Multiscale factors control community and species distribution in mountain peatlands

Joanna M. Lemly and David J. Cooper

Abstract: We studied the vegetation of 166 fens in Yellowstone National Park, USA, to determine the relationship between species distribution in mountain peatlands and regional-, landscape-, and local-scale environmental variables. Plant communities were identified through hierarchical agglomerative cluster analysis, patterns in species distribution were explored using nonmetric multidimensional scaling, and the relative importance of variables was assessed though partial canonical correspondence analysis. Five major bedrock types influenced groundwater feeding fens: three volcanic types, a glacial till complex, and rock altered by acidic geothermal activity. Ionic concentrations generally increased with pH, but acidic geothermal fens had very low pH and high electrical conductivity. Bryophyte distribution was controlled by groundwater chemistry, while vascular plants responded to a broader range of variables. When partitioned by spatial scale, landscape variables accounted for >60% of the variation explained. When partitioned categorically, geochemical and topographic variables were more important than geographic factors. For fens in mountainous regions, the primary gradient is site-level water chemistry, which is strongly linked to regional bedrock geology. Site- and stand-level topography represent a secondary gradient. Most mountain fens fit within the established poor–rich gradient; however, geochemical acid production creates a distinct category outside the conventional paradigm.

Key words: Rocky Mountains, peatlands, vegetation, spatial scale, nonmetric multidimentional scaling (NMS), variance partitioning.

Résumé : Les auteurs ont étudié la végétation de 166 tourbières minérotrophes dans le parc national Yellowstone aux États-Unis, pour déterminer les relations entre la distribution des espèces dans les tourbières de montagne ainsi que les variables environnementales à l'échelle régionale, du paysage et locale. Ils ont identifié les communautés végétales par l'analyse typologique d'agglomération hiérarchique et ont exploré les patrons de distribution des espèces en utilisant l'échelonnage multidimensionnel non-métrique (EMS), et ils ont évalué l'importance relative des variables à l'aide de l'analyse canonique par correspondance partielle (ACCp). Cinq types de roches mères principaux influencent la nappe phréatique nourrissant les tourbières minérotrophes; trois types volcaniques, un till glaciaire complexe et une roche altérée par une activité géothermique acide. Les teneurs ioniques augmentent généralement avec le pH, mais les tourbières minérotrophes avec acidité géothermique montrent des pH très bas avec un EC élevé. La chimie de la nappe phréatique contrôle la distribution des bryophytes alors que les plantes vasculaires réagissent à une amplitude plus large de variables. Lorsque réparties selon l'échelle spatiale, les variables du paysage comptent pour 60 % de la variation expliquée. Lorsque réparties par catégories, les variables géochimiques et topographiques se révèlent plus importantes que les facteurs géographiques. Pour les tourbières minérotrophes situées en montagne, la chimie de l'eau à l'échelle du site constitue le gradient primaire, lequel montre un lien étroit avec la géologie régionale de la roche mère. La topographie à l'échelle du site et du peuplement représente un gradient secondaire. La plupart des tourbières minérotrophes de montagne correspondent au gradient pauvre riche établi; cependant, la production géochimique d'acide crée une catégorie distincte externe au paradigme conventionnel.

Mots-clés : Montagnes Rocheuses, tourbières, végétation, échelle spatiale, échelonnage multidimensionnel non-métrique (EMS), partition de la variance.

[Traduit par la Rédaction]

Introduction

Peatland ecosystems have formed wherever the long-term production of organic matter exceeds the rate of decomposition because of waterlogging (Moore and Bellamy 1974). Globally, peatlands cover ~4 × 10^6 km^2 (Gorham 1991; Joosten and Clarke 2002), approximately one half of the wetland area on earth (Mitsch and Gosselink 2007), and store up to one third of terrestrial carbon (270–370 TgC: Gorham 1991; Turunen et al. 2002). Peatlands contribute valuable ecological services, including the regulation of local and regional hydrologic regimes and habitat for plant and animal species that

Received 11 January 2011. Accepted 7 June 2011. Published at www.nrcresearchpress.com/cjb on xx October 2011.

J.M. Lemly* and D.J. Cooper. Department of Forest, Rangeland, and Watershed Stewardship and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA.

Corresponding author: Joanna M. Lemly (e-mail: joanna.lemly@colostate.edu).

*Present address: Colorado Natural Heritage Program, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523-1474, USA.

require saturated soils. Most peatlands occur in boreal regions of Canada, Alaska, northern Europe, and Russia (Wieder and Vitt 2006). However, peatlands also occur in temperate and tropical regions and can be abundant in temperate mountain ranges, including the Alps (Gerdol et al. 1994; Bragazza and Gerdol 1999), Carpathian Mountains (Hájková et al. 2004; Hájek et al. 2006), Andes (Cooper et al. 2010), and Rocky Mountains (Cooper and Andrus 1994; Johnson and Steingraeber 2003; Chimner et al. 2010).

Peatland vegetation is influenced by several complex ecological gradients at continental to local spatial scales (Bridgham et al. 1996; Wheeler and Proctor 2000; Rydin and Jeglum 2006). Continental-scale climate patterns influence peatland type, which ranges from chiefly ombrotrophic bogs and poor fens in humid maritime regions to few bogs and a variety of fen types in drier inland regions (Gignac and Vitt 1990; Gignac et al. 1991). On a regional scale, climate, elevation and biogeographic history influence the composition of peatland vegetation (Sjörs 1950*b*; Økland 1990*b*; Glaser 1992; Halsey et al. 1997; Clarke and Martin 1999). For fens, which are fed by groundwater flow systems, the chemical content of groundwater is influenced by regional bedrock type (Cooper and Andrus 1994; Reeve et al. 1996; Bedford and Godwin 2003; Tahvanainen 2004; Chimner et al. 2010; Cooper et al. 2010) and the balance of precipitation versus groundwater inputs (Glaser et al. 1990; Vitt and Chee 1990). Resulting groundwater chemistry creates the poor to extreme-rich gradient of fen vegetation (Sjörs 1950*a*). At a local scale, differences in water table depth and soil aeration produced by microtopography, such as hummocks and hollows, and the peatland margin – peatland expanse gradient influence species distribution (Andrus 1986; Malmer 1986; Økland 1990*a*; Hájková and Hájek 2004). While gradients influencing vegetation composition are well known, there have been few attempts to analyze the relative importance of each factor, the interactions between factors, or how multiscale environmental gradients operate in peatlands outside boreal regions.

Mountain landscapes are highly heterogeneous, with steep topography, pronounced elevation gradients, and varied bedrock type and groundwater chemistry across relatively short distances (Chimner et al. 2010). In continental climate regions, deep winter snow covers most high mountains, summers can be warm and dry, and spring snowmelt recharges groundwater aquifers and flushes wetlands with chemically dilute water (Cooper 1990; Winter et al. 1998). Peatlands form in mountain valleys, in basins, or on hillslopes, and most are fens supported by groundwater input, although *Sphagnum*-dominated peatlands floristically similar to boreal bogs occur in high mountain regions of the Italian Alps (Gerdol et al. 1994; Bragazza and Gerdol 1999), the Kosciuszko Massif in Australia (Clarke and Martin 1999), and the Rocky Mountains (Cooper and Andrus 1994; Chimner et al. 2010). While many differences in landscape and climate exist between boreal and mountain peatlands, it remains unclear how regional and local ecological gradients influence species distribution in mountain peatlands.

Fens occupy a small fraction of the Rocky Mountain landscape in the western United States, but they contribute substantially to regional biodiversity of both plants and animals (Chadde et al. 1998). In an otherwise arid region, perennially saturated fens are critical habitat for invertebrate and amphibian species and, because of the relative warmth of discharging groundwater, many fen plants green earlier than upland plants, providing forage for grazers. Often located in the headwaters, Rocky Mountain fens play a key role as groundwater discharge zones that support late-season stream flows (Cooper 1990). Though dry summers prevent the formation of ombrotrophic bogs, fens occur throughout the region. Because of variation in chemical content and landforms, the floristic composition of Rocky Mountain fens is highly variable (Lesica 1986; Cooper 1990, 1996; Cooper and Andrus 1994; Cooper et al. 2002; Johnson and Steingraeber 2003; Chimner et al. 2010). The present study was conducted in Yellowstone National Park, a complex and heterogeneous landscape where environmental gradients at several spatial scales influence the composition of fen vegetation. Our objectives were to characterize the vegetation of mountain fens and analyze regional-, landscape-, and local-scale gradients that influence the distribution of communities and species. We addressed the following questions. (*i*) Are the distribution patterns of vascular plant and bryophyte species influenced by different environmental gradients? (*ii*) What spatial scale is most strongly correlated with species and community distribution? (*iii*) Do the principle gradients known to control fen vegetation operate at multiple spatial scales?

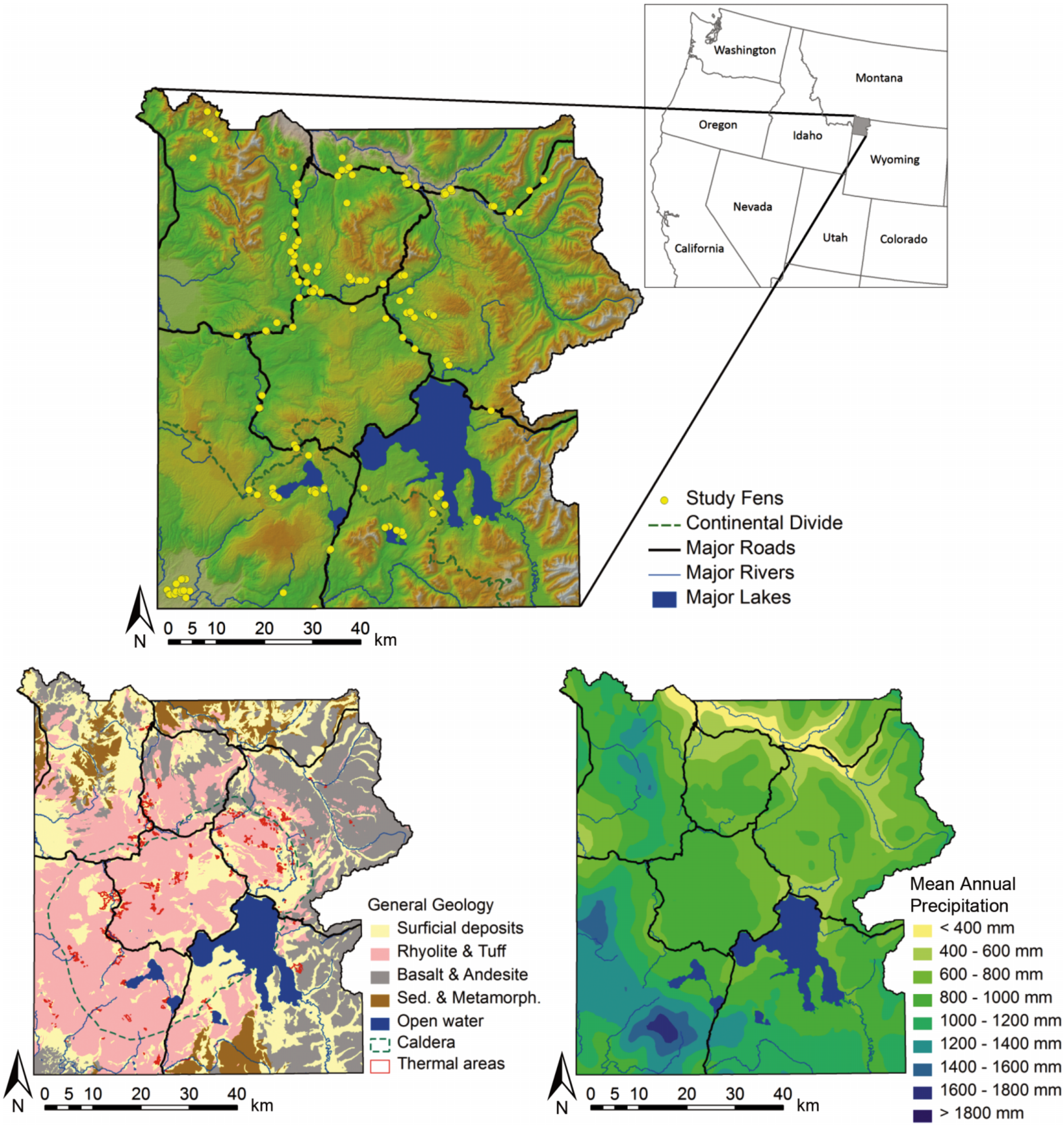
Materials and methods

Study area and site selection

Yellowstone National Park (YNP) occupies the northwest corner of Wyoming and adjacent areas in Montana and Idaho in the western United States (Fig. 1*a*). It covers nearly 9000 km^2 at a mean elevation of ~2500 m. The central portion of YNP is a volcanic plateau formed during the last eruption of the Yellowstone hotspot magma plume ~630 000 years ago (Smith and Siegel 2000). High mountain ranges border the plateau except in the southwest corner, which is more than 500 m lower than the central plateau. Rhyolite from caldera-forming eruptions is the dominant bedrock type, and localized areas of basalt and andesite, as well as metamorphic and sedimentary rocks, occur (Fig. 1*b*: Christiansen 2001). Glaciers covered most of the central plateau and mountain valleys during stages of the Quaternary, and many areas are covered by glacial till, particularly in the north (Despain 1990). The Yellowstone hotspot remains active, supporting a high concentration of geysers, hot springs, mud pots, and fumaroles and discharging both acidic and basic groundwater (Rodman et al. 1996).

YNP's climate has long, cold winters and short, warm summers. The frost-free season is typically less than 5 months. Summer daytime highs reach 20–30 °C, and nighttime lows are <5 °C. Precipitation varies from as little as 300 mm/year in low elevations in the north to 1800 mm/year in the high mountains and 1000 mm/year in the low-elevation southwest corner (Fig. 1*c*; USDA–NRCS 2009). Over three quarters of YNP is mixed conifer forest dominated by *Abies lasiocarpa*, *Picea engelmannii*, *Picea glauca*, *Pinus contorta* var. *latifolia*, and *Pseudotsuga menziesii*. Several large, semiarid valleys are dominated by sagebrush (*Artemisia* spp.). Wetlands constitute <5% of the landscape, and fens likely occupy <1% (Despain 1990; Rodman et al. 1996).

Fig. 1. Map of Yellowstone National Park, USA, showing location within the western United States, specific study fen locations, and elevation gradient (top); generalized geology (bottom left); and precipitation gradient across the park (bottom right).



Using stereo pairs of full-color aerial photographs, approximately 500 fens were identified in YNP based upon identifiable physical features such as a mottled brown photo signature and peat-generated landforms, including patterned topography and floating mats. From these potential sites, 166 fens that spanned the regional gradients of elevation, climate, and bedrock geology were selected for sampling (Fig. 1*a*). Field data were collected during June–August 2004 and 2005. During field visits, sites were verified as fens based on the presence of organic soil at least 40 cm thick.

Vegetation and environmental data collection

Within each verified fen, homogeneous stands of vegetation were identified based on dominant species and analyzed using the relevé method, with plot size based upon minimum area requirements by life form and ranging from 4 to 20 m^2 (Mueller-Dombois and Ellenberg 1974). One to 12 relevés were analyzed per fen depending on the fen's size and vegetation diversity, and a total of 476 relevés were included. Canopy cover was visually estimated for each vascular plant and bryophyte species present in each relevé. Species nomenclature follows Dorn (2001) for vascular plants, Weber and Wittmann (2007) for non-*Sphagnum* bryophytes, and McQueen and Andrus (2007) for *Sphagnum* species. Voucher collections of all species are housed at the Yellowstone Herbarium (YELL). Duplicate collections of non-*Sphagnum* bryophytes are housed at the University of Colorado, Boulder (COLO), and duplicates of *Sphagnum* species are housed at Binghamton University in New York (BING).

Regional-scale variables

Elevation for each site was determined on orthorectified digital USGS 1 : 24 000 scale topographic maps in ArcGIS 9.1 (ESRI 2005). Mean annual precipitation and mean, maximum, and minimum annual temperatures were determined from digital raster data based on 1971–2000 records (USDA–NRCS 2009). Dominant watershed bedrock was determined from a digital geological map (USGS 1972; Christiansen 2001).

Landscape-scale (site level) variables

Within each fen, UTM coordinates were determined with a Garmin GSP 12 (Garmin International, Olathe, Kans.). Groundwater pH and temperature were measured for each site from water that filled a 40 cm pit using an Orion model 250A portable pH meter with combination electrode (Thermo Fisher Scientific, Waltham, Mass.), following the methods of Tahvanainen and Tuomaala (2003). Groundwater was collected from the pit, sealed immediately, and frozen until analyzed at the Soil, Water and Plant Testing Laboratory at Colorado State University. In the lab, electrical conductivity (EC) was measured using an Accumet two-cell conductivity probe (Thermo Fisher Scientific) and corrected for H^+ ions. Concentrations of Ca^{2+}, Mg^{2+}, Na^+, and K^+ were determined by inductively coupled plasma emission spectrography (USEPA 1983), concentration of HCO_3^- was determined by titration, and concentrations of Cl^- and SO_4^{2-} were determined by ion chromatography (Pfaff et al. 1989).

Each fen was categorized into one of four landforms: basin, gentle slope, steep slope, or spring mound. Basin (topogenous or limnogenous) fens occupied peat-filled depressions or pond margins and had floating mats or herbaceous vegetation in shallow standing water. Gently sloping (soligenous) fens (mean slope <10°) occurred on valley margins or at the base of alluvial fans where groundwater discharged to the surface. Steeply sloping fens (mean slope 10°–25°) formed below hillside springs at bedrock discontinuities. Spring mound fens formed around localized points of upwelling groundwater in meadows that otherwise lack organic soils and were up to 2 m high and several metres in diameter.

Local-scale (stand-level) variables

Stand slope was measured with a compass. Stand wetness and microtopography was rated on a four-point scale, which was used as both a categorical and continuous variable in analysis: 4, deep water (≥25 cm above the soil surface); 3, shallow water (<25 cm); 2, saturated soil with no standing water; 1, hummocks raised above the dominant vegetation matrix and water table. The presence of floating mats and seep or spring sources were recorded as categorical variables. Peat thickness was estimated in each stand by pushing a 240 cm steel probe into the soil until it hit rock, sand, or dense mineral substrate. Soil samples were collected from 30 to 40 cm soil depth, stored in paper bags, and air dried. In the laboratory, a sample of each soil was oven dried at 60 °C for 72 h, ground to a fine powder, analyzed for percent organic carbon (OC) and nitrogen (N) using a Truspec C:N analyzer (LECO Corporation, St. Joseph, Mich.), and soil C/N ratios were calculated. See Table 1 for environmental variables used in the analysis.

Statistical analysis

Prior to analysis, species recorded in fewer than five relevés were removed from the data set to reduce noise produced by rare plants. Cover values were square root transformed to maintain the information value of moderate and low abundance species (McCune and Grace 2002). Water chemistry variables were tested for normality (PROC UNIVARIATE; SAS Institute Inc. 2002); all but pH were log-normally distributed and log transformed. No other environmental variables were transformed.

Regional-scale parent material was divided into five bedrock groups: (*i*) rhyolite and rhyolitic tuff; (*ii*) basalt; (*iii*) andesite; (*iv*) glacial till containing a mix of granite, andesite, rhyolite, and sedimentary rocks; and (*v*) acidic geothermal rock. Differences in mean pH and EC between selected sites from watersheds clearly dominated by each bedrock type were compared using ANOVA with Tukey's honestly significant difference multiple comparison test ($P < 0.05$) (PROC GLM; SAS Institute Inc. 2002). Dominant groundwater ions for each bedrock type were identified by trilinear Piper diagram (Deutsch 1997).

Plant communities were identified from relevés through hierarchical agglomerative cluster analysis (van Tongeren 1995) using the Sørensen distance measure and flexible beta linkage method with $\beta = -0.25$ in the computer program PC-ORD 5.0 (McCune and Mefford 2006). Indicator species analysis was used to determine the optimum number of clusters produced by the dendrogram (Dufrene and Legendre 1997; McCune and Grace 2002), and environmental variables were summarized by community type (Appendix Table A1). Patterns in species and community distribution were related to environmental variables using nonmetric multidimensional scaling (NMS) in PC-ORD 5.0 based on the Sørensen distance measure and a three-axis solution, as determined by the stress test (McCune and Grace 2002). To relate environmental variables to the three groups, NMS was run on (*i*) vascular plants only, (*ii*) bryophytes only, and (*iii*) all species. Spearman's rank correlation coefficients of environmental variables with NMS sample scores were calculated for all three axes in each ordination.

To examine the effect of spatial scale on species distribution, the proportion of variation within the species data explained by environmental variable subsets was obtained through partial canonical correspondence analysis following the approach of Borcard et al. (1992) and Økland and Eilertsen (1994). Results for each model were calculated as total variation explained (TVE), the sum of all constrained eigenvalues divided by total inertia, and as %TVE for each varia-

Table 1. Environmental variables by regional, landscape, and local designation and by subset.

			Observed			
Variable	Abbrev.	Units	Mean	SD	Min.	Max.
Regional variables						
Elevation	Elev	m	2264	188	1880	2710
Climate						
Mean annual precipitation	AnnPPT	mm	806	207	330	1300
Mean annual temperature	MeanTemp	°C	1.2	1.0	–0.6	3.9
Max. annual temperature	MaxTemp	°C	23.3	1.6	18.3	26.1
Min. annual temperature	MinTemp	°C	–16.0	1.1	–18.3	–12.8
Dominant geology[a]						
Acidic geothermal	Geoth				12	7.2%
Glacial till	Till				39	23.5%
Rhyolite	Rhy				91	54.8%
Basalt	Bas				14	8.4%
Andesite	And				10	6.0%
Landscape variables						
Site location						
UTM E	UTME	m	na	na	494 166	572 547
UTM N	UTMN	m	na	na	4 886 728	4 990 055
UTM E × UTM N	UTME×N	10^6 m^2	na	na	2 416 737	2 848 893
Groundwater chemistry						
pH	pH	na	6.13	0.99	2.89	7.98
Temperature	WtrTemp	°C	17.3	5.4	5.9	39.0
Electrical conductivity	EC	µS/cm	141.7	150.4	7.8	1250.0
[Ca^{2+}]	Ca^{2+}	mg/L	12.7	13.6	0.3	67.3
[Mg^{2+}]	Mg^{2+}	mg/L	4.1	7.2	0.0	39.6
[Na^+]	Na^+	mg/L	11.0	22.2	0.3	193.8
[K^+]	K^+	mg/L	2.7	3.6	0.0	23.9
[HCO_3^-]	HCO_3^-	mg/L	68.5	77.4	0.5	390.0
[Cl^-]	Cl^-	mg/L	7.6	21.7	0.2	161.0
[SO_4^{2-}]	SO_4^{2-}	mg/L	8.5	21.9	0.2	190.0
Dominant site landform[a]						
Basin fen	Basin				36	21.7
Gently sloping fen	GntSlp				107	64.5
Steeply sloping fen	StpSlp				16	9.6
Spring mound	SpgMnd				7	4.2
Local variables						
Stand slope	Slope	°	2.8	4.1	0	25
Microtopography[a]						
Deep standing water (≥25 cm)	DeepWtr				43	9.0
Shallow standing water (<25 cm)	ShalWtr				179	37.6
Saturated soil	Sat				182	38.2
Raised hummocks	Hum				72	15.1
Wetness scalar (scales 1–4)	Wet				43, 179, 182, 72	9.0, 37.6, 38.2, 15.1
Floating mat	FltMat				31	6.5
Seep–spring	SeepSpg				41	8.6
Soil characteristics						
Peat thickness[b]	Peat	cm	na	na	20	240+
Soil carbon	Car	%	31.9	9.7	10.4	52.6
Soil nitrogen	Nit	%	1.8	0.7	0.5	3.7
Soil carbon/nitrogen ratio	C/N	%	19.8	8.3	11.9	63.3

Note: "Abbrev." refers to abbreviations used elsewhere in the text. Observed mean, standard deviation, minimum, and maximum are by site for regional and landscape variables and by stand for local variables. na, not applicable.

[a]Subset consists of categorical variables. Table values shown under Min. are the number of sites or stands in each category. Values shown under Max. are the percentage of total sites or stands.

[b]Mean and SD are not shown for peat thickness because maximum peat thickness was not known.

ble set within the model (Økland 1999). Eight models were analyzed in two hierarchical sets. The first four models quantified the relative importance of regional, landscape, and local scales and of each variable subset within each scale. For the second four models, variable subsets were reorganized into three different categories that crossed spatial scales: geochemical variables (bedrock geology, water chemistry, and soil chemistry); topographic variables (site landform, stand slope, and stand topography); and geographic variables (climate, elevation, and site location). This set of models explored how the major gradients controlling fen vegetation operate at different spatial scales. Before running partial canonical correspondence analysis, each variable subset was first subjected to manual forward selection (Monte Carlo test, 499 permutations, $P \leq 0.01$), and only significant variables were included.

Results

Environmental characteristics of YNP fens

Study fens occurred at 1880–2710 m elevation (Table 1), and many were on the central volcanic plateau. Mean annual precipitation at study fens ranged from 330 to 1300 mm, was highest in high elevation areas, and decreased along a gradient from southwest to northeast. Fens located on the central plateau occurred predominantly within watersheds dominated by rhyolite bedrock or acidic geothermal rock. Andesitic rock predominated in the northern and southern mountains, while basalt was most common in the southwest. Sites in northern river valleys were located in watersheds dominated by glacial till.

Groundwater pH was significantly different between watersheds with distinct bedrock types ($F_{[4,40]} = 52.41$, $P < 0.0001$) and ranged from 2.89 to 7.98 (Table 1). Fens in glacial till watersheds had significantly higher pH than the three volcanic bedrock types, which were not significantly different from each other. Fens in geothermal watersheds were significantly more acidic than all other types (Table 2). EC was also significantly different among bedrock types ($F_{[4,40]} = 9.54$, $P < 0.0001$) and ranged from 7.8 to 1250.0 µS/cm. Mean EC of groundwater in fens within glacial till and acidic geothermal watersheds was not significantly different, but the EC of both was significantly higher than that of fens in all volcanic bedrock type watersheds (Table 2). HCO_3^- was the dominant anion in glacial till and the volcanic watersheds, while SO_4^{2-} dominated acidic geothermal water. The dominant cation for all bedrock types was Ca^{2+}, although volcanic and geothermal groundwater contained higher concentrations of Na^+ and glacial till contained more Mg^{2+}. Fen groundwater pH was positively correlated with EC (Fig. 2); however, most acidic geothermal fens had pH < 5 and EC > 100 µS/cm.

Of the 166 study fens, 107 were on gentle slopes, 36 were in basins, 16 were on steep slopes, and 7 were spring mounds (Table 1). Stands within fens had slopes of 0°–25° and stand slope was greatest in steeply sloping fens and on the margins of other fen landforms. Nine percent of stands had deep water, 38% had shallow water, 38% had saturated soil with no standing water, and 15% were on hummocks. A number of gently sloping fens had strings and flarks with alternating stands of shallow standing water and saturated soil or hummocks.

Soil OC ranged from 10.4% to 52.0% with a mean of 31.9%. Soil total N ranged from 0.5 to 3.7% with a mean of 1.8% (Table 1). Soil OC was not strongly correlated with slope or peat thickness, was not significantly different between site landforms, but was positively correlated to soil total N concentration ($R^2 = 0.45$, $P < 0.0001$). One hundred of the 476 stands analyzed had peat thickness >240 cm, the length of our sampling tool. The thickest peat bodies occurred in basin or gently sloping fens. Few stands with >5° slope had peat >120 cm thick.

Patterns in community and species distribution

A total of 254 vascular plant species were identified in the study fens, representing ~20% of all vascular plant species known for YNP (J. Whipple, personal communication). *Carex aquatilis* and *Carex utriculata* occurred in ~80% of all study fens, and *Carex* was the most abundant genus with 34 species. The most abundant woody plants were *Salix planifolia* and *Salix wolfii*. Fifty-eight bryophyte species were identified, with *Aulacomnium palustre*, *Ptychostomum pseudotriquetrum*, and *Plagiomnium cuspidatum* being the most common. *Sphagnum* species occurred in one-third of the study fens, with *Sphagnum teres*, *Sphagnum warnstorfii*, and *Sphagnum russowii* being the most common. New Wyoming state records were found for three species, *Sphagnum capillifollium*, *Sphagnum lindbergii*, and *Sphagnum riparium* (Lemly et al. 2007).

Eight plant communities were identified from the relevés, each distinguished by characteristic indicator species (Table 3; Appendix Table A2) and fidelity to certain environmental variables (Appendix Table A1). The most commonly sampled community, *Aulacomnium palustre – Symphyotrichum foliaceus*, occurred on hummocks or saturated soil within sloping fens with intermediate water chemistry. The *Eleocharis quinqueflora – Carex livida* community dominated gently sloping fens with shallow sheet flow and water of intermediate chemical content. The *Carex aquatilis – Carex simulata* community occurred in both high-pH, mineral-rich waters of northern glacial till watersheds and low-pH, mineral-rich geothermal fens. The *Epilobium ciliatum – Plagiomnium cuspidatum* community dominated most spring mounds and seeps in steeply sloping fens. The *Carex utriculata – Rorippa palustris* and *Eleocharis palustris – Schoenoplectus acutus* var. *occidentalis* communities were most common in basin or gently sloping fens with shallow standing water, the latter occupying sites at lower elevations with drier climate and higher groundwater mineral ion content. The *Carex lasiocarpa – Carex limosa* community occupied basin fens within the high-precipitation basalt watersheds of the southwest and formed floating mats. The *Kalmia microphylla – Sphagnum russowii* community dominated acidic geothermal fens, often on hummocks and never in standing water.

NMS ordinations for vascular plants, bryophytes, and all species each resulted in three-dimentional solutions. Final stress and instability were, respectively, 19.03 and 0.00003 for vascular plant species, 23.72 and 0.00022 for bryophytes, and 22.02 and 0.00165 for all species. Based on the cumulative R^2 between ordination distance and Bray–Curtis distances in the original n-dimensional space, NMS ordinations explained 66.9% of the variance in species composition for vascular plants, 54.8% for bryophytes, and 50.6% for all species.

Axes 1 and 3 had the strongest relationships to measured environmental variables within the vascular plant ordination (Table 4) and accounted for 18.8% and 28.9% of the variance in species composition, respectively (Fig. 3). The strongest positive correlations along axis 1 were with groundwater pH,

Table 2. Groundwater chemistry parameters by bedrock type for selected sites.

				Concentration (mg/L)						
Bedrock type	*n*	pH	EC (µS/cm)	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	HCO_3^{-}	Cl^{-}	SO_4^{2-}
Acidic geothermal	10	3.79±0.24c	212.1±47.4a	19.4±5.6	2.7±1.5	16.2±5.4	6.2±2.3	30.7±15.0	7.9±3.4	63.9±19.3
Glacial till	10	7.32±0.13a	233.5±27.0a	25.1±4.0	12.9±2.2	11.4±3.0	1.9±0.5	157.5±21.0	3.0±1.0	7.4±2.4
Rhyolite	10	5.92±0.19b	67.9±9.7b	6.3±1.2	1.3±0.5	3.3±0.8	1.7±0.4	32.5±7.5	1.8±0.2	1.5±0.3
Basalt	10	5.26±0.15b	70.1±8.1b	5.5±0.9	1.0±0.2	2.7±0.4	1.5±0.5	26.3±4.5	2.1±0.6	1.0±0.2
Andesite	5	5.11±0.20b	60.6±9.8b	5.1±0.7	0.5±0.2	2.2±0.5	1.7±0.4	23.2±3.5	1.8±0.5	0.6±0.1

Note: Values shown are means ± SE. For pH and electrical conductivity (EC), letters indicate significant differences (ANOVA, Tukey's honestly significant difference test, $P < 0.05$).

EC, concentrations of Ca^{2+}, Mg^{2+}, and HCO^{-}_3, as well as glacial till bedrock, stand wetness, and deep water, while elevation, annual precipitation, acidic geothermal bedrock, and hummocks were most negatively correlated. The strongest positive correlations along axis 3 were with basalt, basin landforms, stand wetness, and shallow standing water, while the strongest negative correlations were with site location variables (UTME, UTMN, UTME × N) and groundwater SO^{2-}_4 concentrations. In this two-dimensional ordination space, plant communities identified using cluster analysis formed loose groups related to environmental gradients at multiple spatial scales (Fig. 3*b*). Communities associated with high-pH and mineral-rich waters were plotted on the right side of the ordination; those tolerant of standing water were in the upper right, and those with saturated soils were in the lower right. Stands from high-precipitation basaltic watersheds dominated the upper-left portion of the ordination, while acidic geothermal stands were in the lower left.

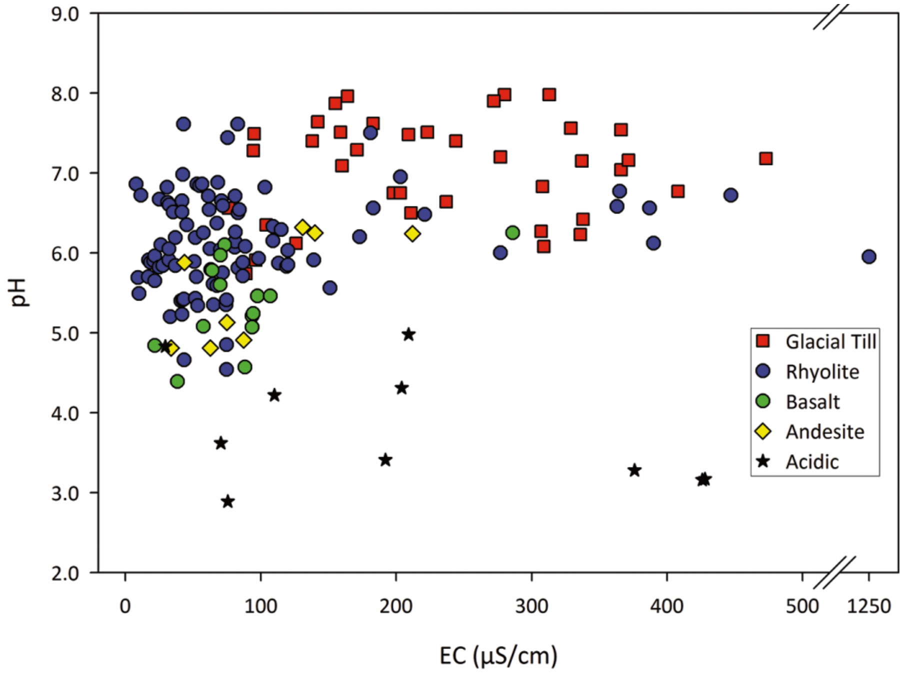
The bryophyte ordination had fewer strong correlations, and plant communities were less evident than in the vascular plant ordination. Axes 2 and 3 accounted for the greatest variation in bryophyte composition among stands, explaining 23.9% and 17.6%, respectively. Only axis 2 was strongly correlated with several variables, including positive associations with glacial till, groundwater pH, and ionic concentrations and negative associations with acidic geothermal bedrock (Table 4). This axis represented a geochemical gradient with mineral-rich fens opposite acidic geothermal fens (Fig. 3*d*). Axis 3 represented a hydrological gradient with shallow water stands plotted on the lower half of the ordination space, where the centroids of character species *Scorpidium scorpioides* and *Campylium stellatum* occur, and stands with saturated soil or hummocks plotted in the upper half with character species *Aulacomnium palustre*, *Tomentypnum nitens*, and several *Sphagnum* spp. Correlations with axes within the NMS for all species reflected the influence of these two species groups (Table 4).

Partitioning the variance between spatial scales

Full variance partitioning models analyzed by spatial scale (Fig. 4*a*) and environmental variable type (Fig. 4*e*) explained 19.2% and 19.0% of variation in the species data, respectively, with a slight difference due to the variable selection process. Within the full model by spatial scale (see Table 1 for breakdown of variables by spatial scale), each scale contributed substantially to the total variation explained (TVE). Landscape-scale variables accounted for the greatest percentage of TVE (28.9%), while regional and local scales accounted for 15.4% and 22.7%, respectively. Strong overlap between regional and landscape scales (20.3%) indicated covariance among certain subsets, such as regional-scale bedrock geology and landscape-scale water chemistry. With interactions included, total variation related to the landscape scale was 61.1%, regional scale 41.1%, and local scale 35.5%. Within each spatial scale, one variable subset accounted for >50% of TVE: bedrock type at the regional scale (Fig. 4*b*), water chemistry at the landscape scale (Fig. 4*c*), and microtopography at the local level (Fig. 4*d*).

When partitioned by environmental variable type (Fig. 4*e*), geochemical and topographic variables were more important than geographic variables, although geochemical and geo-

Fig. 2. Groundwater pH versus electrical conductivity (EC) by bedrock type for all study fens.



graphic subsets overlapped by 16.0%. Without interactions, topography accounted for 31.8% of TVE, geochemistry 30.8%, and geography 12.2%. With interactions included, the relative contribution of geochemistry was 54.2%, topography 40.9%, and geography 33.1%. Within the geochemistry submodel (Fig. 4*f*), landscape-scale water chemistry accounted for 52.6% of TVE, regional scale-bedrock geology 27.2%, and the two sets shared an additional 15.7% of variation. Within the topography submodel (Fig. 4*g*), local-scale microtopography accounted for 60.0% of TVE without interactions and 75.1% when interactions were included; site landform accounted for 17.0% alone and 33.1% with interactions. Within the geography submodel (Fig. 4*h*), climate variables accounted for the greatest proportion of variation (44.4%) and overlapped with both site location and elevation.

Discussion

Distribution of vascular plants versus bryophytes

Vascular plants and bryophytes in YNP fens were influenced by measured environmental variables to differing degrees. The distribution of bryophyte species was primarily influenced by extremes in site-level water chemistry and stand-level microtopography, while the distribution of vascular plant species was related to a broader range of variables, including regional climate, elevation, and site landform. Similarly, bryophyte species in boreal peatlands have a higher fidelity to specific water chemistry conditions than vascular plants and are reportedly the best indicators of the poor–rich water chemistry gradient (Chee and Vitt 1989; Slack 1994). For fens in western Canada (Vitt and Chee 1990) and Italy (Bragazza and Gerdol 2002), the distribution of bryophytes was controlled by pH and mineral elements, like in YNP, while vascular plant distribution was correlated with nitrogen and phosphorus concentrations, not measured in this study. In Carpathian Mountain fens, bryophyte distribution responded to one clear water chemistry gradient, while vascular plant variation was related to multiple gradients of similar importance (Hájkova and Hájek 2004). This suggests that vascular plant root systems allow them to persist in a wider range of water chemistry conditions than bryophytes, which are strongly influenced by hydrogeochemical conditions near the soil surface.

Relative importance of spatial scales

Landscape scale (site level) factors exhibited the strongest relationship to overall plant species distribution in YNP fens. This relationship was driven primarily by water chemistry, which is known to influence peatland vegetation composition worldwide (Sjörs 1950*a*; Malmer 1986; Glaser et al. 1990; Vitt and Chee 1990; Økland 1990*a*; Bragazza et al. 2005; Hájek et al. 2006). Local variables, most notably stand wetness and microtopography, represented the second most important scale. For spring fens in the Carpathian Mountains, site-level water chemistry was similarly the most important driver of vegetation patterns between fens, while local-scale water levels influenced the distribution of species within fens (Hájkova et al. 2004).

Without accounting for shared variance, regional-scale variables were the least important category for YNP fens and had less direct influence on fen vegetation than finer spatial scale variables. Of the variation explained by regional variables, however, more than half was shared with the landscape scale, indicating that the effect of each scale could not be evaluated in isolation because the principal gradients controlling fen vegetation operate at multiple spatial scales.

Multiscale influence of environmental gradients

Bedrock geology, water chemistry, and the poor–rich gradient

Regional bedrock geology strongly influenced site-level

Table 3. Indicator species for plant communities in Yellowstone National Park fens, with up to 10 species shown per community.

Scientific name	Abbrev.	Indic.	Mean cover and constancy class by plant community							
			A	B	C	D	E	F	G	H
(A) *Carex aquatilis* – *Carex simulata* (*n* = 74)										
Carex aquatilis	*Car aqu*	24.5	**30.4, V**	18.0, V	2.3, III	10.4, IV	20.4, V	4.4, III	—	1.3, II
Carex simulata	*Car sim*	11.3	**10.9, III**	—	—	—	—	—	—	—
Drepanocladus longifolius	*Dre lon*	10.9	**6.1, I**	—	—	—	—	—	—	—
Drepanocladus aduncus	*Dre adu*	8.6	**10.4, III**		—	5.2, II	—	7.8, II	1.6, II	—
Calamagrostis canadensis	*Cal can*	7.7	**4.2, III**	1.3, II	—	1.4, II	—	—	—	—
Scutellaria galericulata	*Scu gal*	4.4	**0.2, I**	—	—	—	—	—	—	—
(B) *Aulacomnium palustre* – *Symphyotrichum foliaceum* (*n* = 123)										
Aulacomnium palustre	*Aul pal*	39.0	—	**17.8, IV**	—	4.0, II	—	—	—	—
Symphyotrichum foliaceum	*Sym fol*	35.4	—	**1.2, III**	—	—	—	—	—	—
Salix wolfii	*Sal wol*	31.6	—	**9.8, III**	—	—	—	—	—	—
Salix planifolia	*Sal pla*	30.5	7.1, III	**8.1, III**	—	—	—	—	—	—
Betula glandulosa	*Bet gla*	27.2	—	**2.0, II**	—	—	—	—	—	—
Viola macloskeyi subsp. *pallens*	*Vio mac*	24.9	0.5, III	**2.7, IV**	—	2.0, III	—	—	—	—
Agrostis thurberiana	*Agr thu*	21.8	—	**1.9, II**	—	—	—	—	—	—
Antennaria corymbosa	*Ant cor*	21.5	—	**0.5, II**	—	—	—	—	—	—
Gentianopsis detonsa var. *elegans*	*Gen det*	21.2	—	**0.6, II**	—	—	—	—	—	—
Pentaphylloides floribunda	*Pen flor*	20.8	—	**3.1, II**	—	—	—	—	—	—
(C) *Carex utriculata* – *Rorippa palustris* (*n* = 33)										
Carex utriculata	*Car utr*	34.7	8.7, IV	7.4, IV	**56.7, V**	41.9, V	—	2.4, III	0.6, II	4.4, III
Rorippa palustris	*Ror pal*	12.0	—	—	**0.2, I**	—	—	—	—	—
Carex vesicaria	*Car ves*	10.9	—	—	**2.0, II**	—	—	—	—	—
Veronica scutellata	*Ver scu*	7.0	—	—	**0.1, I**	—	—	—	—	—
(D) *Epilobium ciliatum* – *Plagiomnium cuspidatum* (*n* = 58)										
Epilobium ciliatum	*Epi cil*	50.8	—	0.3, II	—	**3.5, IV**	—	—	—	—
Plagiomnium cuspidatum	*Pla cus*	41.6	4.1, III	6.3, III	—	**18.3, V**	—	—	—	—
Marchantia polymorpha	*Mar plo*	36.3	—	—	—	**2.5, III**	—	—	—	—
Veronica americana	*Ver ame*	28.2	—	—	—	**1.5, II**	—	—	—	—
Galium trifidum	*Gal tri*	26.4	0.5, III	1.0, III	0.3, II	**1.3, IV**	—	—	—	—
Equisetum arvense	*Equ arv*	25.4	—	—	—	**5.3, II**	—	—	—	—
Symphyotrichum eatonii	*Sym eat*	24.9	—	—	—	**4.4, II**	—	—	—	—
Poa palustris	*Poa pal*	23.4	—	—	—	**0.6, II**	—	—	—	—
Glyceria striata	*Gly str*	23.2	—	—	—	**0.5, II**	—	—	—	—
Senecio triangularis	*Sen tri*	22.4	—	—	—	**1.5, II**	—	—	—	—
(E) *Kalmia microphylla* – *Sphagnum russowii* (*n* = 25)										
Kalmia microphylla	*Kal mic*	56.2	—	—	—	—	**13.8, IV**	—	—	—
Sphagnum russowii	*Sph rus*	42.5	—	—	—	—	**37.2, III**	—	—	—
Gymnocolea inflata	*Gym inf*	36.0	—	—	—	—	**10.0, II**	—	—	—
Vaccinium occidentale	*Vac occ*	29.6	—	6.0, II	—	—	**8.8, III**	—	—	—
Pinus contorta var. *latifolia*	*Pin cor*	28.4	—	3.6, II	—	—	**7.7, III**	—	—	—
Sphagnum lindbergii	*Sph lin*	28.0	—	—	—	—	**16.2, II**	—	—	—

Published by NRC Research Press

Table 3 (*concluded*).

Scientific name	Abbrev.	Indic.	Mean cover and constancy class by plant community							
			A	B	C	D	E	F	G	H
Drepanocladus polygamus	*Dre pol*	24.0	—	—	—	—	**3.6, II**	—	—	—
Polytrichum commune	*Pol com*	21.2	—	—	—	—	**6.4, II**	—	—	—
Ledum glandulosum	*Led gla*	19.3	—	—	—	—	**5.2, II**	—	—	—
Sphagnum riparium	*Sph rip*	14.3	—	—	—	—	**10.0, II**	—	—	—
(F) *Eleocharis quinqueflora* – *Carex livida* (*n* = 74)										
Eleocharis quinqueflora	*Ele qui*	61.7	—	3.2, II	—	—	—	**26.2, V**	—	—
Carex livida	*Car liv*	25.7	—	—	—	—	—	**7.6, III**	—	5.5, II
Tofieldia glutinosa subsp. *montana*	*Tof glu*	23.5	—	—	—	—	—	**1.4, II**	—	—
Drosera anglica	*Dro ang*	20.7	—	—	—	—	—	**3.1, II**	—	2.0, II
Triglochin maritimum var. *elatum*	*Tri mar*	19.3	—	—	—	—	—	**2.5, II**	—	—
Scorpidium scorpioides	*Sco sco*	15.6	—	—	—	—	—	**4.7, II**	—	—
Carex buxbaumii	*Car bux*	14.7	—	—	—	—	—	**2.9, II**	—	—
Carex echinata	*Car ech*	14.7	—	—	—	—	—	**0.8, II**	—	—
Campylium stellatum	*Cam ste*	13.2	—	—	—	—	—	**6.1, II**	—	—
Eriophorum angustifolium	*Eri ang*	12.5	—	0.9, II	—	—	—	**1.7, II**	—	1.3, I
(G) *Eleocharis palustris* – *Schoenoplectus acutus* var. *occidentalis* (*n* = 30)										
Eleocharis palustris	*Ele pal*	25.1	—	—	—	—	—	—	**10.8, II**	—
Schoenoplectus acutus var. *occidentalis*	*Sch acu*	23.0	—	—	—	—	—	—	**10.3, II**	—
Carex nebrascensis	*Car neb*	19.1	—	—	—	—	—	—	**5.5, II**	—
Utricularia minor	*Utr min*	17.9	—	—	1.5, I	—	—	—	**4.3, III**	1.4, I
Typha latifolia	*Typ lat*	16.1	—	—	—	—	—	—	**8.0, II**	—
Eleocharis rostellata	*Ele ros*	12.9	—	—	—	—	—	—	**6.2, I**	—
Eleocharis flavescens var. *thermalis*	*Ele fla*	12.1	—	—	—	—	—	—	**9.3, I**	—
Juncus brevicaudatus	*Jun bre*	11.8	—	—	—	—	—	0.7, II	**1.2, II**	—
Nuphar lutea subsp. *polysepala*	*Nup lut*	11.5	—	—	—	—	—	—	**2.3, I**	—
Potamogeton spp.	*Pot* spp.	6.1	—	—	0.8, I	—	—	—	**1.1, I**	—
(H) *Carex lasiocarpa* – *Carex limosa* (*n* = 59)										
Carex lasiocarpa	*Car las*	62.5	—	—	—	—	—	—	—	**22.5, IV**
Carex limosa	*Car lim*	31.8	—	—	—	—	—	—	—	**11.9, III**
Menyanthes trifoliata	*Men tri*	30.9	—	—	—	—	—	—	—	**5.9, III**
Potentilla palustris	*Pol pal*	23.8	—	—	—	—	—	—	—	**5.4, III**
Scheuchzeria palustris	*Sch pal*	17.9	—	—	—	—	—	—	—	**1.1, I**
Mentha arvensis	*Men arv*	16.3	—	—	—	—	—	—	—	**1.3, II**
Sphagnum subsecundum	*Sph sub*	9.7	—	—	—	—	—	—	—	**5.2, I**

Note: Communities are named by the top two indicator species, which are not necessarily the most dominant. "Abbrev." refers to the abbreviation used in Fig. 3. "Indic." is the indicator value, significant at $P < 0.05$ for all species listed. Mean cover value and constancy class shown for each species across all communities. Values are shown in bold under the community for which the species is an indicator. Species with low constancy (class I) were excluded for readability except if among the top indicator species. Constancy classes: I, 0%–20%; II, >20%–40%; III, >40%–60%; IV, >60%–80%; V, >80%.

Published by NRC Research Press

Table 4. Spearman's rank correlation coefficients of environmental variables with nonmetric multidimensional scaling sample scores for ordinations run using all species, vascular plants only, and bryophytes only.

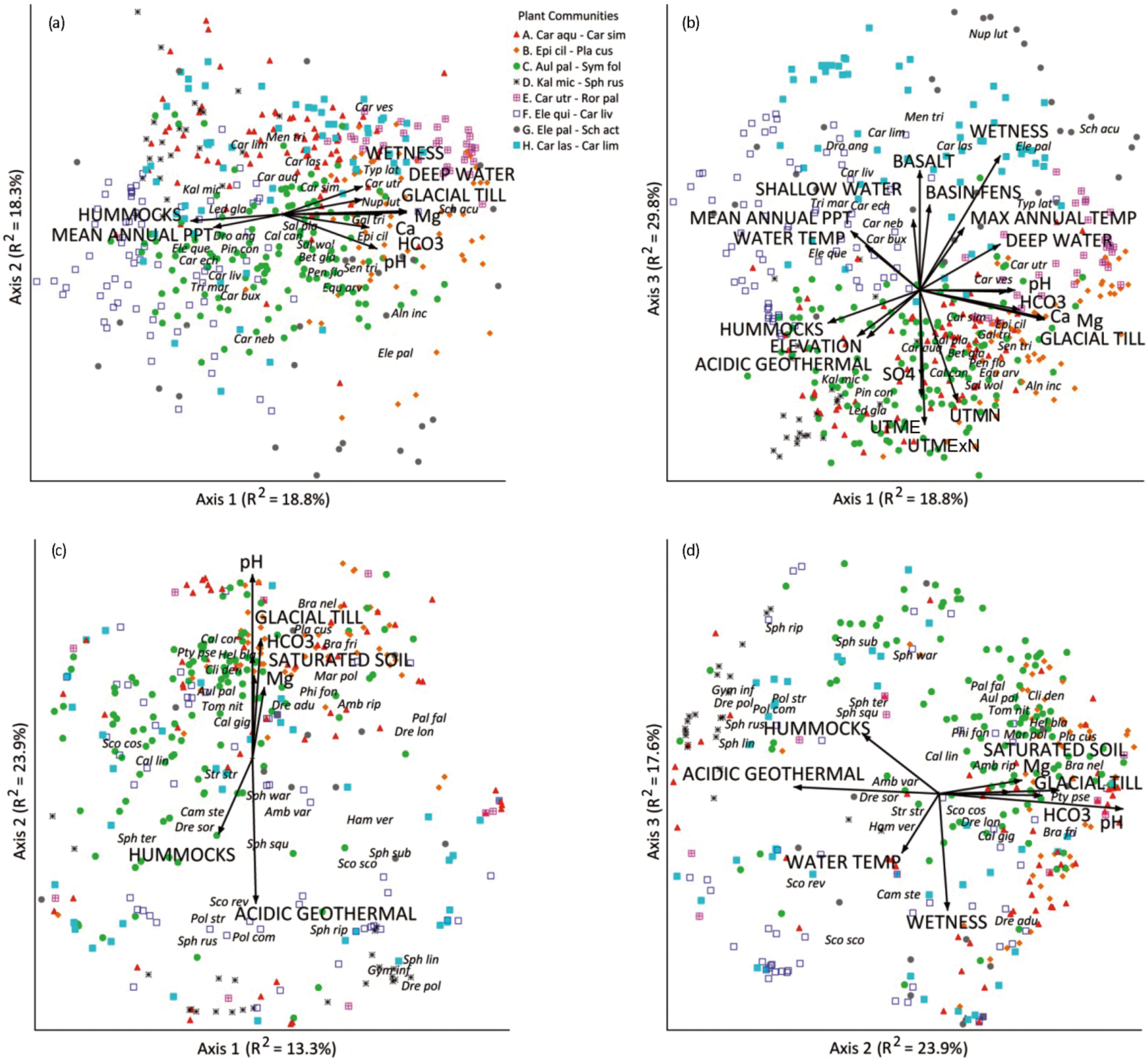
	All species			Vascular plants			Bryophytes		
Variable	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Regional variables									
Elev	0.09	**–0.41** ***	–0.05	–0.30***	0.16**	–0.26***	–0.05	–0.22***	–0.06
AnnPPT	**–0.40** ***	–0.05	0.21***	–0.32***	–0.14**	0.29***	–0.16**	–0.31***	–0.09
MeanTemp	–0.04	0.37***	0.01	0.29***	–0.07	0.21***	0.10	0.21***	0.08
MaxTemp	–0.14**	**0.40** **	0.06	0.25***	–0.13**	0.03***	0.00	0.16**	0.08
MinTemp	0.04	0.21***	–0.05	0.19***	0.06	0.08	0.08	0.10	0.10
Geoth	0.10	**–0.43** ***	–0.10	–0.28***	0.18***	–0.26***	0.07	**–0.46** ***	0.10
Till	0.37***	0.20***	–0.15**	**0.42** ***	0.04	–0.21***	0.11	**0.42** ***	0.07
Rhy	–0.25***	–0.12**	0.19***	–0.27***	–0.19***	0.13**	–0.17**	–0.04	–0.14**
Bas	–0.34***	0.29***	0.07	0.00	0.00	**0.42** ***	0.04	–0.20***	0.12
And	0.12**	0.05	–0.11	0.11	0.13**	–0.09	0.06	0.07	–0.07
Landscape variables									
UTME	0.37***	–0.20***	–0.14**	0.05	0.14**	–0.39***	0.10	0.10	0.04
UTMN	**0.45** ***	–0.09	–0.16**	0.23***	0.11	–0.40***	0.09	0.27***	0.02
UTME×N	**0.42** ***	–0.21***	–0.16**	0.09	0.15**	**–0.44** ***	0.11	0.15**	0.04
pH	0.11	0.32***	0.03	0.37***	–0.22***	0.03	0.03	**0.52** ***	–0.15**
WtrTemp	–0.35***	–0.07	0.14**	–0.28***	–0.10	0.25***	–0.16**	–0.23***	**–0.29** ***
EC	0.27***	0.14**	–0.06	0.31***	–0.06	–0.14**	0.07	0.18***	–0.01
Ca^{2+}	0.33***	0.17***	–0.11	**0.38** ***	–0.02	–0.17***	0.08	0.26***	0.03
Mg^{2+}	0.38***	0.21***	–0.15**	**0.42** ***	0.07	–0.20***	0.13	0.32***	0.04
Na^{+}	0.15**	0.04	0.06	0.15**	–0.17***	–0.10	–0.02	0.10	–0.10
K^{+}	0.02	0.04	0.11	0.01	–0.11	0.01	–0.02	–0.02	–0.05
HCO_3^{-}	0.22***	0.25***	0.01	0.35***	–0.13**	–0.06	0.00	0.39***	–0.06
Cl^{-}	0.13**	0.10	0.04	0.15**	–0.08	–0.06	0.04	0.05	–0.01
SO_4^{2-}	0.33***	–0.23***	–0.12	0.04	0.08	–0.36***	0.13	–0.06	0.07
Basin	–0.24***	0.28***	**–0.22** ***	0.12**	**0.27** ***	0.35***	–0.08	–0.04	–0.10
GntSlp	0.07	–0.36***	0.15**	–0.27***	–0.17***	–0.24***	–0.02	–0.17	0.01
StpSlp	0.20***	0.13**	0.04	0.22***	–0.08	–0.12**	0.07	0.24***	0.09
SpgMnd	0.11	0.07	0.08	0.08	–0.10	–0.05	0.14**	0.14**	0.04
Local variables									
Slope	0.25***	–0.06	0.18***	0.05	**–0.23** ***	–0.27***	0.07	0.24***	0.10
DeepWtr	–0.10	0.24***	**–0.44** ***	0.34***	0.15**	0.26***	0.07	–0.01	–0.17**
ShalWtr	–0.30***	0.13**	0.00	–0.09	0.10	0.32***	0.10	–0.09	**–0.31** ***
Sat	0.33***	0.02	0.12	0.16***	–0.12**	–0.31***	0.05	0.35***	0.14**
Hum	0.04	–0.39***	0.20***	–0.36***	–0.10	–0.22***	**–0.22** ***	–0.33***	**0.29** ***
Wet	–0.25***	**0.40** ***	**–0.38** ***	0.33***	0.20***	**0.44** ***	**0.20** ***	0.11	**–0.41** ***
FltMat	–0.31***	0.12**	–0.08	–0.10	**0.23** ***	0.03***	0.02	–0.19***	0.04
SeepSpg	0.13**	0.12**	0.12	0.17***	–0.22***	–0.05	**0.17** **	0.19***	0.04
Peat	0.03	0.03	–0.05	0.08	0.00	0.00	0.08	0.07	0.08
Car	0.02	0.10	–0.01	0.10	–0.08	0.04	–0.02	0.13	0.10
Nit	0.11	–0.01	–0.03	0.05	–0.02	–0.09	0.07	0.07	0.02
C/N	–0.15**	0.16**	0.03	0.03	–0.03	0.20***	–0.07	0.02	0.09

Note: Variable abbreviations are given in Table 1. Three of the strongest correlations for each axis within each analysis are highlighted in bold. **, $P < 0.01$; ***, $P < 0.001$.

water chemistry, as has been shown for other regions of the Rocky Mountains (Cooper and Andrus 1994; Cooper 1996; Cooper et al. 2002; Chimner et al. 2010) and elsewhere in North America (Halsey et al. 1997; Bedford and Godwin 2003). Site-level groundwater chemistry, however, accounted for greater variation in species composition than regional bedrock geology, and there was not complete overlap between them, indicating that bedrock geology is only a coarse filter for species distribution. Regional-scale bedrock geology broadly influences fen vegetation by controlling the range of groundwater chemistry possible, but the specific chemical composition of groundwater at any given fen may be influenced by annual precipitation, groundwater flow paths, and discharge rates, making site-level water chemistry more important to fen species composition.

Regional bedrock geology and landscape-scale water chemistry can be used to classify fens along the poor–rich gradient. Most individual water chemistry parameters in YNP fens followed the poor–rich gradient, similar to peatland water chemistry across Europe and North America (Sjörs 1950*a*; Glaser et al. 1981, 2004; Malmer 1986; Mullen et al. 2000; Tahvanainen 2004). The relationship between pH and

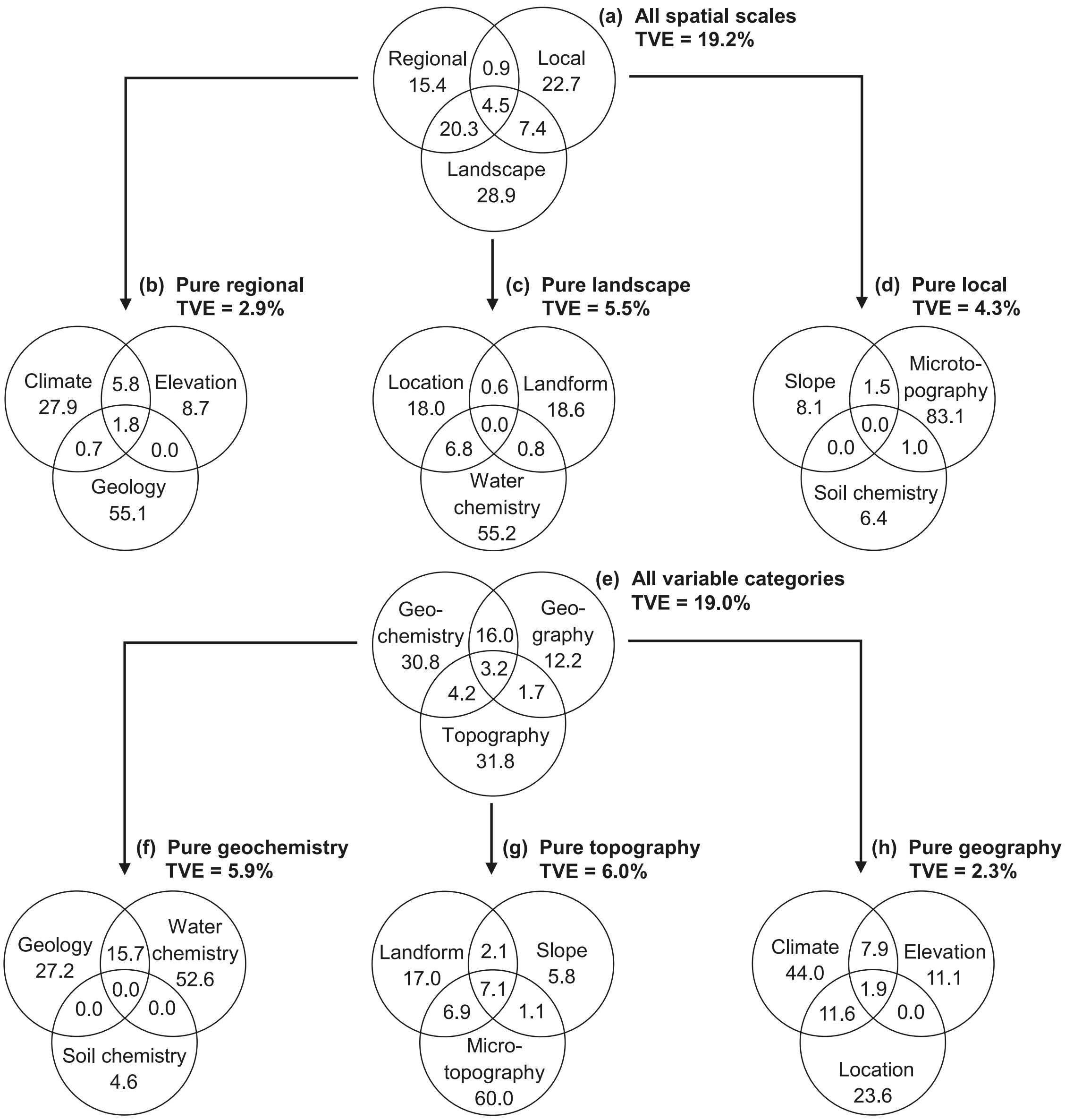
Fig. 3. Nonmetric multidimensional scaling ordination of vegetation plots and selected indicator species based on vascular plants ((*a*) axes 1 and 2; (*b*) axes 1 and 3) and bryophytes ((*c*) axes 1 and 2; (*d*) axes 2 and 3). Symbols represent the eight plant communities identified through cluster analysis. Legend shown in (*a*) applies to the entire figure. Details on each plant community and abbreviations for species names shown in Table 3.



ion concentrations, however, did not exclusively follow traditional categories. Glacial till watersheds had the highest pH and ionic concentrations and supported rich fens. Volcanic watersheds also supported rich fens with indicator species *Tomentypnum nitens*, *Sphagnum warnstorfii*, and *Campylium stellatum*, but were characterized by lower pH and ionic concentrations than found in glacial till watersheds. Although groundwater within volcanic watersheds had lower concentrations of mineral ions, seasonal or summer-long flushing by snowmelt-recharged groundwater likely raised the total annual flux of ions to support rich fen conditions (Cooper 1990; Cooper and Andrus 1994).

Sphagnum-dominated vegetation in YNP's acidic geothermal fens resembled boreal bogs or poor fens, with *Sphagnum* lawns and hummocks, stunted conifer trees, and many species in the family Ericaceae. Although these sites had very low pH values, they contained ion concentrations similar to rich fens. The acidity of geothermal fens is produced when hydrogen sulphide gas from geothermal vents enters groundwater and is oxidized to form sulphuric acid (Mosser et al. 1973). Fens with similar water chemistry and flora occur where the oxidation of iron pyrite creates groundwater rich in sulphuric acid in the San Juan Mountains of Colorado (Cooper et al. 2002, Chimner et al. 2010), the Black Hills of South Dakota, the Warner Mountains of California, and the Andes of Peru (Cooper et al. 2010). In both situations, acid

Fig. 4. Proportion of variance explained by separate variable sets within each of eight partial canonical correspondence analysis models, illustrated by Venn diagrams. (*a*) All variables grouped by spatial scale; (*b*) regional-scale variable sets; (*c*) landscape-scale (site level) variable sets; (*d*) local-scale (stand-level) variable sets; (*e*) all variables grouped by category; (*f*) geochemical variable sets; (*g*) topographic variable sets; (*h*) geographic variable sets. TVE, total variance within the species data explained by the model. All other numbers represent the relative proportion of each variable set within the model. Areas not drawn to scale.



production is driven by geochemical processes not autochthonous *Sphagnum* spp. ion exchange, yet the acidic environment supports vegetation similar in composition to that of bogs and poor fens (Cooper et al. 2002). *Sphagnum russowii*, which commonly dominates poor fens (Andrus 1986), was the most abundant moss in YNP's acidic geothermal fens, and the widely disjunct boreal species *Sphagnum lindbergii* was locally abundant (Lemly et al. 2007). In the most acidic areas of geothermal fens, groundwater pH was as low as 2.9 and *Sphagnum* spp. were replaced by carpets of *Polytrichum commune* and *Gymnocolea inflata*, similar to the composition of communities in boreal bogs and poor fens (Chee and Vitt 1989; Slack 1994) and acidic, mineral-rich waters draining a volcanogenic sulphide deposit in Alaska (Gough et al. 2006). Though the vegetation is not unique, water chemistry within acidic geothermal fens and iron fens in mountainous regions of the western hemisphere represents a distinct type of fen that is poorly characterized by the poor–rich gradient.

Landforms and topography

Topographic variation created by site landform, stand slope, and microtopography is a second important gradient controlling species distribution. Stand microtopography was more strongly correlated with species patterns and explained a greater percentage of the variance than site landform, apparently because plants respond to finer-scale environmental variation. Several communities, however, had high fidelity to particular landforms, indicating that topography functions on both landscape and local scales. The floating mat community *Carex lasiocarpa* – *Carex limosa* occurred primarily in basin fens, while stands of *Aulacomnium palustre* – *Symphyotrichum foliaceus*, often dominated by the woody species *Salix planifolia* and *Salix wolfii*, occurred primarily in sloping fens. While basin fens have restricted outflows and limited water circulation, groundwater in sloping fens flows at or below the peat surface, and the higher discharge rate leads to oxygenated soils more suitable for woody species (Rydin and Jeglum 2006).

Stand microtopography represents variation in water table depth and water retention, which are important drivers of peatland vegetation patterns (Sjörs 1950*b*, Slack et al. 1980; Økland 1990*a*; Bragazza et al. 2005). This was most evident in gently sloping fens with strings and flarks, where microtopography of as little as 10–20 cm resulted in a change from one community to another, typically *Aulacomnium palustre* – *Symphyotrichum foliaceus* on strings and *Eleocharis quinqueflora* – *Carex livida* within flarks. Many peatland species, particularly bryophytes, have a narrow tolerance for water table depth and can be sorted along a water table gradient (Andrus 1986; Gignac 1992; Bragazza and Gerdol 1996). This gradient results in analogous patterns in peatland vegetation throughout the northern hemisphere. Strings and flarks of Red Lake Peatland in Minnesota had a species composition similar to that of YNP fens, with low woody species dominating strings and *Carex livida*, *Triglochin maritima*, and *Scorpidium scorpioides* in flarks (Glaser et al. 1981).

The importance of stand-scale microtopography and slope also reflects, in part, the peatland margin – peatland expanse gradient. Stands on fen margins often had steeper slopes and were drier than peatland centers, and these areas were more likely to be dominated by shrubs and (or) trees. This gradient is an expression of several underlying hydrologic and geochemical processes, including the loss of ions to plant and microorganism uptake and adsorption by the peat body as mineral-rich groundwater flows from the fen margin to the fen centre (Sjörs 1950*b*; Johnson and Steingraeber 2003). Fen margins may also have higher discharge rates, leading to the increased delivery rate of ions (Malmer 1986). In certain locations, margins may experience greater water table fluctuations, which may increase organic matter decomposition rates.

Climate and elevation

Regional gradients of climate and elevation had less direct influence than geochemistry or topography on species distribution patterns. Although a distinct climatic gradient exists across the park, the gradient is correlated with bedrock geology, a stronger driver of vegetation patterns because of its influence on water chemistry. The driest areas of YNP contain glacial till that produces neutral to alkaline groundwater with high mineral content, while the wettest areas contain volcanic bedrock that produces groundwater with low ionic concentrations. The most notable effect of climate was in the southwest corner of YNP, where high annual precipitation, combined with flat topography, contributes to expansive basin fens dominated by the *Carex lasiocarpa* – *Carex limosa* community.

Elevation alone explained little of the vegetation variance in YNP. Low-elevation sites occurred at both ends of the precipitation gradient, within watersheds with different substrates, and did not share uniform characteristics. Acidic geothermal fens often occurred at higher elevations, but low groundwater pH and hummock–hollow topography within these sites were more influential on species composition than elevation. The mountain topography of YNP is steep, with bare slopes in many regions, and fens were not found above 2800 m elevation. In the Wind River range of Wyoming, ~300 km south of YNP, fens occur in high-elevation valleys at up to 3200 m (Cooper and Andrus 1994) and contain several subalpine species, such as *Carex scopulorum*, *Carex illota*, and *Salix eastwoodii*, that were rarely or never encountered in YNP fens. Though elevation was found to be significantly correlated with species distribution in Australian mountain peatlands (Clarke and Martin 1999), the relationship in YNP appears to be limited by the landscape and complexity of other gradients.

Conclusion

Fen vegetation in YNP responded to gradients at regional, landscape, and local spatial scales. Bryophyte species were tightly controlled by groundwater chemistry, while vascular species were influenced by a broader range of factors, including regional climate, elevation, and site landform. Across spatial scales, landscape (site level) factors showed the strongest relationship with species and community distribution. Together, site-level water chemistry, site landform, and location within YNP accounted for over 60% of variation explained within the species data. When variables were grouped categorically, two multiscale gradients were strongly related to vegetation patterns. The first is a geochemical gradient influenced by dominant regional bedrock but most clearly expressed at the landscape scale. The second important gradient is topography, represented by stand microtopography and site landform, both of which influence the distribution of species as well as vegetation communities. Additional regional gradients of elevation and climate showed weaker correlations with patterns of fen vegetation, but these correlations may have been hindered by YNP's geography and may not fully represent relationships to be expected in other high-mountain regions. Most fens in YNP were classified as rich fens, though there was a wide range of water chemistry values. Watershed bedrock geology created three main water chemistry regimes in YNP fens: (*i*) glacial till produced groundwater with high pH and ionic concentrations; (*ii*) volcanic bedrock created groundwater with low pH and ionic concentrations; and (*iii*) acidic geothermal activity produced groundwater with low pH but high ionic concentrations. While differences in water chemistry between glacial till and volcanic bedrock can be interpreted as variation along the poor–rich gradient, acidic geothermal fens represent a distinct category of peatland that does not fit the poor–rich gradient.

Acknowledgments

The Canon Foundation and Yellowstone National Park (YNP) provided funding for this project. Special thanks to YNP staff, including Mary Hektner at the Yellowstone Center for Research; Jennifer Whipple, curator of the Yellowstone Herbarium; Heidi Anderson and Vicki Pecha, park botanists; Christie Hendrix in the research permit office; and Steve Miller, who helped with the park's GIS files. Dr. Richard Andrus of Binghamton University, New York, and Dr. William Weber of the University of Colorado at Boulder provided invaluable help with bryophyte identification. Thanks to Sarah Vincent for field assistance, to committee members Jill Baron and Dave Steingraeber for helpful insight, and to fellow students within the Cooper lab.

References

Andrus, R.E. 1986. Some aspects of *Sphagnum* ecology. Can. J. Bot. **64**(2): 416–426. doi:10.1139/b86-057.

Bedford, B.L., and Godwin, K.S. 2003. Fens of the United States: distribution, characteristics, and scientific connection versus legal isolation. Wetlands, **23**(3): 608–629. doi:10.1672/0277-5212(2003)023[0608:FOTUSD]2.0.CO;2.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology, **73**(3): 1045–1055. doi:10.2307/1940179.

Bragazza, L., and Gerdol, R. 1996. Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy). Ann. Bot. Fenn. **33**(1): 11–20.

Bragazza, L., and Gerdol, R. 1999. Hydrology, groundwater chemistry and peat chemistry in relation to habitat conditions in a mire on the south-eastern Alps of Italy. Plant Ecol. **144**(2): 243–256. doi:10.1023/A:1009868113976.

Bragazza, L., and Gerdol, R. 2002. Are nutrient availability and acidity–alkalinity gradients related in *Sphagnum*-dominated peatlands? J. Veg. Sci. **13**(4): 473–482. doi:10.1111/j.1654-1103.2002.tb02074.x.

Bragazza, L., Rydin, H., and Gerdol, R. 2005. Multiple gradients in mire vegetation: a comparison of a Swedish and an Italian bog. Plant Ecol. **177**(2): 223–236. doi:10.1007/s11258-005-2182-2.

Bridgham, S.D., Pastor, J., Janssens, J.A., Chapin, C., and Malterer, T.J. 1996. Multiple limiting gradients in peatlands: a call for a new paradigm. Wetlands, **16**(1): 45–65. doi:10.1007/BF03160645.

Chadde, S.W., Shelly, J.S., Bursik, R.J., Moseley, R.K., Evenden, A.G., Mantas, M., Rabe, F., and Heidel, B. 1998. Peatlands on National Forests of the northern Rocky Mountains: ecology and conservation. RMRS-GTR-11. U.S. Forest Service, Rocky Mountain Research Station, Ogden, Utah.

Chee, W.L., and Vitt, D.H. 1989. The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada. Wetlands, **9**(2): 227–261. doi:10.1007/BF03160747.

Chimner, R.A., Lemly, J.M., and Cooper, D.J. 2010. Mountain fen distribution, types and restoration priorities, San Juan Mountains, Colorado, USA. Wetlands, **30**(4): 763–771. doi:10.1007/s13157-010-0039-5.

Christiansen, R.L. 2001. The Quaternary and Pliocene Yellowstone Plateau volcanic field of Wyoming, Idaho, and Montana. Geological Survey Professional Paper 729-G. U.S. Geological Survey, Washington, D.C.

Clarke, P.J., and Martin, A.R.H. 1999. *Sphagnum* peatlands of Kosciuszko National Park in relation to altitude, time and disturbance. Aust. J. Bot. **47**(4): 519–536. doi:10.1071/BT97129.

Cooper, D.J. 1990. Ecology of wetlands in Big Meadows, Rocky Mountain National Park, Colorado. Biological Report 90(15). U.S. Fish and Wildlife Service, Washington, D.C.

Cooper, D.J. 1996. Water and soil chemistry, floristics, and phytosociology of the extreme rich High Creek Fen, in South Park, Colorado, USA. Can. J. Bot. **74**(11): 1801–1811. doi:10.1139/b96-217.

Cooper, D.J., and Andrus, R.E. 1994. Patterns of vegetation and water chemistry in peatlands of the west-central Wind River Range, Wyoming, USA. Can. J. Bot. **72**(11): 1586–1597. doi:10.1139/b94-196.

Cooper, D.J., Andrus, R.E., and Arp, C.D. 2002. *Sphagnum balticum* in a southern Rocky Mountain iron fen. Madrono, **49**(3): 186–188.

Cooper, D.J., Wolf, E.C., Colson, C., Vering, W., Granda, A., and Meyer, M. 2010. Alpine peatlands of the Andes, Cajamarca, Peru. Arct. Antarct. Alp. Res. **42**(1): 19–33. doi:10.1657/1938-4246-42.1.19.

Despain, D.G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Boulder, Colo.

Deutsch, W.J. 1997. Groundwater geochemistry: fundamentals and applications to contamination. Lewis Publishers, New York.

Dorn, R.D. 2001. Vascular plants of Wyoming. 3rd ed. Mountain West Publishing, Cheyenne, Wyo.

Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. **67**(3): 345–366.

ESRI. 2005. ArcGIS version 9.1. Environmental Systems Research Institute, Inc., Redlands, Calif.

Gerdol, R., Tomaselli, M., and Bragazza, L. 1994. A floristic-ecologic classification of five mire sites in the montane-subalpine belt of South Tyrol (South Alps, Italy). Phyton-Annales Rei Bot. **34**(1): 35–56.

Gignac, L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climactic and ecological gradients in western Canada. Bryologist, **95**(4): 406–418. doi:10.2307/3243564.

Gignac, L.D., and Vitt, D.H. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. Bryologist, **93**(1): 7–22. doi:10.2307/3243541.

Gignac, D.L., Vitt, D.H., Zoltai, S.C., and Bayley, S.E. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. Nova Hedwigia, **53**(1–2): 27–71.

Glaser, P.H. 1992. Raised bogs in eastern North America: regional controls for species richness and floristic assemblages. J. Ecol. **80**(3): 535–554. doi:10.2307/2260697.

Glaser, P.H., Wheeler, G.A., Gorham, E., and Wright, H.E., Jr. 1981. The patterned mires of the Red Lake Peatland, northern Minnesota: vegetation, water chemistry and landforms. J. Ecol. **69**(2): 575–599. doi:10.2307/2259685.

Glaser, P.H., Janssens, J.A., and Siegel, D.I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota. J. Ecol. **78**(4): 1021–1048. doi:10.2307/2260950.

Glaser, P.H., Siegel, D.I., Reeve, A.S., Janssens, J.A., and Janecky, D.R. 2004. Tectonic drivers for vegetation patterning and landscape evolution in the Albany River region of the Hudson Bay Lowlands. J. Ecol. **92**(6): 1054–1070. doi:10.1111/j.0022-0477.2004.00930.x.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable response to climatic warming. Ecol. Appl. **1**(2): 182–195. doi:10.2307/1941811.

Gough, L.P., Eppinger, R.G., Briggs, P.H., and Giles, S. 2006. Biogeochemical characterization of an undisturbed highly acidic, metal-rich bryophyte habitat, east-central Alaska, USA. Arct. Antarct. Alp. Res. **38**(4): 522–529. doi:10.1657/1523-0430(2006)38[522:BCOAUH]2.0.CO;2.

Hájek, M., Horsák, M., Hájková, P., and Dítě, D. 2006. Habitat diversity of central European fens in relation to environmental gradients and an effort to standardize fen terminology in ecological studies. Perspect. Plant Ecol. Evol. Syst. **8**(2): 97–114. doi:10.1016/j.ppees.2006.08.002.

Hájková, P., and Hájek, M. 2004. Bryophyte and vascular plant response to base-richness and water levels gradients in western Carpathian *Sphagnum*-rich mires. Folia Geobot. **39**(4): 335–351. doi:10.1007/BF02803207.

Hájková, P., Wolf, P., and Hájek, M. 2004. Environmental factors and Carpathian spring fen vegetation: the importance of scale and temporal variation. Ann. Bot. Fenn. **41**(4): 249–262.

Halsey, L.A., Vitt, D., and Zoltai, S. 1997. Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. Wetlands, **17**(2): 243–262. doi:10.1007/BF03161413.

Johnson, J.B., and Steingraeber, D.A. 2003. The vegetation and ecological gradients of calcareous mires in the South Park Valley, Colorado. Can. J. Bot. **81**(3): 201–219. doi:10.1139/b03-017.

Jootsen, H., and Clarke, D. 2002. Wise use of mires and peatlands: background and principles including a framework for decision-making. International Mire Conservation Group and International Peat Society, Finland.

Lemly, J.M., Andrus, R.E., and Cooper, D.J. 2007. *Sphagnum lindbergii* Schimp. in Lindb., and other new records of *Sphagnum* in geothermal fens, Yellowstone National Park, Wyoming, USA. Evansia, **24**(2): 31–34. doi:10.1639/0747-9859-24.2.31.

Lesica, P. 1986. Vegetation and flora of Pine Butte Fen, Teton County, Montana. Great Basin Nat. **46**(1): 22–32.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. **64**(2): 375–383. doi:10.1139/b86-054.

McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore.

McCune, B., and Mefford, M.J. 2006. PC-ORD, Multivariate analysis of ecological data. Version 5.0. MjM Software Design, Gleneden Beach, Ore.

McQueen, C.R., and Andrus, R.E. 2007. *Sphagnum–Sphagnaceae*. Flora of North America north of Mexico. Vol. 27: bryophytes: mosses, Part 1. *Edited by* Flora of North America Editorial Committee. Oxford University Press, New York.

Mitsch, W.J., and Gosselink, J.G. 2007. Wetlands. 4th ed. John Wiley & Sons, Inc., N.J.

Moore, P.D., and Bellamy, D.J. 1974. Peatlands. Springer, New York.

Mosser, J.L., Mosser, A.G., and Brock, T.D. 1973. Bacterial origin of sulfuric acid in geothermal habitats. Science, **179**(4080): 1323–1324. doi:10.1126/science.179.4080.1323. PMID:17835938.

Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Mullen, S.F., Janssens, J.A., and Gorham, E. 2000. Acidity of and the concentration of major and minor metals in the surface waters of bryophyte assemblages from 20 North American bogs and fens. Can. J. Bot. **78**(6): 718–727.

Økland, R.H. 1990*a*. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. II. Identification of gradients by detrended (canonical) correspondence analysis. Nord. J. Bot. **10**(1): 79–108. doi:10.1111/j.1756-1051.1990.tb01755.x.

Økland, R.H. 1990*b*. Regional variation in SE Fennoscandian mire vegetation. Nord. J. Bot. **10**(3): 285–310. doi:10.1111/j.1756-1051.1990.tb01774.x.

Økland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. J. Veg. Sci. **10**(1): 131–136. doi:10.2307/3237168.

Økland, R.H., and Eilertsen, O. 1994. Canonical correspondence-analysis with variation partitioning: some comments and an application. J. Veg. Sci. **5**(1): 117–126. doi:10.2307/3235645.

Pfaff, J.D., Brockhoff, C.A., and O'Dell, J.W. 1989. The determination of inorganic anions in water by ion chromatography: Method 300.0. U.S. Environmental Protection Agency, Cincinnati, Ohio.

Reeve, A.S., Siegel, D.I., and Glaser, P.H. 1996. Geochemical controls on peatland pore water from the Hudson Bay Lowland: a multivariate statistical approach. J. Hydrol. **181**(1–4): 285–304. doi:10.1016/0022-1694(95)02900-1.

Rodman, A., Shovic, H., and Thoma, D. 1996. Soils of Yellowstone National Park. YCR-NRSR-96-2. Yellowstone Center for Resources, Yellowstone National Park, Wyo.

Rydin, H., and Jeglum, J. 2006. The biology of peatlands. Oxford University Press, New York.

SAS Institute Inc. 2002. SAS version 9.1. SAS Institute Inc., Cary, N.C.

Sjörs, H. 1950*a*. On the relation between vegetation and electrolytes in North Swedish mire waters. Oikos, **2**(2): 241–258. doi:10.2307/3564795.

Sjörs, H. 1950*b*. Regional studies in north Swedish mire vegetation. Bot. Notiser, **2**: 173–222.

Slack, N.G. 1994. Can one tell the mire type from the bryophytes alone? J. Hattori Bot. Lab. **75**: 149–159.

Slack, N.G., Vitt, D.H., and Horton, D.G. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. Can. J. Bot. **58**(3): 330–350. doi:10.1139/b80-034.

Smith, R.B., and Siegel, L.J. 2000. Windows into the Earth: the geologic story of Yellowstone and Grand Teton National Parks. Oxford University Press, New York.

Tahvanainen, T. 2004. Water chemistry of mires in relation to the poor-rich vegetation gradient and contrasting geochemical zones of the north-eastern Fennoscandian Shield. Folia Geobot. **39**(4): 353–369. doi:10.1007/BF02803208.

Tahvanainen, T., and Tuomaala, T. 2003. The reliability of mire water pH measurements — a standard sampling protocol and implications to ecological theory. Wetlands, **23**(4): 701–708. doi:10.1672/0277-5212(2003)023[0701:TROMWP]2.0.CO;2.

Turunen, J., Tomppo, E., Tolonen, K., and Reinikainen, A. 2002. Estimating carbon accumulation rates of undrained mires in Finland: application to boreal and subarctic regions. Holocene, **12**(1): 69–80. doi:10.1191/0959683602hl522rp.

USDA–NRCS. 2009. Processed annual precipitation, derived for the 30-year period of 1971–2000. U.S. Department of Agriculture, National Resource Conservation Service, National Cartography and Geospatial Center, Fort Worth, Tex. Available from http://datagateway.nrcs.usda.gov [accessed 13 February 2009].

USEPA. 1983. Methods for chemical analysis of water and wastes. EPA-600-4-79-020. US Environmental Protection Agency, Cincinnati, Ohio.

USGS. 1972 Geologic map of Yellowstone National Park. Miscellaneous Geologic Investigations I-711. US Geological Survey, Washington, D.C.

van Tongeren, O.F.R. 1995. Cluster analysis. *In* Data analysis in community and landscape ecology. *Edited by* R.H.G. Jongman et al. Cambridge University Press, New York.

Vitt, D.H., and Chee, W.L. 1990. The relationships of vegetation to surface-water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio, **89**(2): 87–106. doi:10.1007/BF00032163.

Weber, W.A., and Wittmann, R.C. 2007. Bryophytes of Colorado: mosses, liverworts, and hornworts. Pilgrims Process, Inc., Santa Fe, N.M.

Wheeler, B.D., and Proctor, M.C.F. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. J. Ecol. **88**(2): 187–203. doi:10.1046/j.1365-2745.2000.00455.x.

Wieder, R.K., and Vitt, D.H. 2006. Boreal peatland ecosystems. Ecological Studies, Vol. 188. Springer, N.Y.

Winter, T.C., Harvey, J.W., Franke, O.L., and Alley, W.M. 1998. Ground water and surface water — a single resource. U.S. Geological Survey Circular 1139. U.S. Department of the Interior, Denver, Colo.

Appendix A

Tables A1 and A2 are found in the following pages.

Table A1. Observed mean (standard deviation in parentheses) of environmental variables by plant community (see Table 3 for plant community codes and indicator species).

Variable	Abbrev.	Units	A (*n* = 74)	B (*n* = 123)	C (*n* = 33)	D (*n* = 58)	E (*n* = 25)	F (*n* = 74)	G (*n* = 30)	H (*n* = 59)
Regional variables										
Elevation	Elev	m	2302 (195)	2301 (166)	2283 (203)	2155 (173)	2460 (67)	2294 (160)	2223 (143)	2151 (190)
Climate										
Mean annual precipitation	AnnPPT	mm	720 (186)	822 (206)	742 (191)	620 (214)	757 (79)	921 (168)	819 (193)	916 (151)
Mean annual temperature	MeanTemp	°C	1.1 (0.9)	1.0 (0.8)	1.2 (1.0)	1.7 (0.9)	0.6 (0.0)	1.0 (0.8)	1.2 (0.9)	1.9 (1.2)
Max. annual temperature	MaxTemp	°C	23.0 (1.5)	23.0 (1.4)	23.3 (1.7)	23.9 (1.4)	21.8 (0.6)	23.1 (1.3)	23.6 (1.0)	24.4 (1.6)
Min. annual temperature	MinTemp	°C	–15.9 (1.1)	–16.1 (1.1)	–16.0 (1.1)	–15.8 (0.9)	–16.3 (0.4)	–16.3 (1.0)	–16.2 (1.2)	–15.4 (1.4)
Dominant geology[a]										
Acidic geothermal (*n* = 33)	Geoth	No. of stands	9	—	—	—	20	3	1	—
Glacial till (*n* = 114)	Till	No. of stands	27	26	11	40	—	3	4	3
Rhyolite (*n* = 267)	Rhy	No. of stands	28	88	14	16	5	63	23	30
Basalt (*n* = 35)	Bas	No. of stands	1	1	2	—	—	5	2	24
Andesite (*n* = 27)	And	No. of stands	9	8	6	2	—	—	—	2
Landscape variables										
Site location										
UTM E	UTME	m	534 037 (15 271)	530 788 (14 546)	53 2121 (18 648)	540 105 (18 406)	544 216 (9939)	524 503 (12 363)	523 108 (14 483)	515 471 (19 874)
UTM N	UTMN	m	4 953 571 (23 506)	4 944 375 (28 318)	4 945 382 (30 812)	4 963 844 (18 872)	4 949 632 (8835)	4 929 428 (26 860)	4 936 018 (25 425)	4 914 002 (29 105)
UTM E × UTM N	UTME×N	10^6 m^2	264 529 (7312)	262 430 (6908)	263 144 (9045)	268 104 (9330)	269 361 (4580)	258 559 (6625)	258 216 (7595)	253 331 (10 600)
Groundwater chemistry										
pH	pH	na	6.14 (1.26)	6.27 (0.76)	6.4 (0.8)	6.85 (0.75)	4.07 (0.72)	6.26 (0.68)	6.37 (0.79)	5.74 (0.85)
Temperature	WtrTemp	°C	17.6 (5.5)	16.7 (5.1)	16.9 (4.5)	13.8 (5.0)	18.1 (2.9)	21.3 (5.9)	22.2 (8.5)	17.9 (3.8)
Electrical conductivity	EC	µS/cm	192.7 (142.3)	114.9 (109.7)	158.1 (111.1)	175.4 (107.6)	160.1 (158.4)	83.0 (76.5)	256.7 (311.9)	82.2 (60.5)
$[Ca^{2+}]$	Ca^{2+}	mg/L	20.2 (18.5)	10.7 (11.0)	16.8 (13.2)	20.9 (15.1)	13.4 (14.3)	6.7 (7.6)	14.2 (11.5)	7.0 (7.8)
$[Mg^{2+}]$	Mg^{2+}	mg/L	8.4 (11.1)	3.4 (6.0)	7.4 (9.5)	6.5 (7.6)	3.0 (5.7)	1.2 (3.5)	3.0 (5.8)	1.5 (3.6)
$[Na^{+}]$	Na^{+}	mg/L	12.0 (13.7)	8.9 (15.6)	8.0 (8.5)	10.8 (12.2)	10.7 (13.3)	7.4 (9.7)	32.8 (52.9)	4.7 (4.8)
$[K^{+}]$	K^{+}	mg/L	3.5 (5.3)	2.1 (2.5)	2.0 (1.8)	2.6 (3.4)	4.1 (5.3)	2.4 (2.6)	6.6 (11.5)	2.3 (2.1)
$[HCO_3^{-}]$	HCO_3^{-}	mg/L	107.7 (102.0)	53.0 (57.5)	90.2 (77.2)	105.6 (77.7)	25.0 (36.6)	39.5 (49.4)	103.0 (84.5)	35.3 (36.3)
$[Cl^{-}]$	Cl^{-}	mg/L	6.5 (11.7)	10.7 (32.0)	8.5 (23.5)	8.3 (21.0)	5.6 (9.3)	3.1 (3.6)	23.6 (45.1)	4.9 (17.2)
$[SO_4^{2-}]$	SO_4^{2-}	mg/L	16.8 (34.5)	3.5 (5.4)	5.3 (8.9)	6.2 (7.9)	43.9 (55.4)	3.6 (7.9)	8.2 (15.5)	1.1 (0.7)
Dominant site landform[a]										
Basin fen (*n* = 138)	Basin	No. of stands	25	22	18	4	4	8	8	49
Gently sloping fen (*n* = 282)	GntSlp	No. of stands	48	81	14	26	21	63	19	10
Steeply sloping fen (*n* = 41)	StpSlp	No. of stands	1	18	1	19	—	2	—	—
Spring mound (*n* = 15)	SpgMnd	No. of stands	—	2	—	9	—	1	3	—
Local variables										
Stand slope	Slope	°	1.43 (1.57)	4.29 (4.91)	0.06 (0.35)	6.55 (6.24)	1.72 (1.54)	3.23 (2.75)	1.07 (2.2)	0.07 (0.37)
Microtopography[a]										
Deep standing water (*n* = 43)	DeepWtr	No. of stands	4	—	20	1	—	—	15	3
Shallow standing water (*n* = 179)	ShalWtr	No. of stands	24	16	12	21	4	51	13	38
Saturated soil (*n* = 182)	Sat	No. of stands	36	75	1	36	6	12	2	14
Raised hummocks (*n* = 72)	Hum	No. of stands	10	32	—	—	15	11	—	4
Floating mat (*n* = 31)	FltMat	No. of stands	3	4	1	—	2	1	1	19
Seep–spring (*n* = 41)	SeepSpg	No. of stands	1	7	—	23	—	4	6	—
Soil characteristics										
Peat thickness[b]	Peat	cm	30–240	20–240	40–240	30–240	30–240	20–240	30–240	20–240

Published by NRC Research Press

Table A1 (*concluded*).

Variable	Abbrev.	Units	A (n = 74)	B (n = 123)	C (n = 33)	D (n = 58)	E (n = 25)	F (n = 74)	G (n = 30)	H (n = 59)
Soil carbon	Car	%	31.4 (9.6)	33.4 (10.1)	34.3 (8.1)	33.6 (7.8)	27.6 (8.0)	32.9 (9.5)	34.2 (10.6)	31.8 (10.0)
Soil nitrogen	Nit	%	1.8 (0.8)	1.7 (0.6)	1.9 (0.6)	1.9 (0.5)	1.5 (0.5)	1.8 (0.6)	1.7 (0.7)	1.5 (0.7)
Soil carbon/nitrogen ratio	C/N	%	18.1 (5.3)	21.0 (8.3)	19.2 (8.5)	19.0 (7.3)	18.4 (3.3)	19.8 (7.1)	24.2 (15.6)	25.3 (15.3)

Note: "Abbrev." refers to abbreviations used elsewhere in the text. Full species presence–absence is shown in Table A2.

[a]Values shown are the number of stands in each category.

[b]Values shown are the min.–max. of peat thickness. Mean (SD) not shown because maximum peat thickness was not known.

Published by NRC Research Press

Table A2. Complete list of vascular plant and bryophyte species encountered in Yellowstone National Park fens.

Family	Scientific name	Count of occurrence		Presence and dominance by plant community							
		By site (n = 166)	By stand (n = 476)	A	B	C	D	E	F	G	H
Trees											
Pinaceae	*Abies lasiocarpa*	6	7		+		+	+			
Pinaceae	*Picea* sp.	19	30	+	+		+	+			
Pinaceae	*Pinus albicaulis*	1	1					+			
Pinaceae	*Pinus contorta* var. *latifolia*	45	59	+	+		+	+	+		
Pinaceae	*Pinus flexilis*	1	1					+			
Shrubs											
Betulaceae	*Alnus incana* var. *occidentalis*	4	8				+				
Betulaceae	*Betula glandulosa*	39	48	+	+		+		+		
Caprifoliaceae	*Linnaea borealis*	5	7		+		+				
Caprifoliaceae	*Lonicera caerulea*	33	44	+	+			+	+		
Caprifoliaceae	*Lonicera involucrata*	7	10		+		+				
Cornaceae	*Cornus canadensis*	1	1		+						
Cornaceae	*Cornus sericea*	1	1		+						
Cupressaceae	*Juniperus communis*	2	2		+						
Ericaceae	*Gaultheria humifusa*	7	7	+	+			+			
Ericaceae	*Kalmia microphylla*	24	35	+	+			++			+
Ericaceae	*Ledum glandulosum*	13	16		+		+	+	+		
Ericaceae	*Vaccinium occidentale*	36	49	+	+			+	+		+
Ericaceae	*Vaccinium scoparium*	5	5		+			+			
Grossulariaceae	*Ribes hudsonianum*	1	2				+				
Grossulariaceae	*Ribes lacustre*	1	2				+				
Rhamnaceae	*Rhamnus alnifolia*	3	5		+		+		+		
Rosaceae	*Pentaphylloides floribunda*	31	51	+	+		+		+		
Rosaceae	*Rosa woodsii*	6	10		+		+				
Rosaceae	*Rubus acaulis*	6	6	+	+						
Rosaceae	*Spiraea splendens*	2	2		+						
Salicaceae	*Salix bebbiana*	7	10	+	+		+				
Salicaceae	*Salix boothii*	9	14		+		+				
Salicaceae	*Salix candida*	5	9	+	+		+				+
Salicaceae	*Salix drummondiana*	4	4		+						
Salicaceae	*Salix geyeriana*	8	8	+	+		+				
Salicaceae	*Salix planifolia*	77	118	+	+		+	+	+		+
Salicaceae	*Salix pseudomonticola*	4	8		+		+				
Salicaceae	*Salix wolfii*	60	82	+	+		+				
Graminoids											
Cyperaceae	*Carex aquatilis*	133	317	++	++	+	++	++	+	+	+
Cyperaceae	*Carex aurea*	18	21	+	+		+		+		
Cyperaceae	*Carex brunnescens*	2	2		+						
Cyperaceae	*Carex buxbaumii*	20	30	+	+				+		+
Cyperaceae	*Carex canescens*	61	94	+	+	+	+	+	+		+
Cyperaceae	*Carex capillaris*	5	6		+		+		+		
Cyperaceae	*Carex cusickii*	2	6		+		+			+	
Cyperaceae	*Carex diandra*	4	11	+	+	+				+	+
Cyperaceae	*Carex disperma*	11	14		+		+				
Cyperaceae	*Carex echinata*	20	40		+				+	+	+

Published by NRC Research Press

Table A2 (*continued*).

Family	Scientific name	Count of occurrence		Presence and dominance by plant community							
		By site (n = 166)	By stand (n = 476)	A	B	C	D	E	F	G	H
Cyperaceae	*Carex flava*	2	5		+		+				
Cyperaceae	*Carex gynocrates*	1	1		+						
Cyperaceae	*Carex haydeniana*	2	2		+						
Cyperaceae	*Carex illota*	5	5		+				+		
Cyperaceae	*Carex interior*	10	24		+		+		+		
Cyperaceae	*Carex laeviculmis*	1	3		+				+		+
Cyperaceae	*Carex lasiocarpa*	27	55	+	+	+			+		++
Cyperaceae	*Carex leporinella*	1	1			+					
Cyperaceae	*Carex leptalea*	3	6		+		+				
Cyperaceae	*Carex limosa*	17	41	+	+	+		+	+		++
Cyperaceae	*Carex livida*	31	64	+	+				+		+
Cyperaceae	*Carex luzulina* var. *ablata*	11	17		+				+	+	
Cyperaceae	*Carex microglochin*	3	5		+				+		
Cyperaceae	*Carex microptera* var. *microptera*	2	2				+				
Cyperaceae	*Carex nebrascensis*	6	13		+		+		+	+	+
Cyperaceae	*Carex neurophora*	10	10		+		+				
Cyperaceae	*Carex norvegica* ssp. *stevenii*	1	1		+						
Cyperaceae	*Carex pellita*	4	5	+	+						
Cyperaceae	*Carex praegracilis*	1	1		+						
Cyperaceae	*Carex saxatilis*	1	1	+							
Cyperaceae	*Carex simulata*	28	51	++	+		+		+	+	+
Cyperaceae	*Carex utriculata*	130	291	+	+	++	++	+	+	+	+
Cyperaceae	*Carex vesicaria*	19	28	+	+	+	+				+
Cyperaceae	*Carex viridula*	8	16		+				+	+	
Cyperaceae	*Dulichium arundinaceum*	1	3								+
Cyperaceae	*Eleocharis flavescens* var. *thermalis*	4	5						+	+	
Cyperaceae	*Eleocharis palustris*	7	10			+	+			++	
Cyperaceae	*Eleocharis quinqueflora*	63	128	+	+		+	+	++	+	+
Cyperaceae	*Eleocharis rostellata*	4	5						+	+	
Cyperaceae	*Eleocharis tenuis* var. *borealis*	9	17						+	+	+
Cyperaceae	*Eriophorum angustifolium*	42	74	+	+			+	+		+
Cyperaceae	*Eriophorum chamissonis*	20	34	+	+			+	+		
Cyperaceae	*Eriophorum gracile*	8	11	+	+				+		+
Cyperaceae	*Eriophorum viridicarinatum*	6	12		+			+	+		+
Cyperaceae	*Schoenoplectus acutus* var. *occidentalis*	9	14			+			+	++	+
Cyperaceae	*Schoenoplectus subterminalis*	2	2							+	
Juncaceae	*Juncus balticus*	21	32	+	+		+		+		
Juncaceae	*Juncus brevicaudatus*	24	38	+	+				+	+	+
Juncaceae	*Juncus drummondii*	3	3		+						
Juncaceae	*Juncus ensifolius*	41	66		+		+		+	+	+
Juncaceae	*Juncus filiformis*	1	1	+							
Juncaceae	*Juncus* sp.	2	3		+		+				
Juncaceae	*Juncus longistylis*	1	2				+				
Juncaceae	*Juncus nevadensis*	1	2							+	
Juncaceae	*Juncus regelii*	1	1	+							
Juncaceae	*Luzula multiflora*	1	1		+						

Table A2 (*continued*).

Family	Scientific name	Count of occurrence		Presence and dominance by plant community							
		By site (n = 166)	By stand (n = 476)	A	B	C	D	E	F	G	H
Juncaceae	*Luzula parviflora*	22	22		+		+	+			
Poaceae	*Agrostis exarata*	16	19	+	+		+			+	
Poaceae	*Agrostis idahoensis*	2	3		+						
Poaceae	*Agrostis scabra*	56	97	+	+	+	+	+	+	+	+
Poaceae	*Agrostis thurberiana*	32	46		+	+	+		+	+	+
Poaceae	*Alopecurus aequalis*	2	2			+					
Poaceae	*Bromus ciliatus*	27	37		+		+				
Poaceae	*Calamagrostis canadensis*	46	63	+	+	+	+	+	+		+
Poaceae	*Calamagrostis stricta*	47	85	+	+	+	+		+	+	+
Poaceae	*Danthonia intermedia*	3	3		+						
Poaceae	*Deschampsia caespitosa*	64	89	+	+	+	+	+	+	+	
Poaceae	*Elymus albicans* var. *griffithsii*	1	1		+						
Poaceae	*Elymus trachycaulus* var. *trachycaulus*	3	2				+				
Poaceae	*Festuca idahoensis*	1	3		+						
Poaceae	*Glyceria striata*	23	30		+		+			+	
Poaceae	*Hierochloe odorata*	2	2		+						
Poaceae	*Hordeum brachyantherum*	2	2			+	+				
Poaceae	*Muhlenbergia andina*	2	2		+				+		
Poaceae	*Muhlenbergia filiformis*	55	75	+	+		+	+	+		+
Poaceae	*Muhlenbergia glomerata*	1	1						+		
Poaceae	*Phleum alpinum*	21	21	+	+				+		
Poaceae	*Phleum pratense*	11	14	+	+		+				
Poaceae	*Poa interior*	15	23	+	+	+	+				
Poaceae	*Poa leptocoma*	2	2		+		+				
Poaceae	*Poa palustris*	30	48	+	+		+				
Poaceae	*Poa reflexa*	1	1		+						
Poaceae	*Torreyochloa pallida* var. *pauciflora*	1	1				+				
Poaceae	*Trisetum wolfii*	8	8		+						
Nongraminoid herbs											
Alliaceae	*Allium brevistylum*	3	4		+		+		+		
Alliaceae	*Allium schoenoprasum*	5	6		+						
Apiaceae	*Angelica arguta*	6	8		+		+				
Apiaceae	*Angelica pinnata*	29	33	+	+		+		+		
Apiaceae	*Heracleum maximum*	4	6		+		+				
Apiaceae	*Ligusticum canbyi*	7	9		+		+				
Apiaceae	*Osmorhiza* sp.	1	1				+				
Asteraceae	*Achillea millefolium* var. *lanulosa*	7	7		+		+				
Asteraceae	*Agoseris* sp.	1	1		+						
Asteraceae	*Anaphalis margaritacea*	1	1				+				
Asteraceae	*Antennaria corymbosa*	32	38		+			+	+		
Asteraceae	*Antennaria pulcherrima*	4	4		+						
Asteraceae	*Arnica longifolia*	1	1		+						
Asteraceae	*Arnica mollis*	8	10		+				+		
Asteraceae	*Cirsium* sp.	11	11		+		+				
Asteraceae	*Crepis runcinata*	12	17	+	+				+		
Asteraceae	*Erigeron acris* var. *kamtschaticus*	1	1	+							

Published by NRC Research Press

Table A2 (*continued*).

Family	Scientific name	Count of occurrence		Presence and dominance by plant community							
		By site (n = 166)	By stand (n = 476)	A	B	C	D	E	F	G	H
Asteraceae	*Packera pseudaurea*	27	34	+	+		+		+		
Asteraceae	*Packera subnuda*	50	73	+	+		+	+	+		
Asteraceae	*Senecio hydrophilus*	1	2				+				
Asteraceae	*Senecio integerrimus* var. *exaltatus*	3	4		+		+				
Asteraceae	*Senecio serra*	7	7	+	+	+	+				
Asteraceae	*Senecio sphaerocephalus*	41	53	+	+		+		+		+
Asteraceae	*Senecio triangularis*	25	34	+	+		+				
Asteraceae	*Solidago canadensis*	2	2		+		+				
Asteraceae	*Symphyotrichum eatonii*	25	42		+		+		+	+	
Asteraceae	*Symphyotrichum foliaceum*	74	101	+	+	+	+	+	+		+
Asteraceae	*Taraxacum officinale*	2	2		+						
Brassicaceae	*Barbarea orthoceras*	2	2		+		+				
Brassicaceae	*Cardamine* sp.	1	1							+	
Brassicaceae	*Cardamine pensylvanica*	19	24	+	+		+				
Brassicaceae	*Erysimum cheiranthoides*	1	1				+				
Brassicaceae	*Rorippa palustris*	9	11	+		+	+			+	
Callitrichaceae	*Callitriche palustris*	1	2			+				+	
Calochortaceae	*Streptopus amplexifolius*	3	5				+				
Caryophyllaceae	*Cerastium fontanum*	13	16		+	+	+				
Caryophyllaceae	*Moehringia lateriflora*	1	2		+		+				
Caryophyllaceae	*Stellaria borealis*	2	2		+						
Caryophyllaceae	*Stellaria crassifolia*	4	5	+	+		+				
Caryophyllaceae	*Stellaria longifolia*	23	39	+	+	+	+				
Caryophyllaceae	*Stellaria longipes*	19	34		+		+				
Convallariaceae	*Maianthemum stellatum*	7	8		+		+				
Crassulaceae	*Sedum rhodanthum*	14	14	+	+						
Droseraceae	*Drosera anglica*	23	48		+			+	+	+	+
Fabaceae	*Lupinus polyphyllus* var. *prunophilus*	2	2		+						
Fabaceae	*Trifolium hybridum*	3	4	+	+						
Fabaceae	*Trifolium longipes* ssp. *reflexum*	3	3		+		+				
Gentianaceae	*Gentianopsis detonsa* var. *elegans*	50	74	+	+		+		+		
Gentianaceae	*Swertia perennis*	10	17	+	+				+		
Geraniaceae	*Geranium richardsonii*	12	19		+		+				
Hippuridaceae	*Hippuris vulgaris*	5	5			+	+			+	
Iridaceae	*Sisyrinchium idahoense*	5	6		+				+		
Isoetaceae	*Isoetes*sp.	1	1			+					
Juncaginaceae	*Triglochin maritimum* var. *elatum*	28	49	+	+				+	+	+
Juncaginaceae	*Triglochin palustris*	19	23	+	+		+		+	+	
Lamiaceae	*Mentha arvensis*	14	26	+	+		+				+
Lamiaceae	*Prunella vulgaris*	1	1		+						
Lamiaceae	*Scutellaria galericulata*	5	7	+	+		+				
Lemnaceae	*Lemna* sp.	1	1				+				
Lentibulariaceae	*Utricularia minor*	31	48	+		+			+	+	+
Melanthiaceae	*Zigadenus elegans*	1	2				+				
Menyanthaceae	*Menyanthes trifoliata*	20	43	+	+	+		+	+	+	+
Nymphaeaceae	*Nuphar lutea* ssp. *polysepala*	5	7							+	+

Table A2 (*continued*).

Family	Scientific name	Count of occurrence		Presence and dominance by plant community							
		By site (n = 166)	By stand (n = 476)	A	B	C	D	E	F	G	H
Onagraceae	*Chamerion angustifolium*	4	7		+		+				
Onagraceae	*Epilobium anagallidifolium*	7	8	+	+				+		
Onagraceae	*Epilobium ciliatum*	44	75	+	+	+	+			+	
Onagraceae	*Epilobium clavatum*	7	8	+	+	+			+		
Onagraceae	*Epilobium halleanum*	3	3	+	+						
Onagraceae	*Epilobium hornemannii*	10	14	+	+						
Onagraceae	*Epilobium lactiflorum*	1	1		+						
Onagraceae	*Epilobium palustre*	52	93	+	+	+	+		+	+	+
Orchidaceae	*Listera cordata*	3	3		+		+	+			
Orchidaceae	*Platanthera dilatata*	46	61	+	+		+		+		+
Orchidaceae	*Platanthera huronensis*	14	20		+		+	+	+	+	+
Orchidaceae	*Platanthera hyperborea*	1	1		+						
Orchidaceae	*Platanthera obtusata*	1	1				+				
Orchidaceae	*Platanthera stricta*	4	5		+						
Orchidaceae	*Spiranthes romanzoffiana*	32	59	+	+			+	+	+	+
Parnassiaceae	*Parnassia fimbriata*	3	8	+	+		+		+		
Parnassiaceae	*Parnassia palustris* var. *montanensis*	16	27		+		+		+	+	
Polemoniaceae	*Polemonium occidentale*	13	19		+		+			+	
Polygonaceae	*Polygonum amphibium* var. *stipulaceum*	3	4	+			+				+
Polygonaceae	*Polygonum bistortoides*	1	1		+						
Polygonaceae	*Polygonum viviparum*	1	1		+						
Polygonaceae	*Rumex aquaticus* var. *fenestratus*	10	15	+	+	+	+			+	+
Portulacaceae	*Montia chamissoi*	2	2		+						
Potamogetonaceae	*Potamogeton* sp.	15	25	+		+			+	+	+
Potamogetonaceae	*Stuckenia filiformis*	1	1			+					
Primulaceae	*Dodecatheon pulchellum*	7	9		+				+		
Primulaceae	*Lysimachia thyrsiflora*	2	3								+
Pyrolaceae	*Moneses uniflora*	1	1				+				
Pyrolaceae	*Orthilia secunda*	2	2		+						
Pyrolaceae	*Pyrola asarifolia*	12	12	+	+		+				
Pyrolaceae	*Pyrola chlorantha*	1	1				+				
Ranunculaceae	*Aconitum columbianum*	6	6		+		+				
Ranunculaceae	*Actaea rubra*	2	2				+				
Ranunculaceae	*Caltha leptosepala*	14	15		+		+		+		
Ranunculaceae	*Delphinium occidentale*	1	1		+						
Ranunculaceae	*Ranunculus alismifolius* var. *davisii*	3	3		+						
Ranunculaceae	*Ranunculus cymbalaria*	1	1						+		
Ranunculaceae	*Ranunculus gmelinii*	4	4			+	+				
Ranunculaceae	*Ranunculus macounii*	1	1				+				
Ranunculaceae	*Ranunculus sceleratus* var. *multifidus*	1	2			+				+	
Ranunculaceae	*Ranunculus uncinatus*	1	1		+						
Ranunculaceae	*Thalictrum alpinum*	3	3		+		+				
Ranunculaceae	*Thalictrum sparsiflorum* var. *saximontanum*	5	5		+		+				
Ranunculaceae	*Trollius albiflorus*	7	7		+						
Rosaceae	*Fragaria virginiana*	38	47	+	+		+		+		
Rosaceae	*Geum macrophyllum* var. *perincisum*	44	64	+	+	+	+				+

Table A2 (*continued*).

Family	Scientific name	Count of occurrence		Presence and dominance by plant community							
		By site (n = 166)	By stand (n = 476)	A	B	C	D	E	F	G	H
Rosaceae	*Potentilla anserina*	1	1						+		
Rosaceae	*Potentilla diversifolia* var. *diversifolia*	2	2		+						
Rosaceae	*Potentilla gracilis*	4	4		+						
Rosaceae	*Potentilla palustris*	39	66	+	+		+	+	+	+	+
Rubiaceae	*Galium boreale*	4	5		+		+				
Rubiaceae	*Galium trifidum*	98	176	+	+	+	+		+		+
Rubiaceae	*Galium triflorum*	1	1				+				
Saxifragaceae	*Mitella pentandra*	7	10	+	+		+				
Saxifragaceae	*Saxifraga odontoloma*	3	4				+				
Scheuchzeriaceae	*Scheuchzeria palustris*	6	12						+		+
Scrophulariaceae	*Castilleja miniata*	8	8	+	+		+				
Scrophulariaceae	*Mimulus guttatus*	19	29		+		+		+	+	
Scrophulariaceae	*Mimulus moschatus*	6	8		+		+				
Scrophulariaceae	*Pedicularis groenlandica*	79	133	+	+		+		+	+	+
Scrophulariaceae	*Veronica americana*	17	27	+	+	+	+			+	
Scrophulariaceae	*Veronica scutellata*	3	6	+		+					
Scrophulariaceae	*Veronica serpyllifolia* ssp. *humifusa*	2	3		+				+		
Scrophulariaceae	*Veronica wormskjoldii*	6	6	+	+						
Sparganiaceae	*Sparganium emersum*	3	3	+		+				+	
Sparganiaceae	*Sparganium natans*	1	3			+				+	+
Tofieldiaceae	*Tofieldia glutinosa* ssp. *montana*	13	30		+				+		+
Typhaceae	*Typha latifolia*	9	11		+		+			+	+
Valerianaceae	*Valeriana edulis*	9	10		+		+				
Violaceae	*Viola* sp.	98	164	+	+		+	+	+		+
Violaceae	*Viola sororia* var. *affinis*	2	3		+						
Unknown	Unidentifiable vascular species	2	2		+						
Ferns and fern allies											
Equisetaceae	*Equisetum arvense*	35	50		+		+		+	+	+
Equisetaceae	*Equisetum laevigatum*	15	28		+		+		+		
Lycopodiaceae	*Lycopodiella inundata*	1	3								+
Bryophytes											
Amblystegiaceae	*Amblystegium riparium*	28	32	+	+	+	+		+	+	+
Amblystegiaceae	*Amblystegium serpens* var. *juratzkanum*	1	3				+				
Amblystegiaceae	*Amblystegium varium*	3	5	+	+	+		+			
Amblystegiaceae	*Calliergon cordifolium*	7	10	+	+	+	+		+		
Amblystegiaceae	*Calliergon giganteum*	9	22	+	+		+		+	+	+
Amblystegiaceae	*Calliergon richardsonii*	2	2	+			+				
Amblystegiaceae	*Calliergonella cuspidata*	2	3		+					+	
Amblystegiaceae	*Calliergonella lindbergii*	15	27	+	+	+	+	+	+	+	+
Amblystegiaceae	*Campylium stellatum*	22	35	+	+		+		+		+
Amblystegiaceae	*Cratoneuron filicinum*	2	2	+			+				
Amblystegiaceae	*Drepanocladus aduncus*	64	101	++	+		+		+	+	+
Amblystegiaceae	*Drepanocladus longifolius*	17	25	+	+	+	+		+		+
Amblystegiaceae	*Drepanocladus polygamus*	2	6					+			
Amblystegiaceae	*Drepanocladus sordidus*	8	12		+				+		+
Amblystegiaceae	*Hamatocaulis vernicosus*	9	20	+	+				+	+	+

Table A2 (*concluded*).

Family	Scientific name	Count of occurrence		Presence and dominance by plant community							
		By site (n = 166)	By stand (n = 476)	A	B	C	D	E	F	G	H
Amblystegiaceae	*Palustriella falcatum*	5	8				+		+		
Amblystegiaceae	*Pseudocalliergon turgescens*	1	2		+						
Amblystegiaceae	*Scorpidium cossonii*	4	6	+	+				+		+
Amblystegiaceae	*Scorpidium revolvens*	6	9						+		+
Amblystegiaceae	*Scorpidium scorpioides*	16	24						+	+	+
Amblystegiaceae	*Straminergon stramineum*	18	24	+	+	+		+	+	+	+
Aulacomniaceae	*Aulacomnium androgynum*	1	1		+						
Aulacomniaceae	*Aulacomnium palustre*	86	116	+	++		+		+	+	+
Bartramiaceae	*Philonotis fontana*	36	58	+	+		+		+	+	+
Brachytheciaceae	*Brachythecium erythrorrhizon*	2	3			+	+			+	
Brachytheciaceae	*Brachythecium frigidum*	8	11	+	+		+				
Brachytheciaceae	*Brachythecium nelsonii*	10	16	+	+		+				
Brachytheciaceae	*Tomentypnum nitens*	33	42	+	+		+		+		
Bryaceae	*Ptychostomum pseudotriquetrum*	82	132	+	+	+	+	+	+	+	+
Cephaloziaceae	*Cephalozia connivens*	1	1					+			
Cephaloziaceae	*Cladopodiella fluitans*	1	1					+			
Cladoniaceae	*Cladonia ecmocyna*	1	1		+						
Climaciaceae	*Climacium dendroides*	9	9		+						
Dicranaceae	*Dicranum scoparium*	2	2		+						
Dicranaceae	*Dicranum tauricum*	1	1				+				
Ditrichaceae	*Ditrichum gracile*	1	1				+				
Helodiaceae	*Helodium blandowii*	30	47	+	+		+		+		+
Hypnaceae	*Platydictya jungermannioides*	2	4	+							
Jungermanniaceae	*Gymnocolea inflata*	3	9					++			
Jungermanniaceae	*Nardia compressa*	1	1					+			
Marchantiaceae	*Marchantia polymorpha*	30	45	+	+		+			+	
Meesiaceae	*Meesia triquetra*	3	3						+		
Mniaceae	*Plagiomnium cuspidatum*	80	141	+	+	+	++		+	+	+
Polytrichaceae	*Polytrichum commune*	10	17	+	+			+			
Polytrichaceae	*Polytrichum strictum*	6	10	+	+			+			
Sphagnaceae	*Sphagnum angustifolium*	1	1		+						
Sphagnaceae	*Sphagnum capillifolium*	2	3		+			+			
Sphagnaceae	*Sphagnum fimbriatum*	3	4	+							
Sphagnaceae	*Sphagnum fuscum*	2	2					+			+
Sphagnaceae	*Sphagnum lindbergii*	2	7					++			
Sphagnaceae	*Sphagnum platyphyllum*	2	3		+				+		+
Sphagnaceae	*Sphagnum riparium*	4	8		+			++			
Sphagnaceae	*Sphagnum russowii*	14	21	+	+			++			
Sphagnaceae	*Sphagnum squarrosum*	4	5		+		+	+	+		+
Sphagnaceae	*Sphagnum subsecundum*	3	7						+		+
Sphagnaceae	*Sphagnum teres*	25	36	+	+	+	+	+	+		+
Sphagnaceae	*Sphagnum warnstorfii*	19	25	+	+			+	+		
Tetraphidaceae	*Tetraphis pellucida*	1	1				+				
Unknown	Unidentified liverwort, leafy	4	4		+				+		+

Note: The count of occurrencesis shown by site and by stand. Presence within each plant community is noted "+". Species with mean cover >10% within a particular community are noted "++". Plant community codes and indicator species are shown in Table 3. Species nomenclature follows Dorn (2001) for vascular plants, Weber and Wittmann (2007) for non-*Sphagnum* bryophytes, and McQueen and Andrus (2007) for *Sphagnum* species.

Published by NRC Research Press