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Alpine Peatlands of the Andes, Cajamarca, Peru

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Abstract

An ecological analysis of wetlands in the high mountain jalca above 3700 m elevation in the Andes near Cajamarca, Peru, indicated that most wetlands are groundwater-supported peat-accumulating fens. The floristic composition of fen communities was controlled largely by groundwater chemistry, which was highly variable and influenced by watershed bedrock composition. Watersheds with highly mineralized rock discharged water as acidic as pH 3.7, which was high in $CaSO_4$, while watersheds with limestone, marble, and skarn produced groundwater as basic as pH 8.2 and high in $CaHCO_3$. Of the 125 plots sampled in 36 wetland complexes, >50% of plots had at least 3 m of peat, and 21 plots had peat thicker than 7 m. Most soil horizons analyzed had 18 to 35% organic carbon, indicating high C storage. A total of 102 vascular plants, 69 bryophytes, and 10 lichens were identified. Study plots were classified using TWINSPAN into 20 plant communities, which were grouped into four broad categories by dominant life form: (1) cushion plant communities, (2) sedge- and rush-dominated communities, (3) bryophyte and lichen communities, and (4) tussock grass communities. Direct gradient analysis using canonical correspondence analysis indicated that Axis 1 was largely a water chemistry gradient, while Axis 2 was a complex hydrology and peat thickness gradient. Bryophytes and lichens were more strongly separated in the ordination space than vascular plants and were better indicators of specific environmental characteristics.

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Introduction

In the world's tropical regions, the largest area of alpine vegetation above the limit of closed canopy forest and below the permanent snowline is in the Andes Mountains of northern South America (Smith and Young, 1994). This landscape includes broad continuous highlands and isolated peaks that rise to elevations of 3500 m to over 6000 m. The northern Andes in Venezuela, Colombia, and Ecuador receive abundant rainfall, and their alpine ecosystems are termed páramo (Troll, 1968; Walter, 1985). From central Peru south to central Chile the climate is drier, and the alpine ecosystems are termed puna (Smith and Young, 1994). The transition between páramo and puna occurs in northern Peru, between 4.5 and 8°S latitude, and is termed jalca (Rundel et al., 1994; Luteyn, 1992). Cloud forest forms the upper treeline in the east, while deep valleys on the Andes' western slopes are in rain shadows and support thorn scrub and desert below the montane vegetation. In the jalca, tree-sized *Polylepis* (Rosaceae) and *Lupinus* (Fabaceae) occur in scattered patches within a high-elevation steppe.

The alpine flora of South America is the most species-rich of all high mountain regions in the tropics (Smith and Cleef, 1988). It contains the smallest number of boreal and temperate zone species and the greatest proportion of endemics (Luteyn and Churchill, 2000). There have been analyses of regional biota, endemism, and historical and biogeographic relationships of the flora (Young and Reynel, 1997; Weigend, 2002; Young et al., 2002). However, relatively little is known about factors controlling vegetation composition (Squeo et al., 2006; Ginocchio et al., 2008).

Uplands in the jalca, páramo, and puna are dominated by grass species in the genera *Calamagrostis*, *Poa*, and *Festuca*. Taller rosette plants including species of *Puya* are common, along with woody species of *Senecio* and other genera, particularly in Asteraceae. Most areas are cultural landscapes (Young and Reynel, 1997) heavily grazed by domestic livestock and burned annually (Suárez and Medina, 2001).

Seasonally abundant precipitation has allowed the development of numerous wetlands in the jalca, which have been referred to as cushion mires (Bosman et al., 1993), highland bogs (Wilcox et al., 1986), and soligenous (formed on slopes) peatlands (Earle et al., 2003), and are locally and regionally known as bofedales (Squeo et al., 2006). Ombrogenous (rain-fed) bogs are known to occur in southern Chile (Kleinebecker et al., 2008) but are unlikely to occur in the seasonally wet jalca. Few wetlands in the jalca are known to be *Sphagnum*-dominated (Earle et al., 2003), and not all are soligenous or dominated by cushion plants (Squeo et al., 2006). It is unclear what proportion of wetlands have accumulated peat and should be termed mires, bogs, or peatlands. Little is known about the physical factors controlling wetland distribution, wetland types, and their floristic composition in the jalca. The goals of this study were to (1) characterize the types of wetlands and the plant communities occurring within them in a region of jalca in northern Peru, (2) compile a list of species occurring in the wetlands, (3) determine the proportion of wetlands that are peat-accumulating, and (4) identify the physical factors controlling the floristic composition of vegetation.

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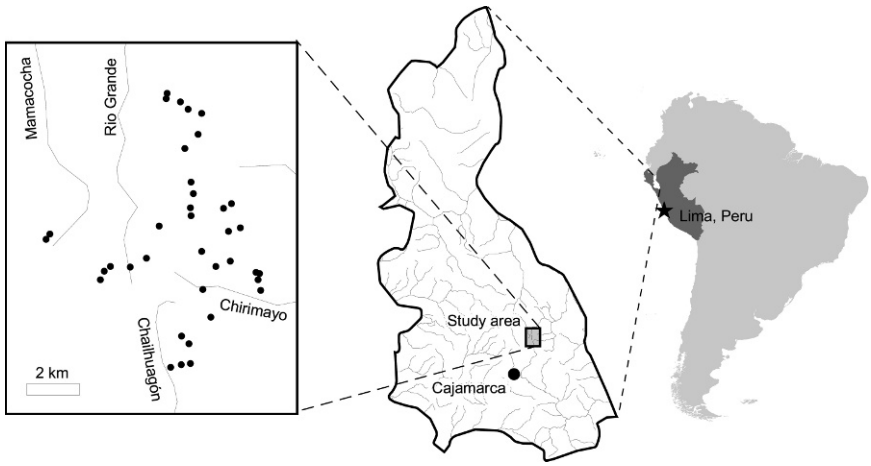

FIGURE 1. Location of study sites (dots on left panel) in the Department Cajamarca (middle panel) in Peru, South America. The study area is centered at 6°54′S, 78°22′W.

Study Area

LANDSCAPES, LANDFORMS, AND HYDROLOGY

The study area is approximately 150 km^2, located in Cajamarca Department, in the Andean Cordillera of northern Peru at elevations ranging from 3700 m to 4200 m (Fig. 1). Four rivers originate in the study area: Chirimayo to the east, Challhuagón to the south, Rio Grande to the north, and Mamacocha to the west. Most wetlands occur on slopes or at the toe of slopes and appear to be supported by groundwater discharging from relatively localized and small hillslope aquifers. Terminal moraines deposited perpendicular to valley bottoms retard runoff and have created the hydrologic template for wetland formation in many areas. Other wetlands occur up-gradient from and adjacent to lakes or pond basins that had filled with peat.

GEOLOGY

Bedrock in the study area is complex and highly variable, consisting of five major rock types: Cretaceous sedimentary rocks including limestone, Pliocene volcanic rocks, Eocene/Miocene intrusive igneous rocks, metamorphic rocks where the original parent material has been altered, and surficial Pleistocene sediments (Davies, 2002).

Cation and anion concentrations, and acidity, differ in groundwater originating in each bedrock type. Water emerging from highly mineralized metamorphic rock is acidic due to the formation of sulfuric acid from pyrite weathering (Cooper et al., 2002; Verplank et al., 2006), while the dissolution of calcium carbonate from limestone or marble (metamorphosed limestone) produces alkaline water (Macpherson et al., 2008). Because of the numerous lithologic contact zones, where two or more rock types are adjacent to each other, a single wetland may straddle bedrock types and receive runoff and groundwater from more than one chemically distinct water source (Fig. 2)

CLIMATE

The rainy season in the jalca occurs from October to April, contrasting strongly with the dry season from May through September. Precipitation arrives from northeasterly winds that bring warm and humid air masses from the Amazon Basin. Mean annual precipitation is 1180 mm at Brillantana and 1400 mm at Minas Sipan, both privately operated weather stations located near the study area, and is highly variable from year to year. Sites that are saturated to the surface with water-filled pools during the rainy season may have dry pools and water tables >40 cm below the soil surface during the dry season. Monthly temperatures are relatively consistent year round, with January being the warmest month with a mean temperature of 7.8 °C.

Methods

FIELD METHODS AND SPECIES NOMENCLATURE

We sampled all 36 major wetland complexes in the study area (Fig. 1). In each complex we identified homogeneous stands of vegetation and collected data on the physical environment and floristic composition of each stand. The number of stands analyzed in each wetland depended upon its size and heterogeneity, and varied from one to seven. One 20 m^2 plot was analyzed in each stand for plant species composition, and we visually estimated percent canopy coverage by species. A total of 125 plots were analyzed. All data were collected in September and October 2005. Collections of unknown vascular plants were identified at Herbario de la Facultad de Ciencias (MOL), Universidad Nacional Agraria La Molina, Lima, Peru, where all vouchers are housed. We used the APG II (Angiosperm Phylogeny Group) system of plant classification (Stevens, 2001; Angiosperm Phylogeny Group, 2003; http://www.mobot.org/MOBOT/research/APweb/) for species nomenclature. The geographic distri-

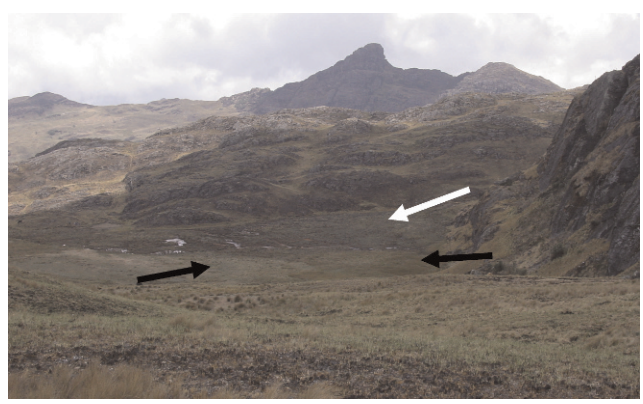

FIGURE 2. View of wetland Cocañes 3 looking southeast, illustrating its three major groundwater flow systems indicated by arrows. The water flowing from the near side of the wetland (two black arrows) has pH ranging from 6.4 to 6.7, while that from the far side (white arrow) is highly acid with pH ranging from 4.3 to 4.7. The two areas support different plant species and plant communities.

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bution of vascular plant taxa were investigated using the U.S. Department of Agriculture PLANTS database <http://plants.usda.gov> and The Missouri Botanical Garden's website database TROPICOS <http://www.tropicos.org>.

In each plot we measured the pH of groundwater that filled a 20- to 40-cm-deep soil pit using an Orion model 250A pH meter with combination electrode. We measured the wetland's slope using a Suunto clinometer, aspect with a compass, peat thickness with a tile probe pushed until rock or dense mineral soil was encountered, groundwater level in the open soil pit after it had equilibrated for 1 h, and soil temperature at 13 and 28 cm depth with thermometers.

Lichens were identified by Dr. S. Will-Wolf, *Sphagnum* by Dr. Richard Andrus, other mosses and liverworts were identified by Dr. W. Weber with the exception of *Scorpidium* and *Drepanocladus* (L. Hedenäs), *Breutelia* and *Philonotis* (Dana Griffin III), *Campylopus* (Jan-Peter Frahm), *Leptodontium* (Richard Zander), and *Dicranum* (Robert Ireland). Voucher specimens of all cryptogams are at the University of Colorado at Boulder (COLO).

LABORATORY ANALYSIS OF WATER AND SOIL SAMPLES

Water was collected from 32 wetland complexes for analysis of dissolved ions, metals, and nutrients. The lack of shallow groundwater made it impossible to collect water from 4 wetlands. Two 1 L sample bottles were filled from the 40-cm-deep soil pit after it filled with fresh clean groundwater. Samples were stored on ice in the field and for transport, and in a refrigerator until analyzed by ALS Environmental in Lima, Peru. One sample bottle from each site was acidified in the field to stabilize the metals. All samples were filtered in the laboratory. We used standard analytical procedures recommended by the American Public Health Association (APHA, 2005) for analysis: Ca, Cu, Mg, and Fe using direct nitrous oxide-acetylene flame method (APHA 3111-D), Na and K using flame photometric method (APHA 3500-K-B), HCO_3 and CO_3 using titration (APHA 2320-B), SO_4 using turbidimetric method (APHA 4500-SO_4 E), and total P using persulfate digestion method (APHA 4500-P-E). Total N was determined using the Kjeldahl method, following ASTM method D5176-91 (standard method for total chemically bound N, http://amaec.kicet.re.kr/cd_astm/PAGES/D5176.htm). Percent organic carbon (OC) for one soil sample in each stand was collected at ~30–40 cm depth from a soil pit and analyzed using a LECO soil analyzer.

SOIL CLASSIFICATION

Soils in the upper 40 cm horizon were analyzed for % OC and organic horizon thickness. Soils containing <18% OC were classified as mineral horizons, while those with >18% OC were classed as organic horizons following USDA Soil Taxonomy (USDA, 1999). If organic horizons were >40 cm thick, the soils were considered to be peat, and wetlands with peat soils to be peatland ecosystems. Sloping wetlands that lacked peat soils were classified as wet meadows, while those on lake shores that flooded deeply were classified as marshes.

DATA ANALYSIS

Divisive cluster analysis using Two Way Indicator Species Analysis (TWINSPAN) was performed with the computer program PC Ord (McCune and Mefford, 1999) to sort plots into groups based upon their floristic composition. Braun-Blanquet table sorting methods (Mueller-Dombois and Ellenberg, 1975) were used to further refine the plot groupings and produce a vegetation classification.

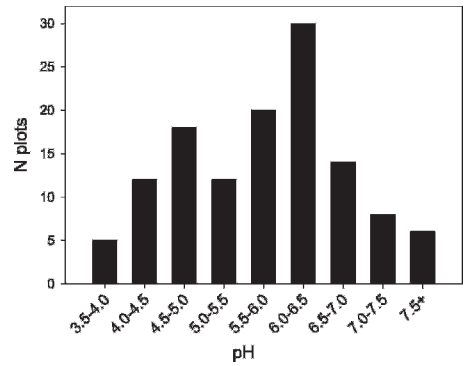

FIGURE 3. Number (*N*) of plots with groundwater pH in 0.5 unit categories.

Direct gradient analysis was used to identify the major environmental gradients controlling the floristic composition of study stands. Canonical correspondence analysis (CCA) was performed using the default settings in the computer program CANOCO (ter Braak, 1986, 1992; ter Braak and Prentice, 1988). Forward selection was used to test the main environmental variables. Variables were tested for their significance using a Monte Carlo permutation test (499 permutations), and significant variables ($P < 0.05$, except Cu which was accepted at $P < 0.01$) were included in the analysis and are shown on the canonical ordination diagrams. A Monte Carlo permutation test (499 runs) was performed to evaluate the significance of the environmental variables and the first ordination axis in explaining the vegetation composition ($P < 0.05$). In addition, a Monte Carlo permutation test (499 runs) was used to test the significance of all canonical eigenvalues. Raw data were not transformed prior to analysis. Two CCA diagrams are presented, one for vegetation composition of plots, and a second for plant species.

Results

WATER CHEMISTRY

Wetland groundwater pH ranged from 3.7 to 8.2. For the 125 stands analyzed, 35 had pH readings from 3.7 to 5.0 indicating highly acid conditions, 32 from 5.0 to 6.0 indicating moderately acid conditions, and 58 from 6.0 to 8.2 indicating slightly acid, neutral to alkaline conditions. Using the geochemical classification of peatlands developed by Sjörs (1950), the three groups of pH ranges listed above would be classified as bogs or poor fens, intermediate fens, and rich to extreme rich fens, respectively. Most stands had pH values from 4.5 to 7.0, but many stands had more acid or basic values (Fig. 3) indicating the broad range of geochemical environments affecting wetland water chemistry in the study area.

The most abundant anions in sampled groundwater were HCO_3, SO_4, and Ca (Table 1). HCO_3 ranged from undetectable in the most acidic sites to >200 mg L^{-1} for sites in limestone watersheds. Bicarbonate concentration was positively correlated with pH ($r = 0.667$). SO_4 varied from <10 to >90 (with one extreme value of 590) mg L^{-1} and was highest in watersheds with the most acid waters. Calcium was the most abundant cation in most samples, and its concentration was positively correlated with both pH ($r = 0.486$) and HCO_3 ($r = 0.580$). The relatively low correlation of Ca with pH was due to Ca concentration having a bimodal distribution, being high in both basic and highly acid

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TABLE 1

Ion and metal concentrations, in mg L^{-1}, for samples from the study wetlands listed by site. Ca = calcium, Mg = magnesium, Na = sodium, K = potassium, HCO_3 = bicarbonate, Cl = chloride, Cu = copper, Fe = iron, SO_4 = sulfate. Sum of cations, anions, and sum of ions are presented as well as the water type based upon the major cations and anions present. Cells that are left blank are below detection levels (0.5 mg L^{-1} for Cl, 0.005 mg L^{-1} for Cu, and 0.01 mg L^{-1} for Fe).

Wetland	Ca	Mg	Na	K	HCO_3	Cl	Cu	Fe	SO_4	Sum cations	Sum anions	Sum ions	Water type
LC	69.63	1.42	5.48	1.28	203				11	77.8	214.5	292.3	$CaHCO_3$
MC	55.42	1.88	5.75	5.00	138	3.1	0.02		11	68.1	152.1	220.1	$CaHCO_3$
UP-10	9.45	1.20	3.95	1.60	0		0.078	1.98	45	16.2	45.5	61.7	$CaSO_4$
UP-3	17.82	1.28	4.60	2.22	13		0.005	1.43	55	25.9	68.5	94.4	$CaSO_4$
LP	0.46	0.24	3.33	1.58	0	3.0	0.044	0.05	16	5.6	19	24.6	$NaSO_4$
PL	5.78	2.08	4.10	5.36	1	4.0	0.012	0.84	33	17.3	38	55.3	$CaKHCO_3$
SLA	4.63	1.67	4.05	1.31	1			0.03	37	11.6	38.5	50.1	$CaSO_4$
ELA	9.36	1.56	4.73	0.76	3			0.03	33	16.4	36.05	52.4	$CaSO_4$
ULA	23.42	0.89	6.05	2.80	14	2.5			68	33.2	84.5	117.6	$CaSO_4$
VLA	8.50	0.52	6.55	3.28	25		0.027	0.65	50	18.8	75.5	94.3	$CaNaHCO_3$
WBV	5.18	2.17	5.92	4.88	0	4.5		0.06	61	18.1	65.5	83.6	$CaNaHCO_3$
CL	1.83	2.39	5.59	1.45	0	2.4	0.007	0.1	54	11.3	56.4	67.6	$NaSO_4$
C2	3.83	0.28	0.85	0.45	8				4	5.4	12.5	17.9	$CaHCO_3$
C1	5.63	0.42	1.01	0.79	10				9	7.8	19.5	27.3	$CaHCO_3$
C3-1	245.08	3.42	9.12	1.50	42				590	259.1	632.5	891.6	$CaSO_4$
C3-2	4.66	1.03	1.90	0.85	0			0.21	20	8.4	20.5	28.9	$CaSO_4$
C5	15.70	1.03	2.50	0.75	17				44	19.9	61.5	81.5	$CaSO_4$
H1	5.06	0.34	4.70	3.17	0	1.0		0.14	32	13.3	33	46.3	$CaSO_4$
H5	9.13	0.66	3.35	1.32	3			0.08	23	14.5	26.5	41.0	$CaSO_4$
A1	47.63	2.21	4.21	1.03	100				32	55.1	132.5	187.6	$CaHCO_3$
A2	5.62	1.27	3.24	3.63	17	1.5	0.007	0.63	15	13.8	33.5	47.2	$CaSO_4$
A3	85.47	0.52	3.18	0.87	176				34	90.0	210.5	300.5	$CaHCO_3$
A4	10.79	1.61	3.84	1.56	1			0.23	36	17.8	37.5	55.3	$CaSO_4$
T6	23.68	3.55	6.44	2.32	1		0.06	0.4	104	36.0	105.5	141.5	$CaSO_4$
T4	38.83	2.52	9.12	2.50	140			3.8	22	53.0	162.5	215.5	$CaHCO_3$
SR5	26.07	20.9	10.5	2.49	0			0.23	98	60.0	98.5	158.5	$CaMgSO_4$
M2	62.92	4.37	4.59	1.09	214			0.03	8	73.0	222.5	295.5	$CaHCO_3$
SA-1	5.69	1.29	3.51	1.13	0			0.066	59	11.6	59.5	71.1	$CaSO_4$
SA-4	2.02	0.69	2.68	1.74	0			0.05	30	7.1	30.5	37.6	$NaSO_4$
LM	85.80	2.90	2.82	31.65	252	8.8			44	123.1	304.8	428.0	$CaKHCO_3$
TL	62.81	1.79	0.29	0.48	165				7	65.4	172.5	237.9	$CaHCO_3$
L1	69.85	6.71	2.01	6.26	213				25	84.8	238.5	323.3	$CaHCO_3$
Mean	**32.12**	**2.34**	**4.37**	**3.03**	**55**	**2.9**	**0.029**	**0.552**	**53**	**41.9**	**109.6**	**151.5**	
SD	**47.26**	**3.65**	**2.33**	**5.43**	**82**	**2.4**	**0.026**	**0.923**	**100**	**50.1**	**122.8**	**172.6**	

waters, and lower in waters with moderate acidity. The concentration of Mg was low at most sites, and Na concentration was high in acidic waters.

A Piper plot of anions and cations (Fig. 4) illustrates the relative abundance of ions in the waters sampled. On a proportional basis, Ca was the dominant cation in most samples; however, at seven sites >50% of cations were Na and/or K. Waters were classified based upon their most abundant ions, and a relatively equal number of sites had $CaHCO_3$-dominated and $CaSO_4$-dominated type water, indicating that the influence of carbonate and sulfide rocks on the study wetlands were dominant and of equal importance. Three sites had $NaSO_4$-dominated water (Table 1). Our water samples were collected during the dry season after months without significant rains and reflect the chemistry of local and regional groundwater discharge.

SOIL ORGANIC CARBON CONTENT AND PEAT THICKNESS

Soils were grouped into seven categories to represent their percent (%) organic carbon content (Fig. 5). Soils with <18% OC were considered mineral soils. Soils with ≥18% OC were organic. Most soils analyzed had 18 to 35% OC, and all but 17% of the soils analyzed had organic horizons at least 40 cm thick (Fig. 6) and are classified as peat soils. Ten of the 16 soil samples that had <12% OC were from one wetland complex, Cocañes, indicating that the soil in most other wetland complexes was organic. Mineral soils also occurred where highly mineralized groundwater discharge led to high rates of mineral deposition, for example in pools within acidic wetland complexes.

Using USDA (1999) criteria for organic soil thickness and organic carbon content, 65% of sample stands had organic soils of sufficient thickness to be classified as peatlands, while the remaining sites are classified as wet meadows and marshes. Eleven plots had organic layers <40 cm thick, 17% had <18% OC, and 7% had both <40 cm soil and <18% OC. At least one sampled stand within 31 of the 36 study wetland complexes had peat soils indicating that peat accumulating communities occurred throughout the study area.

Peat bodies in many wetlands were very thick. In 22 plots the peat was >7 m thick, >25% of plots had peat >5 m thick, and nearly 50% had peat >3 m thick (Fig. 6). Thick and rapidly growing peat bodies have been identified in the Andes Mountains in Chile (Earle et al., 2003) where peat accumulated at a rate of approximately 2 m per 1000 years, which is 2–10 times faster than accumulation rates in boreal or mountain peatlands in the northern hemisphere (Chimner et al., 2002). The rapid peat accumulation is likely due to the 12 month growing season, and the very dense carbon-rich peat formed by cushion plants, *Carex* spp., and bryophytes.

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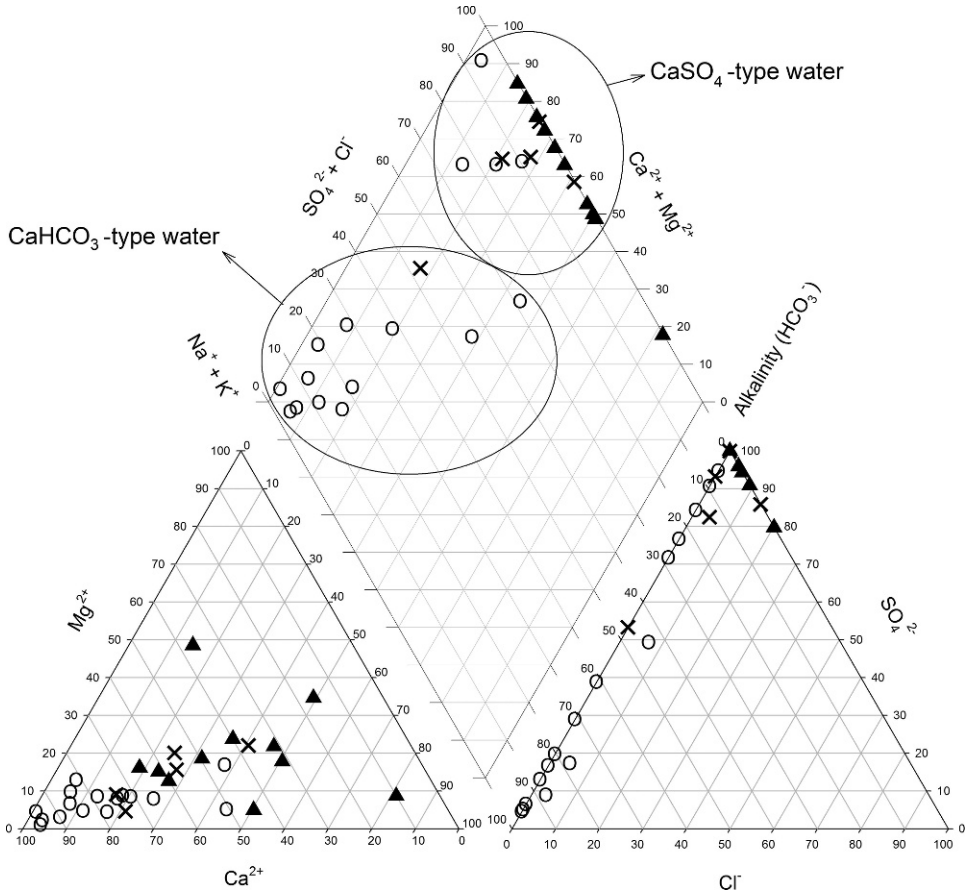

FIGURE 4. Piper plot showing proportion of Ca, Mg, and Na+K in bottom left ternary plot; SO_4, HCO_3, and Cl in the bottom right ternary plot; and the combined ion combinations in the top plot. Triangles are plots with pH < 5.0, x plots with pH 5.0–6.0, and circles plots with pH > 6.0.

FLORA

A total of 102 vascular plants (Appendix A), 69 bryophyte (Appendix B), and 10 lichen taxa (Appendix C) were identified in the study wetlands. Most *Sphagnum* spp. are unidentified. Vascular plants comprised 56% of the flora, bryophytes 38%, and lichens 6%, indicating that non-vascular plant species richness was nearly equal to vascular plant species richness. A total of 49% of vascular taxa are in just three families, Asteraceae with 12 taxa, Cyperaceae 14, and Poaceae 24 (Table 2). The geographic distribution of 54 vascular taxa (53%) was limited to the Andes. A number of taxa are widely distributed along the Cordillera from the Antarctic to the Arctic, including *Carex microglochin*, *Carex praegracilis*, *Eleocharis acicularis*, *Juncus arcticus*, *Poa annua*, and *Veronica serpyllifolia*. Because our collections occurred at the end of the dry season, it is possible that some herbaceous species were not collected.

Carex microglochin is a calciphile in the northern hemisphere, and in the study area was found only in wetlands with high pH waters. However, the very similar *Carex camptoglochin* is endemic to South America and restricted to acidic *Sphagnum magellanicum*–dominated peatlands in the study area and elsewhere in South America (Wheeler and Guaglianone, 2003). *Carex camptoglochin* has not been previously reported for Peru, although it occurs from Ecuador and Colombia, as well as southern Chile and Argentina (Wheeler and Guaglianone, 2003). The Amotape-Huancabamba zone of northern Peru is known to have many endemic taxa (Weigend, 2002, 2004); however, no species new to science have been identified from our collections to date.

Bryophytes covered the ground in many wetland communities. In particular, *Sphagnum magellanicum*, *Breutelia chrysea*, *B. polygastria*, *B. subarcuata*, *B. tomentosa*, *Campylopus argyrocaulon*, *C. cucullatifolius*, *C. sharpii*, *Cratoneuron filicinum*, *Drepano-*

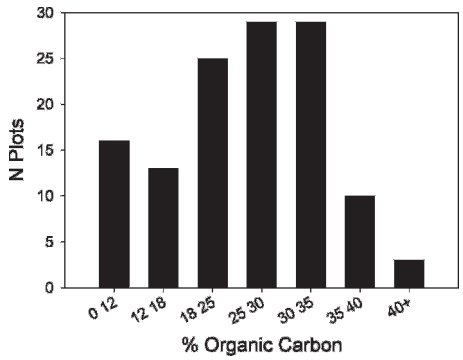

FIGURE 5. Number (*N*) of plots containing percent (%) soil organic carbon in seven categories.

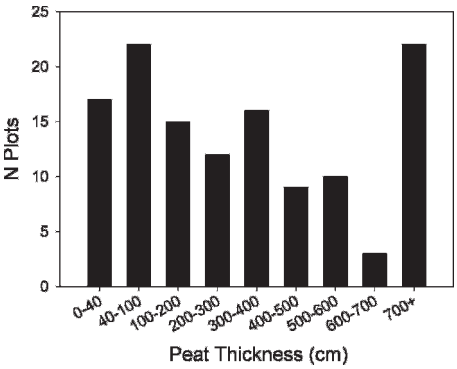

FIGURE 6. Number (*N*) of plots containing peat soil thickness in nine categories.

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TABLE 2

Number of vascular plant taxa and proportion of flora by family.

Family	N Taxa	% Flora
Apiaceae	1	0.98
Araliaceae	1	0.98
Asteraceae	12	11.76
Brassicaceae	2	1.96
Bromeliaceae	1	0.98
Campanulaceae	1	0.98
Caryophyllaceae	2	1.96
Cyperaceae	14	13.73
Ericaceae	2	1.96
Fabaceae	2	1.96
Gentianaceae	5	4.90
Geraniaceae	1	0.98
Hypericaceae	1	0.98
Isoetaceae	1	0.98
Juncaceae	5	4.90
Lamiaceae	1	0.98
Lentibulariaceae	1	0.98
Lycopodiaceae	1	0.98
Melastomataceae	1	0.98
Onagraceae	1	0.98
Orchidaceae	2	1.96
Orobanchaceae	2	1.96
Phrymaceae	1	0.98
Plantaginaceae	3	2.94
Poaceae	24	23.53
Polygonaceae	1	0.98
Ranunculaceae	4	3.92
Rosaceae	5	4.90
Rubiaceae	1	0.98
Salviniaceae	1	0.98
Valerianaceae	1	0.98
Violaceae	1	0.98
Total	**102**	**100**

cladus longifolius, *Hamatocaulis vernicosus*, *Polytrichum juniperinum*, *Scorpidium cossonii*, *S. scorpioides*, and *Warnstorfia exannulata* had high canopy coverage in many stands and characterized some wetland community types. Bryophytes, because they lack roots, are highly sensitive indicators of environmental conditions at the soil surface, particularly water pH and chemical content, and water table depth and duration of soil saturation (Vitt and Chee, 1990; Cooper and Andrus, 1994).

Because bryophytes and lichens comprise >40% of the flora and dominate the vegetation at many sites, they are essential to include in wetland classification and characterization studies. This is particularly important in the study area where many vascular plant species—for example *Carex pichinchensis*, *C. bonplandii*, *Werneria nubigena*, and some species of *Calamagrostis*—occurred in both acid and alkaline wetlands, making them poor indicators of specific environmental conditions. Classifications based solely upon vascular plant taxa could miss even the most important environmental differences among communities.

The bryophytes *Straminergon stramineum*, *Scorpidium cossonii*, *Scorpidium scorpioides*, *Warnstorfia exannulata*, *Drepanocladus longifolius*, *Drepanocladus polygamus*, *Drepanocladus sordidus*, and *Meesia uliginosa* are characteristic of basic to slightly acid peatlands throughout the northern hemisphere, and occupy similar environments in the study area. Species of *Sphagnum*, *Polytrichium*, and many *Campylopus* and *Breutelia* were indicative of acidic waters in the study area. Lichens were common only in acid peatlands, and the fruticose species *Cladina confusa*, *C. arbuscula*, and *Cladia aggregata* formed dense patches.

VEGETATION

Plant communities of the study area were placed into four broad categories based upon the dominant life form: (1) cushion plant, (2) sedge and rush, (3) bryophyte and lichen, and (4) tussock grasses. Within these broad categories 20 plant communities were identified from the 125 plots using TWINSPAN, and are briefly described below.

Cushion Plant Communities

Wetlands with cushion-forming vascular plants have been reported only for the southern hemisphere including the Andes, New Zealand (Wardle, 1991), and Africa (Hedberg, 1964, 1979, 1992). Typically termed cushion bogs (Bosman et al., 1993), these wetlands are fens supported by groundwater discharge, not solely by direct precipitation. The most common cushion-forming species were *Plantago tubulosa*, *Oreobolus obtusangulus*, *Werneria pygmaea*, *Distichia acicularis*, *Aciachne pulvinata*, and *D. muscoides*, with the first two species being most abundant. Cushion communities dominated by species of *Oreobolus* occur in many other regions; for example *O. pectinatus* in New Zealand (Wardle, 1991) and *O. cleefii* in Ecuador (Bosman et al., 1993). *Distichia muscoides*, *Plantago rigida*, and *Oreobolus cleefii* dominate cushion wetlands in the Andes of Colombia (Cleef, 1981) and *D. muscoides* dominates similar wetlands in Chile (Squeo et al., 2006). *Donatia fascicularis* and *Astelia pumila* dominate cushion plant communities in southern Chile (Kleinebecker et al., 2008). Cushion community soils had the highest organic carbon content of any community type, ranging from 30 to 40%. The high organic content, and nearly year-round growth of the dense cushions has produced peat deposits >7 m thick in many sites. These communities are heavily used for livestock forage, are deeply hummocked by cattle trampling, and sod has been cut from many sites for use as a building material and for fuel, and in some areas all of the vegetation and peat has been removed. Three cushion plant communities were identified:

(1) *Plantago tubulosa–Oreobolus obtusangulus–Werneria pygmaea–Distichia acicularis*: This cushion community is common and widespread in the study area. The vegetation can be dominated by any species for which the community is named, but all stands have prostrate forms and most have thick peat accumulations (Fig. 7A).

(2) *Distichia muscoides–Breutelia polygastria*: This cushion-forming community is rare in the study area and characterized by dense turfs of *Distichia muscoides*.

(3) *Werneria nubigena–Campylopus spp.*: This is one of the most characteristic communities in many wetlands because the leaves and flowers of *Werneria nubigena* are distinctive.

Sedge- and Rush-dominated Communities

Species of Cyperaceae and Juncaceae dominate wetlands on the margins of lakes and ponds where seasonal standing water occurs, and in some sloping wetlands. Stands of *Schoenoplectus californicus* and *Juncus arcticus* form dense stands bordering many lakes and ponds (Fig. 8). Stands of short stature *Carex crinalis* dominated pool margins in acid wetlands. The most common sedge was *Carex pichinchensis* but *Carex bonplandii*, *C. hebetata*, *C. praegracilis*, *C. camptoglochin*, *Uncinia hamata*, and *Eleocharis albibracteata* were also common. Fourteen sedge and rush community types are described, indicating the high diversity of this type of wetland.

(4) *Carex pichinchensis–Scorpidium scorpioides–Cratoneuron filicinum*: This community is dominated by the tall sedge *Carex*

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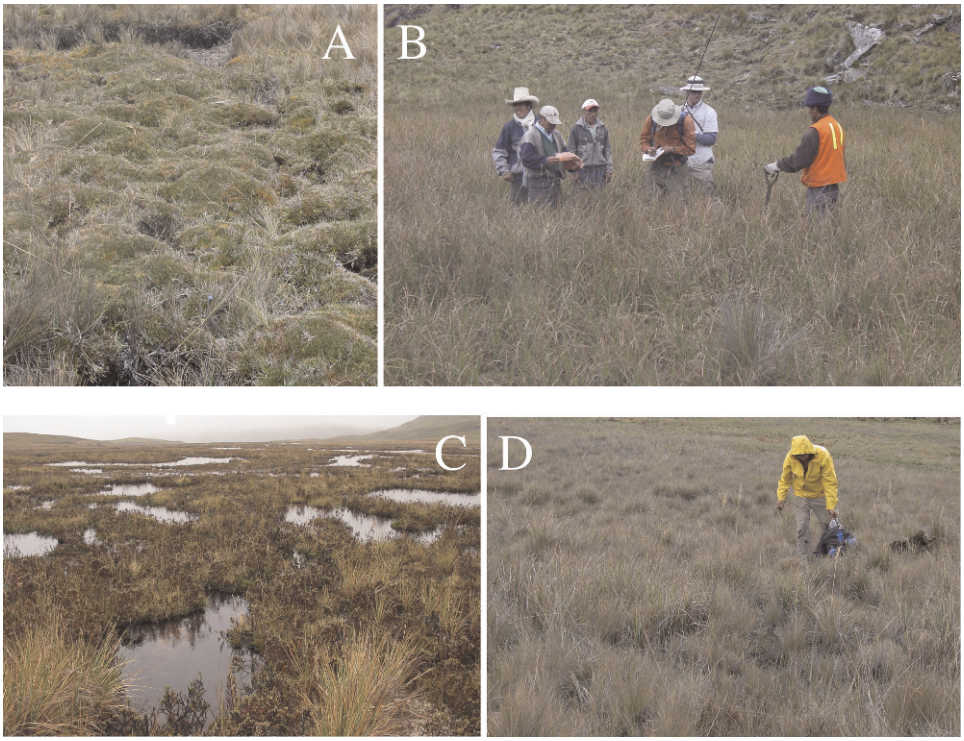

FIGURE 7. Photographs of four of the major vegetation types. (A) Cushion plant community heavily damaged by livestock trampling showing the *Plantago tubulosa–Oreobolus obtusangulus–Werneria pygmaea–Distichia acicularis* community. (B) Sedge vegetation in plot showing the *Carex pichinchensis–Scorpidium scorpioides–Cratoneuron filicinum* community. (C) Bryophyte- and lichen-dominated vegetation showing the *Sphagnum magellanicum–Cladina confusa–Loricaria lycopodinea* community. The dark plant is *Loricaria lycopodinea*. (D) Tussock grass community showing the *Cortaderia hapalotricha–Cortaderia sericantha* community.

pichinchensis and forms dense vegetation in shallow flooded basins with water that has a pH > 6.0. The mosses *Scorpidium scorpioides* and/or *Cratoneuron filicinum* are common in this alkaline wetland type (Fig. 7B).

(5) *Carex pichinchensis–Werneria nubigena*: Sloping wetlands dominated by the tall sedge *Carex pichinchensis* are common in acid sites and have an understory of *Werneria nubigena*.

(6) *Schoenoplectus californicus*: This tall bulrush marsh community occurred on the margins of lakes in the study area.

(7) *Juncus arcticus–Scorpidium scorpioides–Brachythecium stereopoma*: This community dominates flooded marshes on pond margins in alkaline environments where it has an understory of *Scorpidium scorpioides* and other bryophytes.

(8) *Juncus arcticus–Campylopus nivalis*: This community occurs in seasonally or perennially flooded marsh basins with an understory of *Campylopus nivalis* and other bryophytes.

(9) *Carex hebetata–Cratoneuron filicinum*. This tall sedge community occurred in sloping alkaline fens.

(10) *Carex praegracilis–Cratoneuron filicinum*: This community occupies seasonally flooded sloping lake shorelines. *Carex praegracilis* is common in wet meadows and fens in North America.

(11) *Hypsela reniformis–Drepanocladus longifolius*: This community was found in seasonally flooded but sloping lake shorelines.

(12) *Carex camptoglochin–Jensenia erythropus*: This community occurred on sloping acid sites, and has an open canopy of *Carex camptoglochin* and an understory of the liverwort *Jensenia erythropus* and other mosses.

(13) *Carex crinalis–Sphagnum pylaesii*: This community occurred in and around pools in the larger acidic wetlands, with *Sphagnum pylaesii* submerged in pools.

(14) *Carex bonplandii*: Stands dominated by *Carex bonplandii* occurred in several acid wetlands.

(15) *Carex bonplandii–Drepanocladus longifolius*: This highly productive sedge community occurs in areas with a plentiful supply of alkaline water, and nearly constant saturation to the soil surface.

(16) *Uncinia hamata–Puya fastuosa*: A community dominated by the distinctive sedge *Uncinia hamata* was sampled once, but may be regionally common.

(17) *Eleocharis albibracteata–Scorpidium cossonii*: This is the characteristic community of sloping fens in limestone watersheds. The spike rush *Eleocharis albibracteata* has high fidelity to this community type, and the ground layer is covered by mosses that occur only in alkaline substrates, particularly *Scorpidium cossonii*.

Bryophyte- and Lichen-dominated Community

Sphagnum spp. and *Cladina* spp. are characteristic of acidic fens throughout the study area. These wetlands have complex topography with pools and hummocks, although submerged aquatic vascular plants were not seen.

(18) *Sphagnum magellanicum–Cladina confusa–Loricaria lycopodinea*: This is the common and distinctive fen community in acid wetlands. The ground layer is dominated by *Sphagnum* spp., most commonly *S. magellanicum*, several unidentified *Sphagnum* taxa, and the fruticose lichens *Cladina confusa*, *C. arbuscula* ssp. *Boliviana*, and *Cladia aggregata*. *Loricaria lycopodinea* is also distinctive (Fig. 7C).

Tussock Grass Communities

Tussock grass-dominated communities were present in every wetland complex investigated, and are dominated by two genera, *Calamagrostis* and *Cortadaria*. *Calamagrostis tarmensis*, *C. rigida*,

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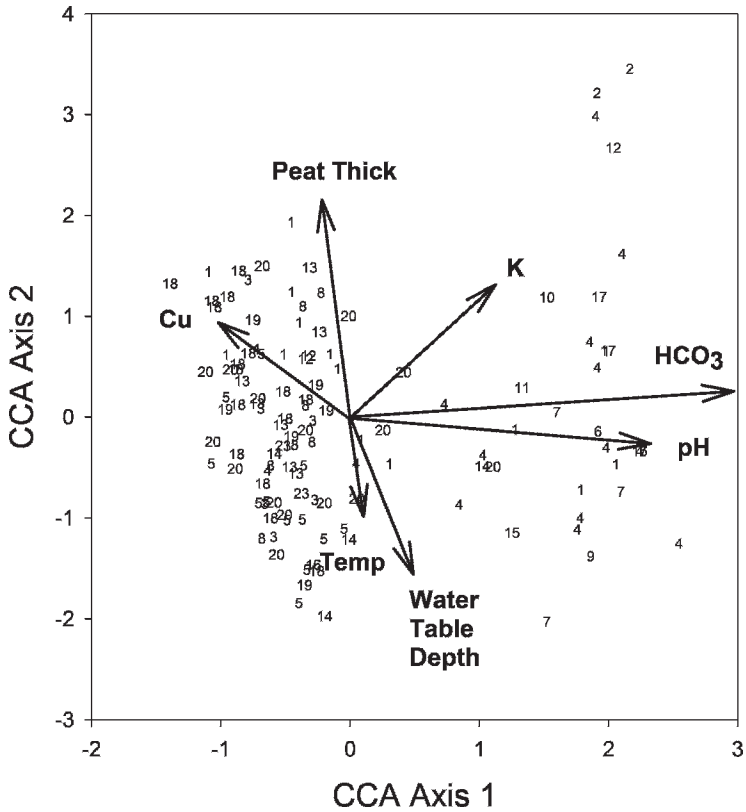

FIGURE 8. CCA analysis of all plots along axes 1 and 2, showing the vectors for statistically significant environmental variables. Eigenvalue of the first canonical axis is 0.507 and is statistically significant at $P < 0.01$ using a Monte Carlo permutation test. The sum of all canonical eigenvalues was also significant at $P < 0.01$, demonstrating that the relation between the species and the environmental variables is highly significant ($P < 0.01$). Numbers are plots assigned to each community type.

and *C. recta* were abundant, as were *Cortaderia hapalotricha* and *C. sericantha*. In the Ecuadorian páramo *C. sericantha* dominates wetland communities (Bosman et al., 1993).

(19) *Cortaderia hapalotricha–Cortaderia sericantha*: Stands dominated by *Cortaderia* were typical of wetlands with acid soils. This community occurred on sites with deeper water tables, some of which lacked peat soils (Fig. 7D).

(20) *Calamagrostis tarmensis–Campylopus cucullatifolius–Scorpidium cossonii*: Bunch grass communities dominated by *Calamagrostis tarmensis*, and other species of *Calamagrostis*, are characteristic of many wetlands, with acid and alkaline soils.

DIRECT GRADIENT ANALYSIS OF THE VEGETATION AND SPECIES DATA

The eigenvalue of the first canonical axis is 0.507 (Table 3), and it was statistically significant at $P < 0.01$ using a Monte Carlo permutation test. The sum of all canonical eigenvalues was also significant at $P < 0.01$, demonstrating that the relation between the species and the environmental variables is highly significant ($P < 0.01$). The canonical coefficients and intra-set correlations of environmental variables from the CCA analyses (Table 3) indicate that Axis 1 is driven by water chemistry, particularly HCO_3 content and pH. Sites with high HCO_3 have low SO_4 concentrations, high pH, and are plotted on the right side of the canonical ordination diagram (Fig. 8), while those with low HCO_3 and low pH are on the left. Acidic wetlands form a relatively tight cluster along Axis 1 between 0 and −1, indicating that these communities are abundant and have relatively similar floristic composition. Most acid waters had detectable concentrations of copper and iron, and other metals are likely present as well.

CCA axis 2 is a complex hydrologic, soil temperature, and peat thickness gradient. Sites with deeper water tables during 2005 had warmer soil temperatures and thinner peat deposits, and plotted at the bottom of the canonical ordination diagram. Sites near the top of the diagram have thicker peat, cooler soil temperatures at 28 cm, and a water table closer to the soil surface.

On the right side of the species canonical ordination diagram (Fig. 9), the mosses *Cratoneuron filicinum*, *Scorpidium scorpioides*, *S. cossonii*, and *Drepanocladus longifolius* along with the vascular plant species *Eleocharis albibracteata* and *Carex praegracilis* are diagnostic of alkaline waters. On the acidic (left) side of the gradient are species of *Sphagnum*, *Polytrichum juniperinum*, and the fruticose lichens *Cladina confusa*, *C. arbuscula*, and *Cladia aggregata*. Among the vascular plants, *Loricaria lycopodinea*, *Cortaderia hapalotricha*, *C. sericantha*, *Carex crinalis*, and *Werneria nubigena* are most abundant in acid wetlands. *Juncus arcticus* and *Carex pichinchensis* are plotted near the center of the ordination space indicating their occurrence in acid and basic wetlands, and those with thick and thin peat deposits. Bryophyte and lichen species were more closely tied to specific hydrological and geochemical environments than vascular plants.

Discussion

Geologically complex mountain systems, such as the northern Andes, are composed of a range of bedrock types, including highly mineralized igneous and metamorphic rocks as well as limestone and other sedimentary rocks. Groundwater contacting each rock type is geochemically distinct, and along with landforms produced by glaciers and hillslope processes form heterogeneous environments that support a diversity of wetlands. Direct gradient analysis indicated that wetland floristic composition is controlled primarily by groundwater geochemistry, which explained more of the total variation in species composition than all other environmental variables combined. Similar controlling gradients occur in boreal (Vitt and Chee, 1990; Nicholson et al., 1996) and mountain wetlands (Gignac et al., 1991; Cooper and Andrus,

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TABLE 3

Results of the canonical correspondence analysis showing eigenvalues for the first four axes, as well as the species environment correlations, and cumulative variance in species and species environment relation data and the total inertia in the data set. The lower portion of the table includes the canonical coefficients, and intraset correlation coefficients of environmental variables with the first two ordination axes are also shown. Axis variables are pH, WT (water table depth), peat thickness (Peat), % organic carbon (%OC), soil temperature at 13 and 28 cm depth (13 cm and 28 cm), wetland slope, aspect, and dissolved HCO_3, total N, total P, Cl, SO_4, Cu, Fe, Mg, K, and Na. Variables in bold explained a statistically significant proportion of the variance as determined using a Monte Carlo permutation test (499 runs) ($P < 0.05$).

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.507	0.323	0.244	0.207	15.149
Species-environment correlations:	0.858	0.773	0.727	0.716	
Cumulative percentage variance					
of species data:	3.3	5.5	7.1	8.5	
of species-environment relation:	18.2	29.9	38.7	46.1	
Sum of all unconstrained eigenvalues					15.149
Sum of all canonical eigenvalues					2.779

	Canonical correlations		Correlation coefficients	
Axis variable	AX1	AX2	AX1	AX2
pH	0.1895	−0.0563	0.6257	−0.0480
WT	−0.0027	−0.2778	0.0722	−0.3432
Peat	−0.0410	0.2631	−0.0866	0.4580
% OC	0.1451	0.0626	0.0775	−0.0104
13 cm	0.1054	−0.0827	−0.0427	0.1263
28 cm	−0.0683	0.6221	−0.0606	0.2464
Slope	0.0741	−0.0173	−0.0312	−0.1880
Aspect	−0.0847	0.1738	−0.0633	−0.0676
HCO_3	0.7878	0.7290	0.7767	0.1336
Total N	0.0766	−0.6476	−0.0357	−0.1650
Total P	0.1072	0.4237	−0.0128	−0.1028
Cl	−0.0906	0.3401	0.1477	0.2217
SO_4	0.1406	0.8201	0.0215	−0.1064
Ca	0.0278	−0.9716	0.5537	−0.0232
Cu	−0.1229	0.1965	−0.2867	0.1656
Fe	−0.2004	0.4619	−0.2525	0.0399
Mg	−0.0136	0.4518	0.0414	0.1280
K	−0.0442	0.1184	0.3375	0.2667
Na	−0.1900	−0.5706	−0.2073	−0.1905

1994) in Canada and the U.S.A., where biogeochemical variables, more than climate, explain the most floristic variation. In the study area, acid and alkaline sloping wetlands have few species in common. This acidic to alkaline gradient is typically referred to as the "rich to poor" gradient (Sjörs, 1950; Malmer, 1986) and provides a conceptual understanding of peatland vegetation variation throughout the world.

Poor fens and bogs are typically dominated by species of *Sphagnum* whose ion exchange capacity acidifies water and soil. However, acidic waters in the study area are produced by the oxidation of mineral sulfides to form sulfuric acid. This water discharges from hillslopes and its pH is little altered during its flow path through the wetland or apparently by ion exchange by *Sphagnum* species. The acid water may leach cations and metals from watershed rock producing acidic and ion-rich water which have been termed iron fens or acid geothermal fens in the Rocky Mountains of the U.S.A. (Cooper et al., 2002; Lemly, 2007). Iron fens occur in watersheds with iron pyrite, which results in precipitation of iron and the formation of iron rich peat, mineral terraces, and bog iron ore formation, similar to those in the study area. Acid geothermal fens occur in volcanic landscapes where sulfur vents produce mineral sulfides. These fens are distinct from poor fens or bogs, which are saturated largely by precipitation and have mineral ion poor waters. The acid fens in our study area were dominated by *S. magellanicum*, which also dominates ombrotrophic (rain fed) bogs in hypermaritime regions of south Patagonia (Kleinebecker et al., 2008) and southeastern Alaska (Klinger, 1996), indicating that water acidity more than climate variables control the distribution and abundance of many peatland species. The alkaline portion of the rich-poor gradient supports *Scorpidium scorpioides* and other brown mosses in the family Amblystegiaceae which dominate rich and extreme rich fens around the world.

Axis 2 of our CCA analysis (Fig. 9) represents a complex hydrologic gradient. Wetlands with perennial discharge of cool groundwater maintained the lowest temperatures, highest water tables, and formed the thickest peat bodies. The hydrologic characteristics of wetlands that formed in basins vs. slopes also produce floristic differences. Basin wetlands dominated by *Carex pichinchensis*, *Juncus balticus*, and *Schoenoplectus californicus* were floristically similar in both alkaline and acid waters because deep flooding limited the species that could occur in these marsh communities, while slope wetland communities were distinctly different in each water type.

Most wetland complexes had at least one area with organic soils of sufficient thickness to be classed as peatlands. Because of the strongly seasonal precipitation regime, peatlands formed only where perennial groundwater discharge occurs, and all peatlands sampled were fens. Previous researchers have termed alpine Andean wetlands cushion mires (Bosman et al., 1993), highland bogs (Wilcox et al., 1986), and soligenous peatlands (Earle et al., 2003). However, communities in the study area are dominated by a wide range of vascular plants, not solely cushion plants. Bogs are ombrogenous (rain-fed) peatland ecosystems (Rydin and Jeglum, 2006) and do not exist in the study area. Peatlands were not all soligenous and many basins with nearly level surfaces supported well developed peat. Our study sites included cushion plant communities, a range of soligenous peatland community types, and topogenous peatlands that had formed in basins. While communities dominated by *Sphagnum* spp. and cushion plants were common, most communities sampled were dominated by species in Cyperaceae.

Biogeographically 53% of vascular plant taxa in the study area are Andean endemics, although no narrow endemics were found. Several species of *Carex* that occur along the Cordillera from the Arctic to Antarctic, such as *Carex microglochin* (Hultén, 1968), were present. In addition, several ruderal taxa, such as *Poa annua*, were found. More than 20% of the bryophyte species are common in the southern and northern hemisphere, and many are worldwide dominants in fens, for example *Scorpidium scorpioides* and *Warnstorfia exannulata*. Of the *Sphagnum* taxa, three occur in the northern hemisphere, and *S. magellanicum* is common in oceanic regions throughout the world.

CONCLUSIONS

A wide diversity of wetland plant communities occur in the study area supported by complex geological and geochemical gradients that produce widely varied groundwater pH and ion concentrations and hydrogeologic settings. Most study wetlands were peat-accumulating fens, and many had peat bodies >5 m

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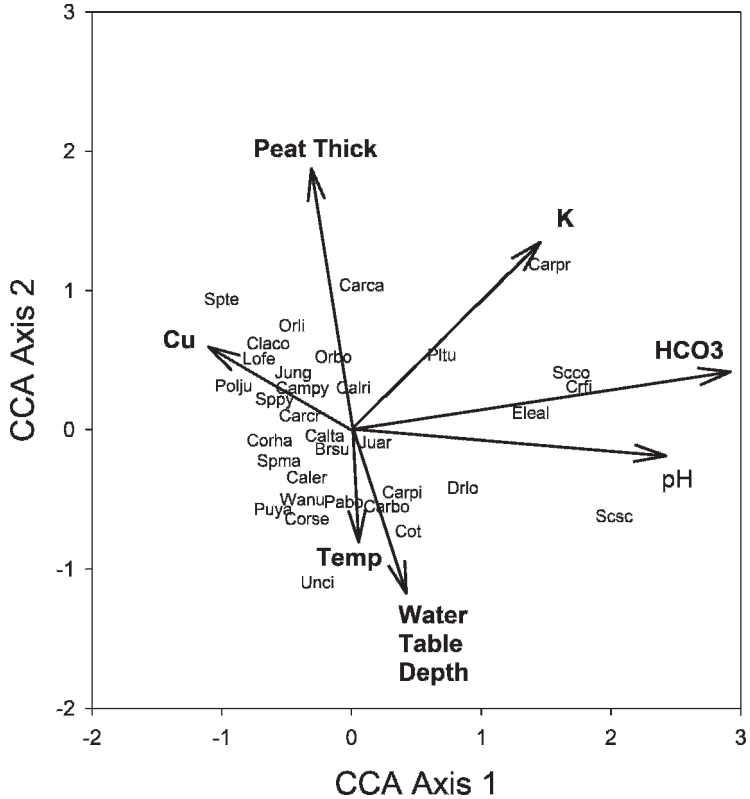

FIGURE 9. CCA analysis showing the centroids of diagnostic plant species along axes 1 and 2, showing the vectors for statistically significant environmental variables. Species shown in the ordination space are: Brsu = *Breutelia subarcuata*, Calta = *Calamagrostis tarmensis*, Capy = *Campylopus* spp., Carca = *Carex camptoglochin*, Carbo = *Carex bonplandii*, Carcr = *Carex crinalis*, Carpi = *Carex pichinchensis*, Claco = *Cladina confusa*, Corha = *Cortaderia hapalotricha*, Corse = *Cortaderia sericantha*, Cot = *Cotula australis*, Crfi = *Cratoneuron filicinum*, Drlo = *Drepanocladus longifolius*, Eleal = *Eleocharis albibracteata*, Juar = *Juncus arcticus*, Jung = *Jungermannia* sp., Lofe = *Loricaria lycopodinea*, Orbo = *Oreobolus obtusangulus*, Orli = *Orithrophium limnophilum*, Pabo = *Paspalum bonplandianum*, Pltu = *Plantago tubulosa*, Polju = *Polytrichum juniperinum*, Puya = *Puya fastuosa*, Scco = *Scorpidium cossonii*, Scsc = *Scorpidium scorpioides*, Spma = *Sphagnum magellanicum*, Spte = *Sphagnum tenellum*, Sppy = *Sphagnum pylaesii*, Sp1 = *Sphagnum* unknown species 1, Wanu = *Werneria nubigena*, Unci = *Uncinia hamata*.

thick. Rapid peat accumulation rates appear to be common in high elevation tropical peatlands in South America, and may not indicate great antiquity. For example, Chimner and Karberg (2008) measured peat accumulation rates of 1.3 mm yr^{-1} in the Ecuadorian páramo while in the puna of northern Chile, Earle et al. (2003) reported that peat bodies had a long-term mean peat accumulation rate of ~2 mm yr^{-1}, and up to 3.5 m of peat had accumulated in no more than 1700 years. In contrast, high elevation peatlands in the Rocky Mountains of Colorado have averaged 0.25 mm yr^{-1} (Chimner et al., 2002), and subarctic and boreal peatlands in Canada average 0.375 mm yr^{-1} and 0.635 mm yr^{-1} (Tarnocai and Stolbovoy, 2006). Thus, tropical montane peatlands appear to support the highest rates of peat accumulation known for mountain wetlands. However, these rates are slower than lowland tropical peatlands, where peat accumulation rates can exceed 10 mm yr^{-1} (Page et al., 2006).

Plant communities in the study area are dominated by cushion plants in basins, sedges and rushes on pond and lake margins and sloping alkaline sites, and bunch grasses on the margins of all fens. Acid fens are widespread in the region, supported by groundwater flow systems discharging from natural acid generating rocks. The acid fens support distinctive *Sphagnum* spp.-dominated communities similar to boreal and austral ombrogenous bogs and geochemically acid fens reported elsewhere in the western hemisphere (Cooper et al., 2002; Lemly, 2007).

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APPENDIX A

Vascular plant taxa found in study plots. *N* is the number of stands in which the taxon was recorded. Mean is the mean canopy cover in all plots, and SD is the standard deviation of mean canopy cover. Distribution is the known geographic distribution of the taxon.

Taxon	*N*	Mean	SD	Distribution
APIACEAE				
Lilaeopsis macloviana (Gand.) A. W. Hill	5	0.05	0.45	South America, Falkland Islands
ARALIACEAE				
Hydrocotyle pusilla A. Rich.				USA; Mexico, Caribbean to Andes; Brazil; Paraguay; Uruguay
ASTERACEAE				
Baccharis genistelloides (Lam.) Pers.	1	0	0.01	Andes: Colombia to N Chile and central Bolivia
Cotula australis (Sieber ex Spreng.) Hook. f.	19	1.72	6.78	New Zealand. Cosmopolitan
Loricaria lycopodinea Cuatrec.	35	4.1	10.2	Andes: Peru
Luciliocline piptolepis (Wedd.) M.O. Dillon & Sagást.				Andes: Venezuela to Argentina (Chile)
Oritrophium limnophilum (Sch. Bip.) Cuatrec.				Andes: Venezuela to Bolivia
Oritrophium peruvianum (Lam.) Cuatrec.	10	0.13	0.55	Andes: Venezuela to Peru
Paranephelius uniflorus Poepp. vel aff.	1	0.04	0.45	Andes: Peru and N Bolivia
Pentacalia andicola (Turcz.) Cuatrec.	4	0.03	0.2	Andes: Venezuela to Peru; Costa Rica; Panama
Senecio canescens (Bonpl.) Cuatrec.	15	0.47	2.1	Andes: Colombia to Bolivia
Werneria nubigena Kunth	55	6.37	11	Andes: Colombia to Bolivia; S Mexico and N Guatemala
Werneria pygmaea Gillies ex Hook. & Arn.	10	1	4.5	Andes: Venezuela to Patagonia
Xenophyllum humile (Kunth) V.A. Funk	7	0.15	0.79	Andes: Colombia to N Peru (and Bolivia)
BRASSICACEAE				
Cardamine bonariensis Pers.	8	0.1	0.45	Andes: Venezuela to Argentina; Uruguay; Mexico to Panama
Rorippa nana (Schltdl.) J.F. Macbr. vel aff.	1	0	0.01	Andes: Colombia to Argentina; Brazil (TROPICOS)
BROMELIACEAE				
Puya fastuosa Mez	24	1.34	4.38	Andes: Ecuador and Peru
CAMPANULACEAE				
Hypsela reniformis (Kunth) C. Presl	1	0.48	5.35	Andes: Colombia to Bolivia and Chile
CARYOPHYLLACEAE				
Arenaria orbignyana Wedd. vel aff.	7	0.2	1.12	Andes: Peru and Bolivia
Cerastium imbricatum Kunth vel aff.	2	0.01	0.09	Andes: Colombia to Bolivia
CYPERACEAE				
Carex bonplandii Kunth	8	0.1	0.45	Andes: Venezuela to Argentina; USA; C America
Carex camptoglochin V.I. Krecz.	15	1.33	5.83	Andes: Colombia to Peru; Argentina-Chile (Falkland Islands)
Carex crinalis Boott vel aff.	22	3.57	12.5	Andes: Colombia to Peru
Carex hebetata Boot	2	0.56	6.24	Andes: Peru
Carex microglochin Wahlenb.	4	0.08	0.52	Canada; USA; South America (Andes); Europe; Asia
Carex pichinchensis Kunth	39	12.12	25.7	Andes: Colombia to Bolivia; Guatemala (TROPICOS)
Carex praegracilis W. Boott	1	0.48	5.35	America
Eleocharis acicularis (L.) Roem. & Schult.	1	0	0.01	America
Eleocharis albibracteata Nees & Meyen ex Kunth	9	1.58	8.06	Andes: Ecuador to Argentina (Chile); Guatemala
Eleocharis radicans (Poir.) Kunth vel aff.	1	0.02	0.27	USA; Mexico; C America; South America (Andes, Brazil, Uruguay)
Isolepis inundata R. Br.	2	0.05	0.45	C America; South America, Oceania
Oreobolus obtusangulus Gaudich.	21	2.35	8.51	Andes: Colombia to Peru; S Chile, Argentina
Schoenoplectus californicus (C.A. Mey.) Soják	2	0.64	7.13	USA (Hawaii); Mexico, C America; South America
Uncinia hamata (Sw.) Urb.	13	1.45	7.06	USA; Mexico; Caribbean; C America; South America (Andes)
ERICACEAE				
Pernettya prostrata (Cav.) DC.	34	0.85	1.81	Central Mexico south through Central America, Andes to NW Argentina
Vaccinium floribundum Kunth				Andes. Venezuela to Argentina; USA; Costa Rica, Panama
FABACEAE				
Trifolium amabile Kunth	3	0.06	0.63	Andes: Ecuador to Argentina (Chile); USA to Guatemala, and Costa Rica
Vicia graminea Sm.	3	0.01	0.09	Andes: Colombia to Argentina (Chile); Brazil and Uruguay; Mexico
GENTIANACEAE				
Gentiana sedifolia Kunth	21	0.05	0.2	Andes: Venezuela to Argentina (Chile); Guatemala to Panama
Gentianella limoselloides (Kunth) Fabris vel aff.	6	0.15	1.09	Andes: Ecuador and Peru
Gentianella stuebelii (Gilg) T.N. Ho & S.W. Liu vel aff.				Andes: Peru
Halenia phyteumoides Gilg vel aff.	3	0.02	0.2	Andes: Peru
Halenia stuebelii Gilg	6	0.07	0.63	Andes: Peru

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APPENDIX A

Continued.

Taxon	*N*	Mean	SD	Distribution
GERANIACEAE				
Geranium sibbaldioides Benth.	27	0.22	0.69	Andes: Venezuela to Bolivia
HYPERICACEAE				
Hypericum laricifolium Juss.	12	0.2	0.81	Andes: Venezuela to Bolivia
ISOETACEAE				
Isoëtes dispora Hickey vel aff.	3	0.01	0.09	Andes: Peru
JUNCACEAE				
Distichia acicularis Balslev & Laegaard	2	0.44	4.47	Andes: Ecuador and Peru
Distichia muscoides Nees & Meyen	5	0.71	5.54	Andes: Colombia to N Argentina
Juncus arcticus Willd.	10	4.35	17	Circumboreal and along the Pacific coast of America to Patagonia
Juncus ebracteatus E. Mey. vel aff.	2	0.02	0.13	Andes: Peru and Bolivia; Mexico and Guatemala
Luzula racemosa Desv.	8	0.06	0.34	Andes: Colombia to Chile
LAMIACEAE				
Stachys pusilla (Wedd.) Briquet				Andes: Colombia to Bolivia
LENTIBULARIACEAE				
Pinguicula calyptrata Kunth vel aff.				Andes: Colombia to Peru
LYCOPODIACEAE				
Huperzia crassa (Humb. & Bonpl. ex Willd.) Rothm. vel aff.	19	0.22	0.6	Andes: Venezuela to Bolivia; Mexico to Panama and Hispaniola
MELASTOMATACEAE				
Miconia chionophila Naudin	4	0	0.02	Andes: Venezuela to Bolivia
ONAGRACEAE				
Epilobium fragile Sam. vel aff.	6	0.1	0.7	Andes: Peru, Bolivia, and Chile
ORCHIDACEAE				
Aa paleacea (Kunth) Rchb. f.				Andes: Venezuela to Bolivia; Costa Rica
Myrosmodes paludosum (Rchb. f.) Ortiz vel aff.	4	0.02	0.13	Andes: Venezuela to Bolivia (Ecuador is a gap)
OROBANCHACEAE				
Castilleja pumila (Benth.) Wedd.	2	0	0.01	Andes: Colombia to Argentina
Bartsia pedicularoides Benth.	2	0	0.01	Andes: Venezuela to N Bolivia
PHRYMACEAE				
Mimulus glabratus Kunth	3	0.14	1.36	Andes: Venezuela to Argentina (Chile); Canada to Central America
PLANTAGINACEAE				
Plantago australis Lam.	2	0.03	0.28	S Arizona, Mexico, C America and most of South America
Plantago tubulosa Decne.	16	3.55	12.6	Andes: Ecuador to Argentina; Mexico and Guatemala
Veronica serpyllifolia L.				America; Africa; temp. Asia; Europe
POACEAE				
Aciachne pulvinata Benth.				Andes: Venezuela, Ecuador to Bolivia; Costa Rica
Agrostis breviculmis Hitchc.	1	0.01	0.09	Andes: Venezuela to Argentina (Chile); Brazil
Agrostis tolucensis Kunth	9	0.81	4.08	Andes: Ecuador to Argentina (Chile); Mexico, Guatemala, Panama
Bromus pitensis Kunth	6	0.05	0.25	Andes: Venezuela to Bolivia
Calamagrostis bogotensis (Vahl) P. Royen vel aff.	2	0.12	0.99	Andes: Venezuela to Ecuador; Costa Rica, Panama
Calamagrostis eminens (J. Presl) Steud.	6	0.53	2.98	Andes: Colombia to Argentina (Chile)
Calamagrostis ligulata (Kunth) Hitchc.	5	0.17	1.12	Andes: Venezuela to Bolivia
Calamagrostis recta (Kunth) Trin. ex Steud.	18	1.74	6.52	Andes: Colombia to Argentina
Calamagrostis rigescens (J. Presl) Scribn.	7	0.28	1.6	Andes: Ecuador to Argentina (Chile); Mexico
Calamagrostis rigida (Kunth) Trin. ex Steud.	17	1.46	5.88	Andes: Ecuador to Argentina (Chile)
Calamagrostis spicigera (J. Presl) Steud. vel aff.				Andes: Peru to Argentina
Calamagrostis tarmensis Pilg.	41	5.42	11.5	Andes: Ecuador to Argentina
Calamagrostis vicunarum (Wedd.) Pilg.	4	0.15	0.93	Andes: Ecuador to Argentina (Chile)
Cortaderia hapalotricha (Pilg.) Conert	22	2.6	8.12	Andes: Venezuela to Bolivia; Costa Rica
Cortaderia sericantha (Steud.) Hitchc.	16	0.86	3.85	Andes: Colombia to Peru
Festuca asplundii E.B. Alexeev	5	0.11	0.68	Andes: Colombia to Peru
Festuca rigescens (J. Presl) Kunth	1	0.01	0.68	Andes: Peru to Argentina
Festuca subulifolia Benth.	4	0.25	1.66	Andes: Colombia to Ecuador
Muhlenbergia ligularis (Hack.) Hitchc.	6	0.14	1.34	Andes: Venezuela to Argentina; Guatemala

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APPENDIX A

Continued.

Taxon	*N*	Mean	SD	Distribution
Paspalum bonplandianum Flügg	32	3.15	8.27	Andes: Colombia to Peru
Poa annua L.	9	0.07	0.33	Andes; Brazil and Uruguay; Canada to Panama; Caribbean; Greenland
Poa cucullata Hack. vel aff.				Andes: Colombia and Ecuador (to Peru?)
Poa pauciflora Roem. & Schult.				Andes: Venezuela to Peru
Poa subspicata (J. Presl) Kunth				Andes: Venezuela to Bolivia
POLYGONACEAE				
Rumex peruanus Rech. f.	2	0.02	0.2	Andes: Ecuador to Bolivia
RANUNCULACEAE				
Caltha sagittata Cav.	1	0.12	1.34	Andes: Ecuador to Argentina (Chile)
Ranunculus flagelliformis Sm.	4	0.03	0.28	Andes: Venezuela to Argentina; Paraguay; Uruguay; Mexico; Caribbean;
Ranunculus peruvianus Pers.				Andes: Colombia to Peru; Mexico; Central America
Ranunculus praemorsus Kunth ex DC.	9	0.44	2.59	Andes: Venezuela to Argentina; Mexico; Central America
ROSACEAE				
Lachemilla aphanoides (Mutis ex L. f.) Rothm.	1	0.02	0.18	California to Bolivia
Lachemilla erodiifolia (Wedd.) Rothm. vel aff.				Andes: Ecuador and Peru
Lachemilla orbiculata (Ruiz & Pav.) Rydb.	3	0.24	1.66	Andes: Colombia to Peru
Lachemilla pinnata (Ruiz & Pav.) Rothm.	12	0.46	1.97	Andes; Mexico to Panama
Lachemilla verticillata (Fielding & Gardner) Rothm. vel aff.	2	0.03	0.28	Andes: Venezuela to Peru; Costa Rica
RUBIACEAE				
Nertera granadensis (Mutis ex L. f.) Druce	7	0.05	0.25	Andes; Mexico; Caribbean; Central America
SALVINIACEAE				
Azolla filiculoides Lam. vel aff.	1	0.04	0.45	S South America to W North America to Alaska; Europe, Asia, Australia
VALERIANACEAE				
Valeriana hirtella Kunth vel aff.	1	0	0.01	Andes: Ecuador and Peru
VIOLACEAE				
Viola pygmaea Juss. ex Poir.	4	0.04	0.29	Andes: Ecuador to Argentina

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APPENDIX B

Bryophyte taxa identified in the study plots. *N* is the number of stands in which the taxon was recorded, mean is the mean percent canopy cover for study stands, and SD is the standard deviation of the mean of percent canopy cover.

Taxon	*N*	Mean	SD
Amblyodon dealbatus (Hedwig) Bruch, Schimper, & Gümbel			
Brachythecium stereopoma (Spruce ex Mitten) Jaeger	9	0.45	1.89
Breutelia chrysea (Müller Halle) Jaeger	4	0.52	3.21
Breutelia polygastria (Müller Halle) Brotherus	5	0.99	7.13
Breutelia subarcuata (C. Müller, Halle) Schimper ex Brotherus	12	1.23	4.68
Breutelia tomentosa (Bridel) Jaeger	5	0.71	4.23
Breutelia trianae (Hampe) Jaeger	1	0.08	0.89
Bryum sp. *sensu stricto*			
Bryum filiforme Dickson			
Campylopus argyrocaulon (C. Müller-Halle) Brotherus			
Campylopus concolor (Hooker) Bridel			
Campylopus cucullatifolius Herzog			
Campylopus nivalis (Bridel) Bridel	19	1.48	4.19
Campylopus richardii Bridel	10	0.85	3.15
Campylopus sharpii J.-P. Frahm, Horton, Vitt	5	0.83	4.55
Campylopus cf. *trichophylloides* Thériot	2	0.16	1.41
Campylopus trivialis C. Müller Halle ex E. G. Britton	5	0.34	1.89
Ceratodon stenocarpus Bruch & Schimp.			
Cratoneuron filicinum (Hedwig) Spruce	12	3.17	13.21
Ctenidium malacodes Mitten			
Dicranum frigidum Müll. Hal.	1	0.04	0.45
Didymodon rigidulus Hedwig var. *gracilis* (Schleicher *ex* Hooker & Greville) Zander	3	0.25	1.93
Drepanocladus longifolius (Wilson *ex* Mitten) Brotherus *ex* Paris	6	1.31	6.88
Drepanocladus polygamus (Schimp.) Hedenäs	1	0.08	0.89
Drepanocladus sordidus (Müller Halle) Hedenäs	1	0.48	5.35
Entodon beyrichii (Schwägrichen) Müller Halle			
Hamatocaulis vernicosus (Mitten) Hedenäs	1	0.63	7.13
Hygrodicranum bolivianum Herzog	1	0.06	0.62
Imbribryum cf. *muehlenbeckii* (Bruch & Schimp.) N. Pedersen			
Jensenia erythropus (Gottsche) Grolle			
Jungermannia sp.	27	3.92	10.36
Leptodontium araucarieti (C. Müller, Halle) Paris			
Marchantia sp.	4	0.47	3.26
Meesia uliginosa Hedwig	1	0.04	0.45
Philonotis andina (Mitten) Jaeger			
Philonotis angulata (Taylor) Brotherus	3	0.18	1.43
Philonotis elegantula (Taylor) A. Jaeger	1	0.04	0.45
Philonotis polygastrica (C. Müller) Brotherus			
Plagiomnium cf. *rhynchophorum* (Hooker) Koponen			
Pohlia wahlenbergii (Weber & Mohr) Andrews in Grout	1	0.04	0.45
Polytrichum juniperinum Hedw.	5	0.64	5.51
Ptychostomum cf. *pallescens* (Schleicher *ex* Schwägrichen.) Spence			
Ptychostomum pseudotriquetrum (Hedwig) Spence & Ramsay			
Racomitrium crispipilum (Taylor) Jaeger			
Rhacocarpus purpurascens (Bridel) Paris	2	0.16	1.41
Riccardia sp.			
cf. Ruizanthus venezuelanus Schuster			
Straminergon stramineum (Bridel) Hedenäs	1	0.08	0.89
Scorpidium cossonii (Schimper) Hedenäs	8	1.09	6.66
Scorpidium scorpioides (Hedwig) Limpricht	7	1.13	5.41
Sphagnum magellanicum Brid.	11	2.74	10.84
Sphagnum tenellum (Brid.) Brid.	3	0.2	1.33
Sphagnum pylaesii Brid.	3	0.31	2.38
cf. Temnoma chaetophylla Schuster			
Thuidium delicatulum (Hedwig) Bruch, Schimper, & Gümbel var. *peruvianum* (Mitten) Crum	1	0.08	0.89
Warnstorfia exannulata (Schimp.) Loeske	2	0.32	2.81

APPENDIX C

Lichen taxa in study plots. *N* is the number of stands in which the taxon was recorded, mean is the mean percent canopy cover for study stands, and SD is the standard deviation of the mean of percent canopy cover.

Taxon	*N*	Mean	SD
Cladia aggregata (Sw.) Nyl.	11	0.72	2.78
Cladina fuliginosa Filson	1	0.04	0.45
Cladina arbuscula ssp. *boliviana* (Ahti) Ahti	9	0.82	3.49
Cladina confusa (R.Santesson) Follmann & Ahti f. *confusa*	12	0.91	3.32
Cladonia andesita Vainio	1	0.08	0.89
Cladonia calycantha Delise ex Nylander			
Cladonia leprocephala Ahti & S. Stenroos			
Peltigera cf. *dolichorrhiza* (Nyl.) Nyl.	1	0.02	0.27
Thamnolia vermicularis (Sw.) Schaer.	1	0.01	0.09

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