum lindbergii</i>	<i>Cephalozia lunulifolia</i>
<i>Carex pauperula</i>	<i>Dicranum elongatum</i>	<i>Sphagnum magellanicum</i>	<i>Cephalozia macrostachya</i>
<i>Carex trisperma</i>	<i>Dicranum flagellare</i>	<i>Sphagnum nemoreum</i>	<i>Cephaloziella hampeana</i>
<i>Chamadaphne calyculata</i>	<i>Dicranum fragilifolium</i>	<i>Sphagnum obtusum</i>	<i>Cephaloziella spinigera</i>
<i>Drosera rotundifolia</i>	<i>Dicranum fuscescens</i>	<i>Sphagnum riparium</i>	<i>Cladopodiella fluitans</i>
<i>Epilobium angustifolium</i>	<i>Dicranum groenlandicum</i>	<i>Sphagnum russowii</i>	<i>Lepidozia reptans</i>
<i>Eriophorum vaginatum</i>	<i>Dicranum polysetum</i>	<i>Sphagnum squarrosum</i>	<i>Lophozia ventricosa</i>
<i>Kalmia polifolia</i>	<i>Dicranum tauricum</i>		<i>Marchantia polymorpha</i>
<i>Ledum groenlandicum</i>	<i>Dicranum undulatum</i>		<i>Mylia anomala</i>
<i>Picea mariana</i>	<i>Drepanocladus exannulatus</i>		<i>Ptilidium ciliare</i>
<i>Rubus chamaemorus</i>	<i>Drepanocladus fluitans</i>		<i>Ptilidium pulcherrimum</i>
<i>Scheuchzeria palustris</i>	<i>Drepanocladus uncinatus</i>		<i>Riccardia latifrons</i>
<i>Smilacina trifolia</i>	<i>Hylocomium splendens</i>		
<i>Vaccinium myrtilloides</i>	<i>Plagiothecium laetum</i>		
<i>Vaccinium oxycoccus</i>	<i>Pleurozium schreberi</i>		
<i>Vaccinium vitis-idaea</i>	<i>Pohlia nutans</i>		
	<i>Pohlia sphagnicola</i>		
	<i>Polytrichum strictum</i>		
	<i>Ptilium crista-castrensis</i>		
	<i>Splachnum ampullaceum</i>		
	<i>Splachnum luteum</i>		