THESIS

ENVIRONMENTAL DRIVERS OF PLANT COMMUNITY COMPOSITION IN SUBALPINE

AND ALPINE FENS OF THE SAN JUAN MOUNTAINS, COLORADO, USA

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ABSTRACT

ENVIRONMENTAL DRIVERS OF PLANT COMMUNITY COMPOSITION IN SUBALPINE

AND ALPINE FENS OF THE SAN JUAN MOUNTAINS, COLORADO, USA

Fens are a widely distributed type of wetland worldwide and offer vital habitat for plant

and animal species in the Rocky Mountains. Fens support a high biodiversity of flora and fauna

given the proportionally small space they occupy on the landscape, often serving as refugia for

disjunct plant species at the extremes of their ranges. While some literature exists on subalpine

fens in the southern Rocky Mountains of the United States, alpine fens in this region remain

understudied. Alpine fens are relatively rare in the southern Rocky Mountains and are

concentrated within the San Juan Mountains where topography and climate favor peat

development in the alpine. While studies of montane and boreal peatlands have identified water

chemistry as a main driver of plant community composition, it is unclear whether the same

drivers of plant community composition are important in alpine fens in the San Juan Mountains.

The goal of this study was to 1.) Describe and classify the vegetation of subalpine and alpine

fens and, 2.) Determine underlying environmental variables influencing plant community

composition. To do this, I mapped fens within the BLM Gunnison Management Unit

(approximately 243,000 hectares). I then visited, verified, and sampled vegetation and

environmental data from 33 subalpine and 32 alpine fens. To classify vegetation data into plant

communities, I used hierarchical cluster analysis. I used non-metric multidimensional scaling

and comparisons of ranked environmental and vegetation distance matrices to investigate

relationships between plant community composition and environmental variables. I compared

the influence of environmental variables on subalpine and alpine plant community composition with cumulative r^2 values from linear regressions with NMS axes and Spearman rank correlations between ranked vegetation and environmental distance matrices. I classified 226 stands of vegetation into 11 plant communities that were correlated with elevation and water chemistry variables. Water chemistry variables, particularly pH, EC, and bicarbonate, were more important in structuring vegetation in subalpine than alpine fens. This was in part due to a lower range in values of alpine water chemistry variables. However, lower variance in water chemistry variables did not correspond to decreased plant community diversity in the alpine. To thoroughly explain alpine fen plant community diversity, future studies should consider measuring additional variables, such as soil temperature and temporal variation in water table. Elevation was a relatively important explanatory variable for plant community composition in alpine fens, suggesting that climatic variables are important influences on community composition. Results of this research indicate that the relative importance of environmental variables differs for alpine and subalpine fen plant communities. Thus, future studies examining mountain fen plant community composition should treat alpine and subalpine fen data separately.

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1. Introduction

Fens are peat-accumulating wetlands that support high plant species richness and plant

community diversity in a small proportion of mountain landscapes in Europe, North and South

America, Africa, and Australia (Cooper 1996, Cooper and Sanderson 1997, Hope 2002,

Tahvanainen 2004, Chong and Stohlgren 2007, Naqinezhad et al. 2009, Cooper et al. 2010,

Holmquist et al. 2011, Horsák et al. 2012). Plant community composition between fens is

closely tied to water chemical composition and depth to water table gradients (Bridgham et al.

1996, Hájková and Hájek 2004, Tahvanainen 2004, Lemly and Cooper 2011). Within fens,

micro-topography such as hummocks and hollows and water table gradients influence local scale

vegetation patterns (Malmer 1986, Gignac and Vitt 1990, Lemly and Cooper 2011). However,

the environmental drivers of fen plant community composition and distribution remain poorly

known in many mountain regions of the world, particularly in comparison to peatlands in boreal

regions (Chimner et al. 2010).

Fens are a common wetland type in mountain regions where suitable topography slows

the runoff of water (Cooper and Andrus 1994, Cooper 1996, Cooper and Wolf 2006). Fens

found in alpine tundra, above the forest line, have received far less attention in North America,

compared with those in forested regions, but they may be of particular importance as vegetation

shifts upward due to climate change. Mountain fens may function as refugia for plant species that

require cold and perennially wet habitats (Cooper 1996, Cooper et al. 2002, Horsák et al. 2012,

Jiménez-Alfaro et al. 2012, Kaplan 2012). Plant species that dominate alpine fens may be

affected by climate change-driven temperature increases (Burkett and Kusler 2000, Bergamini et

al. 2009) while moderating soil temperatures sufficiently to create refugia for other alpine plant species (Scherrer and Körner 2011).

Fens form in areas that are perennially saturated by ground water discharge. Typical sites occur at the base of slopes where water discharges from glacial till, alluvial fans, or colluvium, or they may form in basins that intersect the water table (Woods 2001, Cooper and Andrus 1994, Chimner and Cooper 2003). For long-term peat accumulation to occur, the water table must be maintained at or near the ground surface for most of the snow free season over hundreds to thousands of years. Due to the interaction of the hydrologic requirements and the topographic limitations in mountains, fens in alpine zones (1) depend on a combination of precipitation during the growing season and melting snowpack to recharge aquifers and maintain a high water table, and (2) are limited to the small proportion of land area with relatively level topography conducive to long term water accumulation during the growing season. Because of the rarity of fens in the alpine, little is known about the environmental gradients that influence plant community diversity in fens above the forest line.

The few studies of mountain fens that include alpine areas have noted the context dependence of comparisons between environmental gradients and variation in plant community composition between subalpine and alpine fens. In Bulgaria, Hajkova et al. (2006) found that the statistical correlations between pore water pH and plant community composition were weaker in alpine than in subalpine fens. This was attributed to the lower variance of pH in alpine fens but it was unclear whether reduced plant community diversity in alpine compared to subalpine fens could also have also contributed to weaker correlations.

Ground water pH and ionic content were the primary gradients structuring plant community diversity of alpine fens in the West Carpathian Mountains and Swiss Alps in Europe

as well as the Peruvian Andes (Cooper et al. 2010, Sekulová et al. 2013). Results of research in the San Juan Mountains in Colorado identified pH as an important environmental variable influencing plant community composition in fens yet this study did not differentiate between fens below and above the forest line (Chimner et al. 2010).

Vegetation composition and patterns in alpine and subalpine fens may be influenced by different environmental factors and gradients. The size of the study area and whether it includes zones below and above the forest line may influence the underlying gradients driving plant community composition. Changes in the magnitude of correlations between environmental variables and plant community composition may be the result of decreased plant community variation (beta diversity) and/or environmental variation. The goal of this research was to address the following questions:

1. What is the relative importance of elevation, topography, water chemistry, and water table depth for explaining plant community composition in southern Rocky Mountain fens?

2. Does the relative importance of elevation, topography, water chemistry, and water table in explaining plant community composition differ between alpine and subalpine fens?

3. Are beta diversity and/or environmental variance different between subalpine and alpine fens?

2. Study area

This study was conducted in the southern San Juan Mountains within the BLM Gunnison Management Area, covering an area of approximately 243,000 hectares in southwestern Colorado (Fig. 1). Within the San Juan Mountains, fens occur in alpine and subalpine zones on a range of substrate types, offering an ideal study region to compare vegetation along gradients of elevation, water chemistry, topography, and water tables. Elevations range from 2100 to over 4200 meters. Average annual precipitation ranges from 34 cm in lower elevations to 170 cm in the alpine (Hijmans et al 2005, Carrara 2011). The San Juan Mountains receive most of their precipitation during the winter months but up to 35% of annual precipitation is derived from the North American monsoon during July through September (Carrara 2011). For the purposes of this paper, the subalpine zone includes forests dominated by subalpine fir (*Abies lasiocarpa var. arizonica*) and Engelmann spruce (*Picea engelmannii*) (Zier and Baker 2006), as well as mixed conifer and aspen forests through the forest transition zone to approximately 3600 m (Carrara 2011). Fens occurring above this elevation, or above the forest line, are considered in the alpine zone.

Volcanism and glaciation have shaped the topography and bedrock composition within the study region. Bedrock composition is largely silicic and mafic volcanic rocks (Tweto 1979) (Fig. 1). Quaternary age or younger surficial deposits and alluvium, sandstone, and shale are also common within the study region due in part to past glaciations (Fig. 1). During the last glacial maximum portions of the San Juan Mountains were covered by an ice cap (Atwood and Mather 1932). Deglaciation from the last glacial maximum began ~ 20,000 years ago (Johnson et al. 2013) and ended ~ 12,000 years ago depositing moraines, other till, and alluvial fans and

forming terraces in the San Juan Mountains. Hillslopes stabilized around 9500 years ago.

Subsequent climactic variation in the Holocene has led to smaller scale hillslope destabilization

and alluvial deposition (Johnson et al. 2013).

3. Methods

3.1 *Mapping*

I used Bing maps imagery from Microsoft, Inc. accessed through ArcGIS 10.0 (ESRI

2005) to identify and map sites with mottled brown signatures and patterned topography as key

photographic indicators. I visually identified perennially saturated areas, and some densely

forested fens may have been missed with the photographic interpretation. Thus the number of

forested fens may be underrepresented. Prior to field visits, mapped sites were considered

potential fens. Over 600 potential fens were mapped on private and public land. To sample a

diversity of fens, four environmental variables for mapped potential fens were identified *a priori*

based on their likely influence on plant species distributions: (1) elevation, determined from the

National Elevation Dataset (Gesch et al. 2002, Gesch 2007), (2) average annual precipitation in

the watershed, with HUB-12 Watershed delineations from the Natural Resources Conservation

Service (USDA-NRCS) and average annual precipitation from 1950-2000 from the WorldClim

dataset online (Hijmans et al. 2005) (3) presence/absence of glacier coverage during the last

Pleistocene glacial maximum (Benson et al. 2005), and (4) dominant bedrock geology, one of the

seven bedrock types occurring within the study region, in fen watersheds (Tweto 1979). I used

Multi-Response Permutation Procedure with Ward's method and Euclidian distance in the

program PC-Ord (McCune and Medford 2006) to find the number of stratification groups that

maximized within group agreement. This resulted in fens being sorted into thirteen stratification

groups (Appendix C).

3.2 *Accuracy assessment and sampling*

Mapped fens were field verified before sampling began. Only fens on public land were visited and 10 of the original 13 groups identified by the stratification process were represented on public land. Sites considered to be fens in the subalpine had at least 30 cm of organic soils in the top 60 cm of soil. Sites in the alpine only required 20 cm of organic soils in the top 60cm of soil to be considered fens. Organic soils were identified in the field by a brown to black color, distinctive organic smell, and "spongy" consistency (Soil Survey Staff 2006) and later verified based on a threshold of containing at least 18 % organic matter (OM) content by loss on ignition (Belyea and Warner 1996).

I visited between 5 and 65 randomly selected mapped fens from each of the 10 stratification groups. I sampled vegetation and environmental variables during the summers of 2012 and 2013 (Fig. 1). Because of the grouped nature of fen occurrence on the landscape and the time required to reach selected fens, randomly selected fens were treated as sampling areas. I sampled several fens within the same drainage where possible. Thirty-three of the 65 fens sampled were randomly selected. The remaining 32 were sampled in the same randomly selected watersheds.

Within each fen, homogenous stands of vegetation were sampled using the releve method within a 4 m^2 area (Mueller-Dombois and Ellenberg 1974). Percent cover for each vascular plant and moss species was estimated in each 4 m^2 area. Aspect and slope were measured in each stand with a compass. Location and elevation of the stand was recorded with a Garmin 78s GPS unit. Topography of the stand was classified as basin (slope = 0 degrees), gentle slope (< 10 degrees), steep slope (> 10 degrees), or mound. Mound fens were areas of spring upwelling causing peat accumulation well above mineral soil and were raised above the surrounding

vegetation as a convex feature. For each stand, I dug a soil pit 40 cm in depth and the pit was allowed to fill with ground water. Water electrical conductivity was measured using an Orion EC 105A Meter and pH using an YSI Pro Multimeter. Depth to ground water (DGW) and depth to saturated peat (DSP) were measured in the soil pit after a 1/2 hour. Saturated peat was defined as the point where water was visibly seen glistening and seeping from peat into the soil pit. Water samples were collected from the pit, sealed, and frozen until analyzed. One water sample per fen was randomly selected and analyzed for concentrations of HCO_3^-, Ca^{+2}, Mg^{+2}, and SO_4^{-2}. Ca^{+2}, Mg^{+2}, and SO_4^{-2} concentrations were determined by the Soil Testing Lab at Colorado State University using Inductively Coupled Plasma Atomic Emission Spectroscopy.   I determined HCO_3^- concentrations with titration. A soil sample 5 cm in depth was collected starting at any point between 25 and 40 cm in depth for % organic matter (OM) analysis by loss on ignition (Belyea and Warner 1996). Voucher moss samples were identified by Yelena Kosovich-Anderson (Rocky Mountain Herbarium and Wyoming Natural Diversity Database), William Weber (University of Colorado, Boulder), and Ronald Wittmann. Vascular plant nomenclature follows USDA PLANTS Database (USDA, NRCS 2015). Bryophyte nomenclature follows the Flora of North America (1993).

3. 3 *Statistical analysis*

3.3.1 *Vegetation classification, ordination, and correlation with environmental*
  variables

I used hierarchical agglomerative cluster analysis to classify stands into plant community types. For this analysis, I used a relative Sorenson distance measure and flexible beta linkage of

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-0.25 in the program PC-Ord. I used data from 226 out of 228 sampled stands from the

combined dataset of alpine and subalpine stands (van Tongeren 1995, McCune and Mefford

2006). Two of the 228 stands sampled were removed from this analysis after being identified as

outliers, greater than two standard deviations from the mean distance between stands.

Sparganium emersum dominated one outlier stand while the second outlier stand was dominated

by *Juncus arcticus ssp. littoralis*. *Sparganium emersum* was not detected in any other stands.

While *Juncus arcticus ssp. littoralis* was detected in two other stands, it was not a dominant

species. Rare species, those with one or two occurrences and total cover less than or equal to

three percent, were removed from the vegetation data to reduce noise during cluster analysis.

Forty-one rare species were removed from the analysis. To decrease the influence of dominant

species, I square root transformed the percent covers in the plant composition data. I selected the

final number of plant community types by determining the number that (1) optimized chance

corrected within group agreement using Multi-Response Permutation procedure (MRPP) and (2)

resulted in the lowest average p-value across species using indicator species analysis (ISA). ISA

was also used to determine important species structuring the final vegetation groupings.

I used Non-metric Multidimensional Scaling (NMS) on combined alpine and subalpine

stand samples to analyze stand level species composition. Before running the NMS ordination,

rare species (n = 41 species), outlier stands (n = 2), and stands without a complete set of

corresponding environmental data (n = 11) were removed. The most common missing

environmental data was depth to ground water and depth to saturated peat. Percent cover of

plant composition data was square root transformed. Where possible, I used the Expectation-

Maximization algorithm in Primer-E to fill in missing environmental data (Clarke and Gorley

2006). The NMS analysis was performed on 215 stands from the combined data set. A

Sorenson distance matrix was used for the ordination. A stress test was conducted for NMS ordinations to determine the optimal number of axes for the solution. Monte Carlo tests were used to confirm that NMS ordination explained variation in vegetation better than random.

I used the field environmental data for each stand to examine relationships between plant community composition and selected environmental variables (McCune and Mefford 2006). Continuous environmental data used included pH, EC, concentrations of SO_4^{-2} and HCO_3^-, depth to ground water (DGW), depth to saturated peat (DSP), cover and depth of surface water (CW, DSW), and slope. Pore water concentrations of Ca^{+2} and Mg^{+2} were not used because values were highly correlated with the concentration of SO_4^{-2} (Pearson correlation > 0.9). The same environmental variables were used in subsequent analyses as well.

I compared the influence of environmental variables on plant community composition with cumulative r^2 values. r^2 values were calculated from linear regressions with the NMS axes and environmental variables and then summed across all three axes. Summing r^2 values is analogous to rotating the axis to optimize the correlation of each environmental variable individually. The r^2 values assume a linear relationship between the environmental variable and the NMS axis. I used the BEST procedure in Primer-E (Clarke 1993) to determine the combination of variables which maximize the vegetation-environment correlation. The procedure determines rank correlations between vegetation and environmental distance matrices and does not rely on the assumption of a linear relationship. The BEST procedure compared the Sorenson distance matrix generated for the vegetation NMS ordination and the distance matrix of environmental data using a Euclidian distance measure from normalized data. Although the two matrices use different scales, the BEST procedure compares ranks derived from the information in both matrices. The strength of correlation was calculated by rho, the Spearman rank

correlation coefficient. This coefficient was calculated for each combination of environmental variables to determine the set of variables that maximized the correlation between the two matrices (Clarke 1993). The rank correlation was determined for individual environmental variables and compared to the variables determined to have the highest r^2 values from the NMS ordination.

In addition to slope, topography was described by the categorical variables aspect and topographic position. I used a Permanova procedure to compare vegetation composition across topographic position, aspect, and their interaction. Because only a few steeply sloping fens were encountered, all sloping fens were combined for analysis. Only one mound fen was encountered and its stands were removed for this analysis. Thus topographic position was divided into sloping or basin fens. Aspect was divided into eight categories: N, NE, NW, E, W, S, SW, and SE. Aspect was not recorded for basin or mound fens so all basin fens were removed prior to this analysis (n = 68). The Permanova procedure comparing groups with unequal sample sizes assumes groups have equal variance. When this assumption is not met, results of the Permanova are not reliable (Anderson and Walsh 2013). The PermDisp procedure in Primer-E tests for unequal variance and provided verification of the results of a Permanova comparing groups containing unequal sample sizes. I performed the PermDisp procedure in Primer-E on topographic position and aspect (Clarke and Gorley 2006).

3.3.2 *Comparison of subalpine and alpine fen vegetation*

The transition from subalpine forests to the alpine has been described as a climate shift, or thermal limit, at which tall, upright vegetation can no longer thrive (Körner 2007, Korner et al. 2011). This thermal threshold is the forest line. Sampled fens and stands were divided into

alpine and subalpine groups based on their occurrence above or below the forest line. Sampling

locations were visually assessed in Google Earth and during field sampling to determine if they

occurred above or below the forest line. The steep terrain of the San Juan Mountains has

extensive treeless avalanche zones, and the determination of climatic vs. disturbance caused

forest line was not always clear. By investigating forest line elevations throughout the region

using Google Earth, I determined an approximate elevation of 3615 m as the mean forest line

elevation. The forest line was ambiguous for six out of the 65 sampled fens. When the forest

line boundary was unclear I used the 3615 m in elevation cutoff to separate alpine from

subalpine fens.

3.3.3 *Comparison of subalpine and alpine environmental variables*

To compare differences in the environmental variables between alpine and subalpine

stands the average, standard deviation, and Levene's test of variance, were calculated for each

continuous environmental variable.   Levene's test of variance tests whether the variance, the

standard error squared, between groups is significantly different. A chi-squared test was used to

compare topographic position and aspect distributions between alpine and subalpine fens.

3.3.4 *Subalpine and alpine vegetation comparison and correlations between vegetation*
and environmental variables

I used a Sorenson distance matrix to perform a Permanova analysis in order to determine

differences between subalpine and alpine vegetation using the program Primer-E (Clarke and

Gorley 2006), which allows for unequal sample sizes. The PermDisp procedure was used to

determine if beta-diversity of subalpine and alpine fens differed. In addition, the PermDisp results were used to inform the robustness of the results from the Permanova.

I used NMS to produce separate ordinations of alpine and subalpine vegetation data. Before running the NMS ordination, rare species (subalpine: n = 46; alpine: n = 60), outlier stands (subalpine: n = 2; alpine: n = 0), and stands without a complete set of corresponding environmental data (subalpine: n=10; alpine: n = 1) were removed. Where possible, I used the Expectation-Maximization algorithm in Primer-E to estimate missing environmental data (Clarke and Gorley 2006). Stands with missing environmental data were removed from the NMS analysis. This resulted in 91 subalpine and 124 alpine stands used in the NMS. A stress test was conducted for NMS ordinations to determine the optimal number of axes for the solution. Monte Carlo tests were used to confirm that NMS ordination explained variation in vegetation better than random. I compared the correlation of environmental variables to the NMS axes to determine their relative importance in structuring plant community diversity. Cumulative r^2 values were obtained for each variable by summing across all three axes to compare the relative importance of environmental variables between ordinations. Vegetation data in sloping and basin stands in alpine and subalpine fens was compared using a Permanova analysis.

Correlations of environmental variables with vegetation composition in the NMS ordination consider environmental variables individually and assume linear relationships. However, the BEST analysis allows the identification of combinations of environmental variables that maximize correlations with vegetation composition. The BEST procedure in Primer-E was used to identify the combination of variables that optimized the correlation between vegetation and measured environmental variables (Clark & Gorley 2006) in the alpine and subalpine data sets.

4. Results

4.1 *Fen characteristics*

Two-hundred and twenty-eight stands were sampled in 65 fens at 2700 to 3800 meters in elevation. One hundred and twenty-six stands were sampled in 32 alpine fens and 102 stands in 33 subalpine fens. Approximately 2/3 of stands occurred on gentle slopes and 30% in relatively level basins. Seven stands occurred on steep slopes and one on a mound fen. Soil OM content averaged 49%, with a range of 13% to 81%. Three sampled stands with < 18% OM were retained in the analyses as the stands were not identified as outliers in vegetation composition or environmental variables. However, they would not meet the Natural Resource Conservation Service's organic soils criteria for percent organic matter (Soil Survey Staff 2006).

Concentrations of Mg^{+2}, SO_4^{-2}, and Ca^{+2} were highly correlated (Pearson correlation > 0.90). The pH of pore water in sampled stands ranged from 3.86 to 6.95 (n = 210, mean ± se = 5.71 ± 0.04), HCO_3^- concentrations ranged from 3.2 to 110.6 mg/L (n = 69, mean ± se = 27.5 ± 1.3 mg/L), Mg^{+2} from 0.1 to 62.0 mg/L (n= 64, mean ± se = 5.9 ± 1.7 mg/L), SO_4^{-2} from 0.1 to 990.0 mg/L (n= 64, mean ± se = 62.9 ± 22.4 mg/L) , and Ca^{+2} from 0.3 to 268.0 mg/L (n= 64, mean ± se = 23.8 ± 5.8 mg/L). Fens with median pH greater than or equal to 6.50 and mean HCO_3^- pore water concentrations greater than 50.0 mg/L were classified as rich fens. Six rich fens were sampled. Fens with median pH's less than 5.00 and mean SO_4^{-2} pore water concentrations > 200.0 mg/L were classified as iron fens. Iron fens differ from poor fens in pore water ionic concentrations. The primary water source of poor fens is precipitation. Thus poor fens have low pore water ionic concentrations, often with EC's less than 30, Ca^{+2} < 7 mg/L, and Mg^{+2} < 2 mg/L (Vitt & Chee 1990, Mullen et al. 2000, Bedford & Godwin 2003). Water

supplying iron fens flows from geological deposits where iron pyrite oxidizes to form sulfuric acid. The sulfuric acid dissolves ions from the sediments it flows through producing ground water with high concentrations of many cations and anions. Sampled fens with pH's less than five also had high EC, cation, and SO_4^{-2} concentrations. Thus I classified acid fens in my study sites as iron fens rather than poor fens. Six iron fens were sampled. The remaining fens were classified as intermediate fens with median pH of 5.00 to 6.50 and/or pore water concentrations of HCO_3^- < 50.0 mg/L. Fifty-one intermediate fens were sampled. Two of the 65 fens sampled did not have a water table within the 60 cm of the surface at the time of sampling, so water chemistry could not be determined.

A total of 153 vascular and 43 bryophyte species were identified in the sampled stands. Forty-two bryophyte species and 80 vascular plants were identified in alpine fens while 36 bryophytes and 131 vascular plants were identified in subalpine fens. Total species richness was higher for subalpine fens (richness = 166 species, n = 102 stands) than alpine fens (richness = 121 species, n = 126 stands). However, the mean Shannon diversity index (SDI) per stand for subalpine (SDI = 1.476) and alpine (SDI = 1.552) fens was not significantly different (t = 0.963, p = 0.337)

4.2 *Environmental variation in subalpine and alpine fens*

Subalpine fens had larger variance in pH (p < 0.001), EC (p = 0.013), HCO_3^- (p < 0.001), and elevation (p < 0.001) than alpine fens (Table 1, Fig. 2). The distribution of basin and sloping fens, or topographic position, between subalpine and alpine zones differed significantly (χ^2 = 19.76, p < 0.001), with fewer basin fens in the alpine zone. Alpine fens were found primarily on

flat, E, SE, and S aspects and subalpine fens on flat, SE, SW, and W aspects (χ^2 = 42.19, p < 0.001) (Fig. 3).

4.3 *Vegetation classification and ordination*

Eleven plant communities were identified using hierarchical clustering analysis by optimizing the average species p-value from ISA and within group agreement from MRPP (Table 3). The floristic composition of the communities was significantly different (Permanova, Pseudo-f = 8.431, p = 0.001). Plant communities were named using two species with either significant indicator values or high frequency and abundance within the community type.

Five of 11 communities were differentiated along an elevation gradient, three in the alpine and two in the subalpine (Table 3, Fig. 4). The *Carex scopulorum - Palustriella falcata* (n = 13 stands)*, Eleocharis quinqueflora - Warnstorfia exannulata* (n = 14 stands)*,* and *Carex illota - Podistera eastwoodiae* (n = 59 stands) communities occurred in the alpine, with the exception of three stands of *Carex illota - Podistera eastwoodiae* in the subalpine. Typically these three plant communities occurred in intermediate fens, with mean pH ranging from 5.66 to 5.92 (Table 3). Stands of the *Eleocharis quinqueflora - Warnstorfia exannulata* community occurred in sloping fens with sheet flowing water present. Stands of the *Carex illota - Podistera eastwoodiae* community occurred in sloping intermediate and rich fens. Stands of the *Carex scopulorum - Palustriella falcata* community typically had sheet flowing or shallow standing water present and occurred in both sloping and basin fens. Two communities occurred exclusively in the subalpine, *Triglochin palustris - Carex canescens* (n = 5 stands) and *Salix monticola/brachycarpa - Polemonium occidentale* ssp. *occidentale* (n = 15 stands). Stands of the *Triglochin palustris - Carex canescens* community occurred in basin rich fens with pH's greater

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than 6.5. *Salix monticola/brachycarpa - Polemonium occidentale* ssp. *occidentale* stands occurred in intermediate and rich fens.

Stands of the remaining six plant communities were found in intermediate and rich fens in both alpine and subalpine zones (Table 3, Fig. 4). The *Salix planifolia - Climacium dendroides* community (n = 27 stands) occurred in sloping fens. Stands of the *Carex aquatilis - Caltha leptosepala* community (n = 21 stands) were found in fens with shallow standing water, variable topography, and average pH of 5.6. Stands of the *Carex utriculata - Brachythecium salebrosum* community (n = 20 stands) occurred in both sloping and basin fens where pH's ranged from 4.98 to 6.89 and standing water was often present. Stands of the *Calamagrostis canadensis - Carex aquatilis* (n = 13 stands) community type occurred in sloping fens with intermediate water chemistry but also occurred in iron fens. Stands of the *Warnstorfia fluitans - Polytrichastrum longisetum* community (n = 15 stands) occurred only in iron fens. The *Straminergon stramineum - Amblystegium serpens* (n = 24 stands) community type consistently had high average distances, near 0.80, in the MRPP analysis, regardless of the number of groups chosen (Table 3). Plant species and environmental variables were highly variable across sample stands of this community.

An NMS ordination of the combined (alpine + subalpine) data resulted in a 3-dimensional solution with a final stress of 17.70 and instability of 0.00. The ordination explained 70.9% of the variation in vegetation floristic composition. This was the sum of the explained variation for each of the three axes in order: 21.8%, 22.2%, and 26.8%. Axes one and three represented the water chemistry gradient of increasing pH ($r^2 = 0.128$) and HCO_3^- ($r^2 = 0.151$) while all three axes were correlated with increasing elevation ($r^2 = 0.118, 0.075, 0.311$) (Table 2, Fig. 5). Elevation had the highest correlation with stand level vegetation composition,

and a cumulative r^2 of 0.504. HCO_3^-, pH, and EC were less correlated with vegetation composition with cumulative r^2 of 0.199, 0.165, and 0.147 respectively. Slope and DSW were also correlated with vegetation composition with r^2 values of 0.170 and 0.102.

Elevation, HCO_3^-, EC, pH, and DSW maximized the rank correlation between the vegetation distance matrix and environmental distance matrix (BEST, rho = 0.383, p = 0.002) (Table 4). Analyzed individually, elevation had the highest Spearman rank correlation with the vegetation distance matrix (rho = 0.299), followed by EC (rho = 0.221) and SO_4^{-2} (rho = 0.200).

The vegetation composition of sloping fens was significantly different from basin fens (Permanova, Pseudo-f = 8.960, p = 0.001). Variance in vegetation composition was significantly greater in sloping than basin fens (PermDisp, F = 28.693, p = 0.001). The vegetation of alpine fens was significantly different from subalpine fens (Permanova, Pseudo-f = 24.321, p = 0.001) but had similar variance (PermDisp, F = 1.134, p = 0.342). The interaction between topographic position and alpine/subalpine fens on vegetation composition was significant (p = 0.001). Plant species composition differs significantly between sloping and basin fens in both the alpine and subalpine.

4.4 *Plant community composition explained by environmental variables in subalpine and alpine fens*

The NMS ordination of the alpine vegetation data resulted in a 3-dimensional solution with a final stress of 17.96 and a final instability of 0.00 (Fig. 6). The three axes explained a total of 74.6% of the variation in alpine fen vegetation; however the individual environmental variables explained a relatively low percentage of alpine vegetation composition. Cumulative r^2 values from correlations with NMS axes ranged from 0.010 to 0.133 (Fig. 6, Table 5).

Environmental variables with cumulative r^2 values over 0.100 included elevation ($r^2 = 0.133$), DGW ($r^2 = 0.125$), EC ($r^2 = 0.110$), and HCO_3^- ($r^2 = 0.112$).

NMS ordination of the subalpine fen vegetation resulted in a 3-dimensional solution with a final stress of 16.50 and a final instability of 0.00. The three axes explained a total of 72.2% the vegetation data. The measured environmental variables explained considerably more of the variation in subalpine than alpine vegetation, and ranged from 0.099 to 0.597. Variables that explained the most variation for subalpine vegetation were pH ($r^2 = 0.597$), HCO_3^- ($r^2 = 0.485$), slope ($r^2 = 0.385$), EC ($r^2 = 0.202$), elevation ($r^2 = 0.312$), and DSW ($r^2 = 0.350$) (Table 5). The correlations of environmental variables with vegetation composition were stronger for the subalpine than the combined or alpine data sets. Notable for subalpine vegetation, compared to the ordination of the combined dataset, pH and HCO_3^- were the environmental variables most highly correlated with vegetation composition (Table 5).

Water chemistry and hydrologic variables, particularly DSW, maximized the overall correlation between vegetation composition and environmental variables for both the subalpine and alpine data from the BEST analysis. Elevation, pH, EC, DSW, and CW maximized the rank correlation between alpine vegetation composition and environmental variables (BEST procedure, rho = 0.262, p = 0.002) (Table 4). Compared individually, DSW (rho = 0.142) and CW (rho = 0.164) had the highest Spearman rank correlation with the alpine vegetation distance matrix. This differs from the cumulative r^2 results that identified DGW as more correlated with vegetation composition than CW or DSW. The identification of elevation and EC as environmental variables influencing alpine fen plant species composition reflected a similar result within the alpine NMS ordination (both variables had relatively high cumulative r^2 values). Although pH had the lowest cumulative r^2 value relative to other environmental variables in the

alpine NMS ordination, it was selected by the BEST procedure. As part of the suite of

environmental variables, pH had an important influence on alpine plant community composition.

DSW, pH, HCO_3^-, and SO_4^{-2} maximized the correlation between subalpine vegetation and

environmental distance matrices (BEST procedure, rho = 0.44, p = 0.002) (Table 4). Analyzed

individually, pH (rho = 0.331), HCO_3^- (rho = 0.324), SO_4^{-2} (rho = 0.284), and EC (rho = 0.264)

had the highest Spearman rank correlations with the subalpine vegetation distance matrix.

Elevation and slope did not maximize the correlations between subalpine vegetation and

environmental distance matrices despite their high cumulative r^2 values from the subalpine NMS

ordination. Aside from SO_4^{-2}, the environmental variables identified by the BEST procedure had

some of the highest cumulative r^2 values from the subalpine NMS ordination.

5. Discussion

In the San Juan Mountains, study region fens were common in both subalpine and alpine zones due to the favorable climate and topography. The 13 identified fen plant communities separated out along elevation, topography and water chemistry gradients. Water chemistry, particularly pore water pH and HCO_3^-, influenced plant community composition in both alpine and subalpine fens. However, vegetation composition in subalpine fens had higher correlations with pH, HCO_3^-, and elevation than alpine fens. Alpine fens also had lower variation of pH, EC, HCO_3^-, and elevation than subalpine fens. The lower variation in alpine environmental variables may explain the decreased correlations with vegetation composition. However, weak correlations between environmental variables and plant community composition could not be attributed to lower plant community diversity in alpine fens, as beta diversity was similar for both subalpine and alpine fens.

5.1 *Distribution of subalpine and alpine fens*

This study highlighted the abundance of alpine fens in the Rocky Mountains of Colorado. Subalpine fens are more thoroughly studied in the Rocky Mountains than alpine fens (Driver 2010, Chimner et al. 2010, Johnston et al. 2012). Given the number of alpine fens mapped and visited, alpine fens are more abundant in the San Juan Mountains, compared with other regions of the Rocky Mountains (Cooper and Andrus 1994, Driver 2010, Chimner et al. 2010, Johnston et al. 2012). This is most likely the result of two distinctive features of the San Juan Mountains. First, the geologic history of the mountain range has resulted in large areas of gentle topography and plateaus at high elevation. Second, the precipitation regime of high winter snow packs

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combined with summer monsoons has contributed to the development and productivity of alpine fens. North of this region in the Rocky Mountains such as the Wind River Range in Wyoming (Cooper and Andrus 1994) and Rocky Mountain National Park (Driver 2010) in northern Colorado, alpine fens appear to be relatively uncommon compared to those below the forest line.

Given the relative rarity of alpine landscapes globally, subalpine fens are likely to be more common than alpine fens. In addition, climate and topography must allow for peatland development in the alpine. In the Sierra Nevada in California, a mountain range with dry summers and steep relief in the alpine, few fens occur above the forest line (Sikes et al. 2013). Other regions with large areas of gentle topography above the forest line include the Tibetan Plateau and the Andes. With monsoonal precipitation patterns and expanses of relatively flat topography, the Tibetan Plateau is reported to have the world's largest complexes of alpine peatlands (Zhao et al. 2011). In the Andes, alpine peatlands are most concentrated within the Altiplano-puna plateau and surrounding slopes (Olson et al. 2001, Squeo et al. 2006). In the Andes south of 43°S, peatlands occur mostly below the forest line, in areas of extreme valley glaciation (Arroyo et al. 2005). Alpine and subalpine fens are globally scarce, often have high plant diversity, function as refugia for many plant species, and are susceptible to precipitation and temperature shifts due to climate change. More research is needed to better understand the distribution of mountain fens and the variables that influence mountain fen plant community patterns across the globe.

5.2 *Context dependence of the influence of environmental variables on plant community composition*

An important function of research is to identify the relevant scale to measure observed patterns (Dungan et al. 2002, Legendre et al. 2009). pH is strongly correlated with peatland plant community composition in boreal zones spanning broad latitudinal gradients (Malmer 1986, Gignac and Vitt 1990, Wheeler and Proctor 2000, Bragazza et al. 2005). Thus comparisons of peatland vegetation-environment relationships across the large latitudinal gradient are justified. In this study, a comparison of fen vegetation across a large elevation gradient (alpine versus subalpine zones) showed a marked difference in the explanatory power of measured environmental variables. In particular, pH had only weak correlations with vegetation composition in the alpine.

The elevation range analyzed in the San Juan Mountains clearly points to the relative importance of different environmental variables in determining plant community composition, depending upon the elevation zone. This was also the case in a study of peatlands in the West Carpathian Mountains where elevation played a greater role in structuring plant community composition than pH in alpine as compared to subalpine peatlands (Sekulová et al. 2011). Studies of alpine fens by Sekulová et al. (2011) and Vonlanthen et al. (2006), have suggested that vegetation data from alpine vs. subalpine fens be examined separately. Findings from this research further support separating alpine and subalpine vegetation data.

5.3 *The role of environmental variation in explaining plant community composition and beta*

     diversity

In this study, pH was highly correlated with plant community composition in the subalpine but not in the alpine. In addition, elevation was relatively important for plant community composition in alpine fens. Climate is a key driver of alpine plant communities (Grabherr et al. 2000, Korner 2002, Korner 2003, Pauli et al. 2007) while hydrologic conditions and ground water chemistry are often the key drivers of peatland communities (Malmer 1986). Variations in climate, often inferred using elevation as a surrogate, and water chemistry, can occur across subalpine and alpine fens. Yet water chemistry variables, particularly pH, have often been found to be critical variables in determining plant community composition in both subalpine and alpine fens (Hajek et al. 2006, Cooper et al. 2010, Hettenbererova et al. 2013).

Plant community composition in peatlands in mountain and boreal regions is strongly correlated with variation in water source pH (Malmer 1986, Chimner et al. 2010, Sekulová et al. 2013). The Andes have a broad range of bedrock types from limestone to igneous rocks resulting in a wide range of groundwater geochemistry supplying alpine fens, and this variation was the main influence on fen plant community composition (Cooper et al 2010). The wide pH gradient in European peatlands due to varying bedrock and/or autogenous acidification processes strongly influences peatland plant community composition in the Alps (Gerdol 1995, Gerdol and Bragazza 2001) and Carpathians (Hájek et al. 2002, Sekulová et al. 2013). In the Rocky Mountains, bedrock composition in Yellowstone National Park regulated fen pH, a primary determinant of plant community composition (Lemly and Cooper 2011). In boreal peatlands water chemistry rather than latitude, is a strong driver of plant community composition (Gignac

and Vitt 1990). Researchers have proposed that pH, or the poor- to- rich gradient, is a primary division of peatland plant communities (Gignac and Vitt 1990, Wheeler and Proctor 2000).

Where fen pore water pH is less variable, it has little explanatory value for plant community composition, as was found in this study. Variation of pH was significantly lower in alpine than subalpine fens. Alpine fens in mountain ranges in Bulgaria are found on siliceous bedrock that supports little variation in groundwater pH or conductivity (Hajkova et al. 2006), and pH was not an important driver of plant community composition. In wetlands of the Alborz Mountains of Iran ranging in elevation from 1500 m to 3100 m, pH had low variation (5.9 – 7.7) and inadequately explained vegetation composition (Naqinezhad et al. 2009).

If pH is a driver of vegetation composition, beta diversity should decrease with decreases in the range of pH. However, in this study, beta diversity did not decrease in alpine fens even though pH had less variance in alpine fens as compared to subalpine fens. Thus, a smaller range in pH in alpine fens lead to weaker correlations with vegetation composition, but not decreased beta diversity. Where pH varies little, climatic conditions in the alpine zone may be the main driver of plant community composition. For alpine fens and bogs in the West Carpathian Mountains, elevation rather than pH was the main driver for plant community composition (Sekulová et al. 2011). Elevation was relatively important in explaining plant community composition in alpine fens of this study, despite a lower range of elevation in the alpine compared to the subalpine zone. Elevation was also an important driver of plant communities in high elevation wetlands in the Alborz Mountains in Iran (Naqinezhad et al. 2009) and in Australia mountain peatlands (Clark and Martin 1999). Elevation itself does not describe the environmental conditions of a fen and is more a proxy variable that can represent any number of climate conditions known to structure alpine plant communities. These include growing season

length; maximum, minimum and mean growing season temperature; mean annual precipitation; and duration of snowpack.

In addition to climate variables, environmental variables known to structure alpine plant communities include macronutrient availability (Gerdol 1990), soil temperature (Scherrer and Körner 2011), heavy metal concentrations in soil (Anic et al. 2010), solifluction (Wahren et al. 1999), light and wind exposure (Choler et al. 2001, Sekulová and Hájek 2009), and temporal variation in water table (Tahvanainen and Tuomaala 2003). While vegetation patterns in alpine environments are well studied (Gerdol 1990, Wahren et al. 1999, Choler et al. 2001), these occur across wide variations in soil type and water content. More research is needed for alpine fens to identify gradients structuring these habitats.

6. Conclusion

This study highlighted connections between environmental gradients and fen plant community composition in the San Juan Mountains and suggests areas for future scientific inquiry. Fens are a proportionally high source of regional biodiversity, given the small area they occupy within the Rocky Mountains. To better inform conservation strategies, it is necessary to understand the environmental conditions that influence plant community composition within fens. While water chemistry plays an important role in subalpine and alpine fens, additional research on the influence of temporal variation in water table and elevation on plant community composition should also be considered (Hajkova et al. 2004). Macronutrient availability (Gerdol 1990), soil temperature (Scherrer and Körner 2011), and soil heavy metal concentrations (Anic et al. 2010), are influential in structuring alpine plant communities as a whole and should be considered as variables in future studies of alpine fen vegetation-environment relationships.

Alpine fens are most concentrated within the San Juan Mountains as compared to other regions of the Rocky Mountains. Because of this, land managers within the region will be challenged to address the particular threats to long term alpine fen preservation. This research demonstrated that there may be differing environmental gradients that structure alpine and subalpine fen plant communities. Future studies should consider treating alpine and subalpine fen data separately to better inform land management decisions. The suite of threats to long-term subalpine and alpine fen stability may also differ. Climate change may be a particular threat to alpine fens (Burkett and Kusler 2000). Other likely threats are anthropogenic disturbances such as livestock grazing and roads (Chimner et al. 2010). Alpine fens may be particularly susceptible to destabilization of stream banks from livestock grazing and subsequent erosional forces due to

low plant growth rates. Minimizing anthropogenic disturbance and mitigating the impact of past

disturbance should be priorities for land managers seeking the long term conservation of

subalpine and alpine fens. Understanding the underlying environmental gradients driving fen

plant community composition continues to be an important topic of study, informing future

conservation strategies for these diverse and vital wetlands.

7. Tables and figures

Table 1. Mean, variance, and standard deviation of selected measured environmental variables between alpine and subalpine fens. Units and abbreviations are as follows: SO_4^{-2}, HCO_3^-, and Mg^{+2} (mg/L); Cover of water (CW) (%); Depth of surface water (DSW) (cm); Elevation (m); Electrical conductivity (EC) (μS/cm). * indicates a significant difference in **variance** between subalpine and alpine fens at alpha = 0.05. Significance codes: '***' 0.001 '**' 0.01 '*' 0.05.

	Alpine			Subalpine		
	Mean ± se	Min	Max	Mean ± se	Min	Max
pH***	5.54 ± 0.08	3.86	6.84	5.84 ± 0.05	4.05	6.95
EC*	249 ± 33	26	1772	139 ± 18	12.7	916
Ca^{+2}	30.5 ± 4.4	0.9	172	24.1 ± 5.1	0.3	268
Mg^{+2}	8.4 ± 1.5	0.2	54.2	4.5 ± 1.2	0.1	62
SO_4^{-2}	91.1 ± 18.7	0.6	786	66.8 ± 19.1	0.1	990
HCO_3^-***	32.5 ± 2.5	3.2	110.6	23.5 ± 1.2	6	66
Elevation***	3262 ± 20	2688	3594	3693 ± 5	3609	3792
Slope	2 ± 1	0	10	3 ± 1	0	11
Cover of Water	8 ± 2	0	73	12 ± 2	0	92
DSW	1 ± 1	0	10	1 ± 1	0	7
DGW	13 ± 1	0	48	10 ± 1	0	40
DSP**	6 ± 1	0	40	2 ± 1	0	29
Percent OM	49 ± 1	14	76	51 ± 1	14	81

Table 2. r^2 values from correlations of environmental variables with NMS axes of ordination of combined subalpine and alpine dataset. +/- indicates the direction of the correlation. Abbreviations are as follows: DSW is depth of surface water, DGW is depth to ground water, DSP is depth to saturated peat, and CW is cover of water in stand.

Axis:	1	2	3	Cumulative r^2
HCO$_3^-$	0.029 (+)	0.019 (-)	0.151 (+)	0.199
EC	0.045 (-)	0.01 (-)	0.092 (+)	0.147
pH	0.128 (+)	0.007 (-)	0.030 (+)	0.165
Ca^{+2}	0.012 (-)	0.022 (+)	0.037 (+)	0.071
Mg^{+2}	0.029 (-)	0.020 (+)	0.046 (+)	0.095
SO$_4^{-2}$	0.034 (-)	0.038 (+)	0.023 (+)	0.095
Elevation	0.118 (+)	0.075 (+)	0.311 (-)	0.504
Slope	0.020 (+)	0.027 (-)	0.123 (-)	0.170
DSW	0.001 (-)	0.028 (+)	0.073 (+)	0.102
DGW	0.003 (+)	0.057 (-)	0.032 (-)	0.092
DSP	0.011 (-)	0.007 (-)	0.003 (-)	0.021
CW	0.010 (-)	0.032 (+)	0.019 (+)	0.061

Table 3. MRPP within group distance, number of stands per fen geochemistry type (iron, intermediate, or rich fen), dominant topographic position (basin; sloping, if slope > 0°; or both) and mean (±) standard error of measured environmental variables for each vegetation type classified by hierarchical cluster analysis and grouped by elevation class (alpine, subalpine, or across elevation gradient). Table 3 is continued on next page. DGW is depth to groundwater .

	Plant Community Name with Group ID Number	MRPP: Within Group Distance	Number of Stands/ Fen Geochemistry Type	pH	EC (µS/cm)	HCO$_3^-$ (mg/L)	SO$_4^{-2}$ (mg/L)	Ca^{+2} (mg/L)	Mg^{+2} (mg/L)
Subalpine Fens	(11) *Triglochin palustris - Carex canescens*	0.4864	5/Rich	6.56 ± 0.07	846.46 ± 245.69	57.84 ± 7.15	307.60 ± 66.6	111.96 ± 15.72	28.88 ± 6.12
	(9) *Salix monticola/brachycarpa-Polemonium occidentale ssp. occidentale*	0.6462	7/Intermediate 8/Rich	6.10 ± 0.1	161.25 ± 22.47	50.00 ± 5.29	100.20 ± 51.32	47.65 ± 14.59	11.94 ± 4.56
Alpine Fens	(2) *Carex illota - Podistera eastwoodiae*	0.6627	54/Intermediate 1/Iron 4/Rich	5.79 ± 0.07	109.68 ± 19.43	25.11 ± 2.1	41.95 ± 18.75	17.76 ± 5.27	3.02 ± 1.11
	(5) *Eleocharis quinqueflora - Warnstorfia exannulata*	0.5408	13/Intermediate 1/Iron	5.66 ± 0.14	107.32 ± 60.57	19.47 ± 2.12	71.73 ± 70.64	22.46 ± 18.91	4.93 ± 4.39
	(10) *Carex scopulorum - Palustriella falcata*	0.5457	13/Intermediate	5.92 ± 0.15	77.90 ± 13.60	30.83 ± 3.56	8.61 ± 3.96	8.16 ± 2.71	0.88 ± 0.34
Across Elevation Gradient	(1) *Salix planifolia - Climacium dendroides*	0.5518	24/Intermediate 2/Iron 1/Rich	5.61 ± 0.10	101.90 ± 16.24	23.59 ± 1.40	19.08 ± 10.00	12.71 ± 3.79	2.45 ± 0.86
	(4) *Calamagrostis canadensis - Carex aquatilis*	0.5438	8/Intermediate 4/Iron 1/Rich	5.45 ± 0.25	253.63 ± 99.77	19.08 ± 3.30	162.32 ± 91.03	42.13 ± 21.36	11.31 ± 5.96
	(6) *Carex utriculata - Brachythecium salebrosum*	0.5497	16/Intermediate 1/Iron 3/Rich	5.98 ± 0.10	130.15 ± 20.61	34.93 ± 5.33	31.36 ± 11.48	19.39 ± 5.12	4.13 ± 1.32
	(3) *Carex aquatilis - Caltha leptosepala*	0.6407	18/Intermediate 1/Iron 2/Rich	5.61 ± 0.14	155.17 ± 52.95	21.91 ± 2.08	63.39 ± 38.92	19.16 ± 7.32	5.21 ± 2.72
	(7) *Straminergon stramineum - Amblystegium serpens* (unresolved group)	0.8058	17/Intermediate 1/Iron 6/Rich	5.82 ± 0.14	257.67 ± 69.82	31.17 ± 6.37	48.36 ± 24.81	21.05 ± 7.72	4.96 ± 2.34
	(8) *Warnstorfia fluitans - Polytrichastrum longisetum*	0.6856	15/Iron	4.66 ± 0.19	485.33 ± 106.75	10.00 ± 1.44	344.33 ± 107.83	76.69 ± 27.49	20.79 ± 7.22

Table 3 continued.

	Plant Community Name with ID Number	Topography	Slope (degrees)	Elevation (m)	DGW (cm)	Percent Organic Matter (%)
Subalpine Fens	(11) *Triglochin palustris - Carex canescens*	*Basin*	0.00 ± 0.00	3155.8 ± 6.51	6.60 ± 2.70	56 ± 1
	(9) *Salix monticola/brachycarpa- Polemonium occidentale ssp. occidentale*	*Both*	2.07 ± 0.49	3159.73 ± 37.91	8.85 ± 2.20	56 ± 4
Alpine Fens	(2) *Carex illota - Podistera eastwoodiae*	*Sloping*	3.49 ± 0.35	3699.58 ± 8.93	13.30 ± 1.14	47 ± 2
	(5) *Eleocharis quinqueflora - Warnstorfia exannulata*	*Sloping*	1.93 ± 0.50	3647.43 ± 10.66	10.15 ± 3.66	57 ± 2
	(10) *Carex scopulorum - Palustriella falcata*	*Both*	2.54 ± 0.87	3701.23 ± 17.84	5.46 ± 2.16	45 ± 3
Across Elevation Gradient	(1) *Salix planifolia - Climacium dendroides*	*Sloping*	4.67 ± 0.53	3443.23 ± 48.03	17.74 ± 2.20	53 ± 2
	(4) *Calamagrostis canadensis - Carex aquatilis*	*Sloping*	4.08 ± 1.02	3512.31 ± 76.18	10.92 ± 2.25	47 ± 4
	(6) *Carex utriculata - Brachythecium salebrosum*	*Both*	1.50 ± 0.57	3307.70 ± 60.91	4.73 ± 1.67	48 ± 3
	(3) *Carex aquatilis - Caltha leptosepala*	*Both*	1.62 ± 0.47	3554.05 ± 50.80	8.00 ± 1.96	50 ± 3
	(7) *Straminergon stramineum - Amblystegium serpens* (unresolved group)	*Both*	1.58 ± 0.44	3400.21 ± 42.06	16.21 ± 2.55	55 ± 3
	(8) *Warnstorfia fluitans - Polytrichastrum longisetum*	*Both*	2.47 ± 0.67	3303.27 ± 70.36	10.47 ± 2.43	44 ± 4

Table 4. Spearman rank correlations (SRC) of individual environmental variables as well as the combinations of variables that maximized rho between two to seven environmental variables for the combined, subalpine, and alpine vegetation distance matrices. The BEST procedure produces a rank correlation (rho) for all possible combinations of environmental variables for any given number of environmental variables used. Thus for each number (between two to seven variables used in this instance) there is a combination of specific variables that produces a maximum rank correlation. 'x' denotes which environmental variables were selected at each level that maximized rho between the environmental and vegetation distance matrices. The maximum rho that corresponds to the selected variables at each level is given along the bottom row for each of the three vegetation distance matrices. Rank correlations between individual environmental variables and the three vegetation distance matrices are given in three separate columns. The greyed column shows the combination of variables chosen that had the highest rho overall or when rho plateaued after further addition of variables. Abbreviations are as follows: depth of surface water (DSW), depth to ground water (DGW), depth to saturated peat (DSP), cover of surface water (CW).

	Full Vegetation							Subalpine Vegetation							Alpine Vegetation						
		Number of environmental variables							Number of environmental variables							Number of environmental variables					
	SRC:	2	3	4	5	6	7	SRC:	2	3	4	5	6	7	SRC:	2	3	4	5	6	7
HCO_3^-	0.195				x	x	x	0.324	x	x	x	x	x	x	0.024						
EC	0.221			x	x		x	0.264						x	0.105	x	x	x	x	x	x
pH	0.145	x	x	x	x	x	x	0.331	x	x	x	x	x	x	0.094				x	x	x
SO_4^{-2}	0.200					x	x	0.284			x	x	x	x	0.092					x	x
Elevation	0.299	x	x	x	x	x	x	0.175				x	x	x	0.040		x	x	x	x	x
Slope	0.033							0.117					x	x	0.050						
DSW	0.169		x	x	x	x	x	0.146		x	x	x	x	x	0.142			x	x	x	x
DGW	0.017							0.035							0.065						x
DSP	-0.060							-0.021							-0.052						
CW	0.140					x	x	0.052							0.164	x	x	x	x	x	x
	SRC:	0.330	0.355	0.377	0.383	0.385	0.385	SRC:	0.379	0.420	0.440	0.434	0.433	0.420	SRC:	0.224	0.245	0.256	0.262	0.261	0.258

Table 5. Cumulative r^2 values for measured environmental variables with NMS ordination axes from the combined data set and separated subalpine and alpine stands. DSW is depth of surface water. DGW is depth to ground water. DSP is depth to saturated peat. CW is cover of surface water.

Environmental Variables	Combined Fens	Subalpine Fens	Alpine Fens
HCO_3^-	0.199	0.485	0.112
EC	0.147	0.202	0.110
pH	0.165	0.597	0.010
Ca^{+2}	0.071	0.136	0.094
Mg^{+2}	0.095	0.120	0.098
SO_4^{-2}	0.095	0.163	0.096
Elevation	0.504	0.312	0.133
Slope	0.170	0.385	0.050
DSW	0.102	0.350	0.068
DGW	0.092	0.194	0.125
DSP	0.021	0.109	0.049
CW	0.061	0.099	0.098
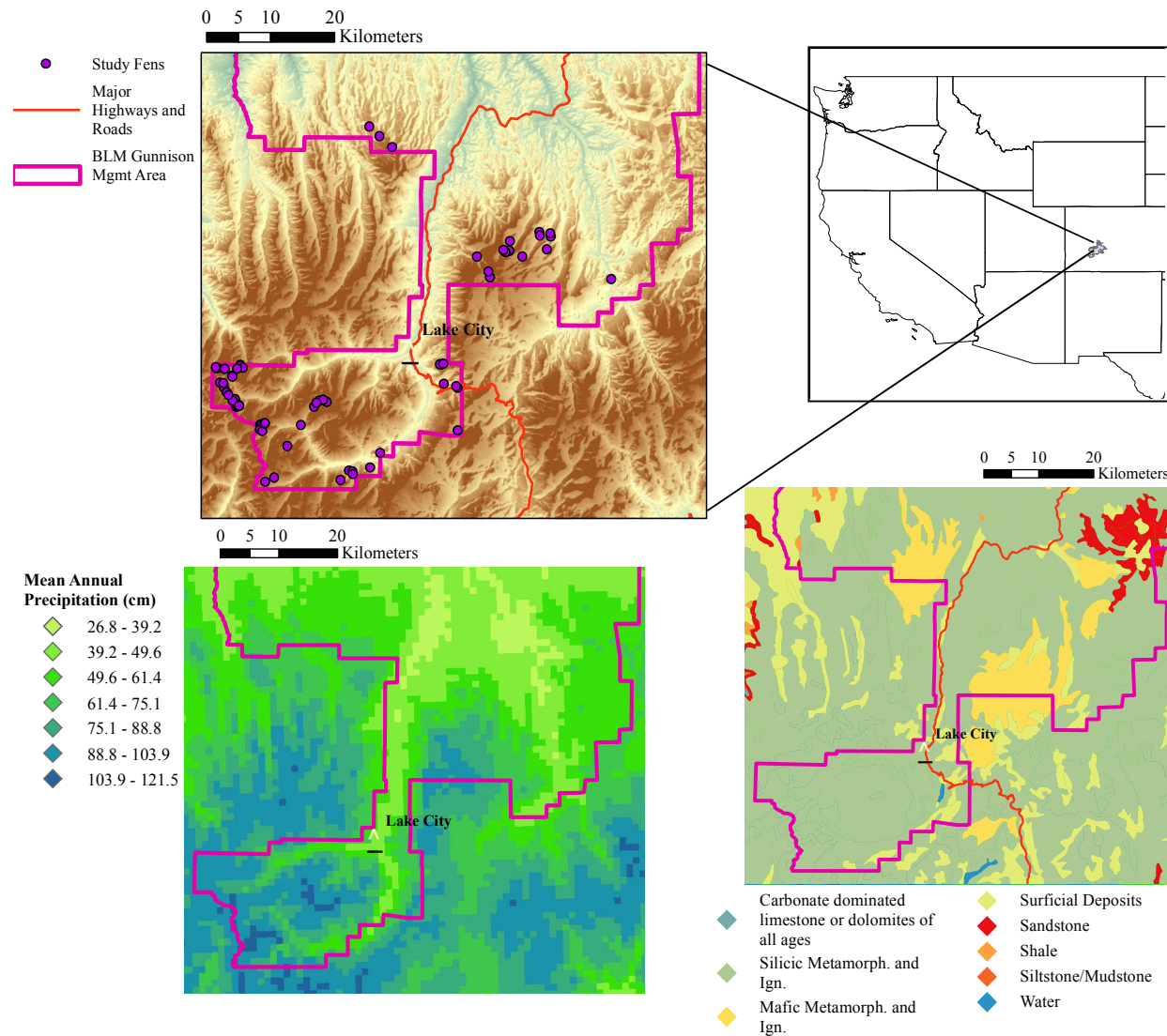
Figure 1. Map of study area within the BLM Gunnison Management Unit in south west Colorado, USA including elevation gradient and locations of sampled fens (top) (Gesch et al. 2002); precipitation gradient (bottom left) (Hijmans et al. 2005); and geology (bottom right) (Tweto 1979).
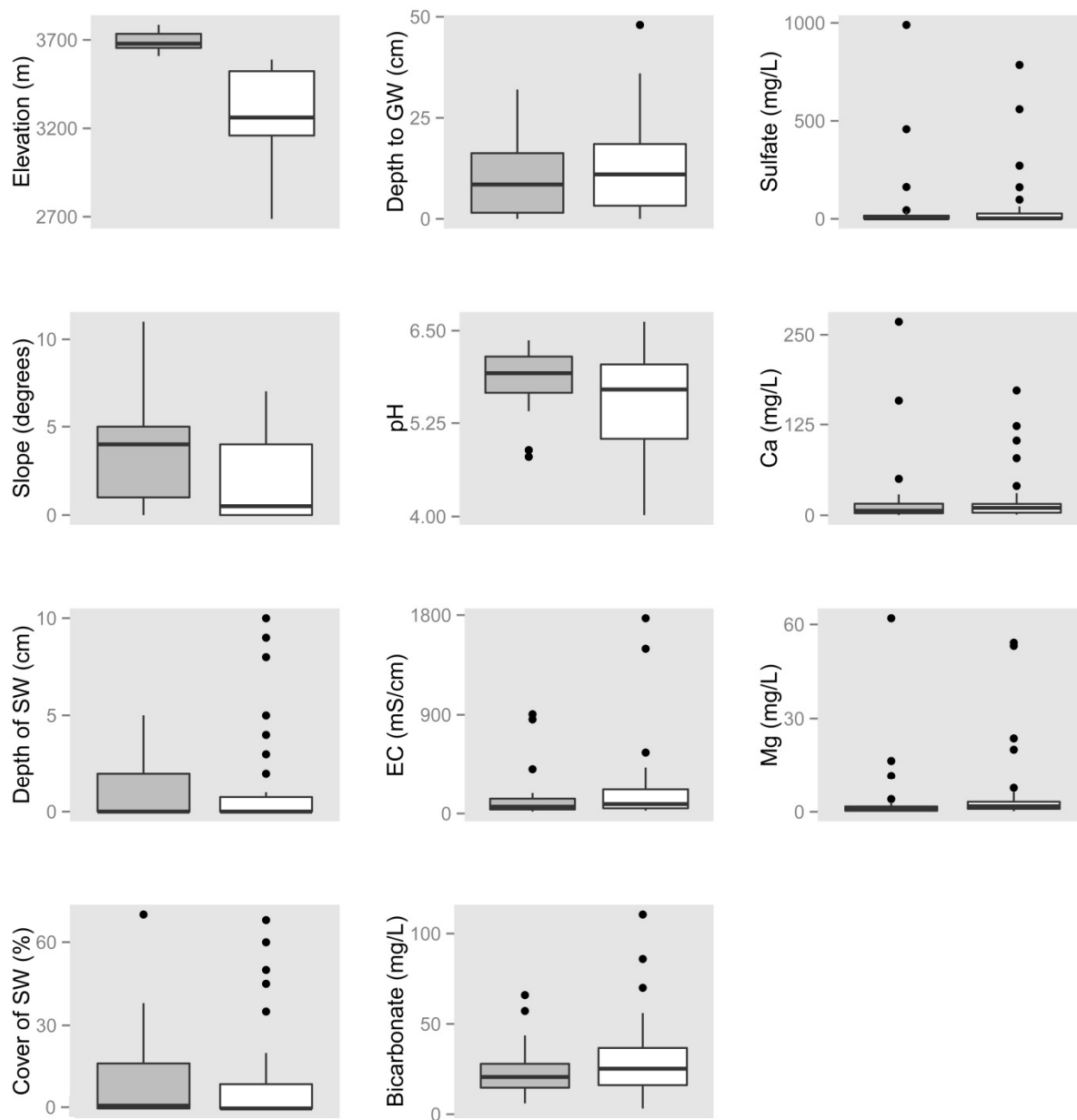
Figure 2. Boxplots comparing selected measured environmental variables for alpine and subalpine fens. Points reflect outliers, occurring past the 95th percentile denoted by the end of the whisker. The upper and lower boundary of the box represents the 75th and 25th quartile. EC is electrical conductivity.
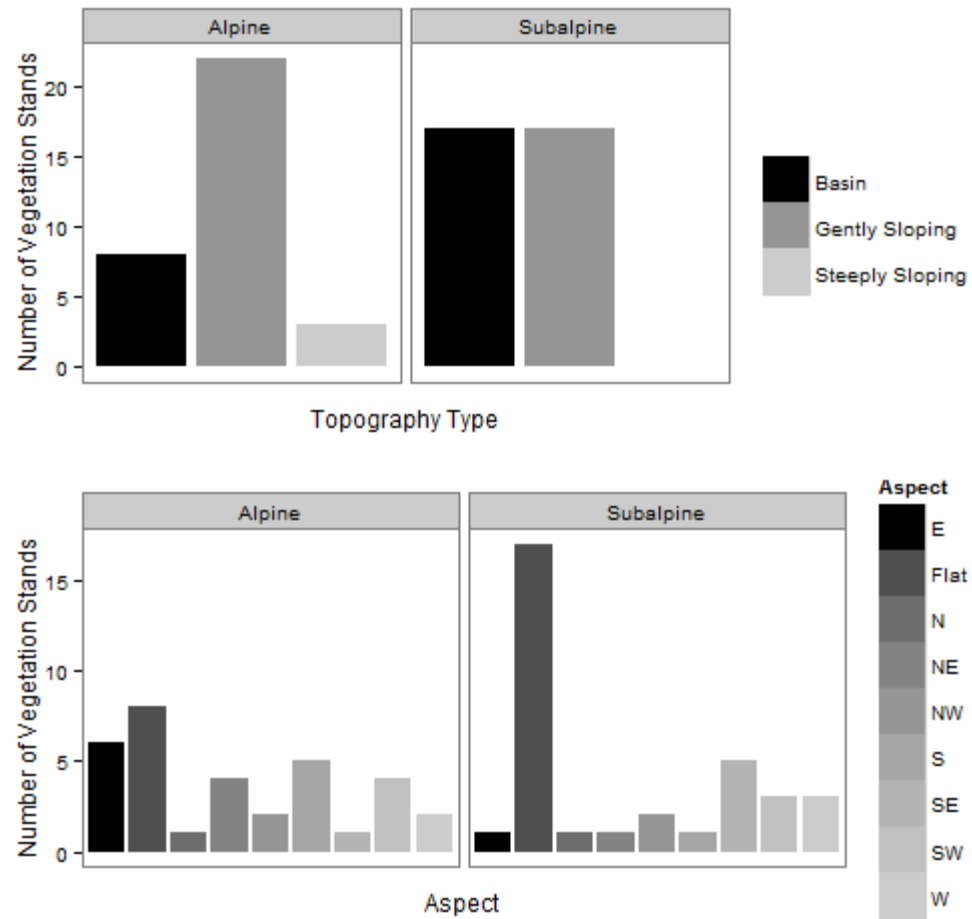
Figure 3. Histograms showing the distribution of *(a)* topographic position and *(b)* aspect categories between alpine and subalpine vegetation stands. Topographic positions are defined as basin (slope = 0), gently sloping (slope < 10º), and steeply sloping (slope > 10º).
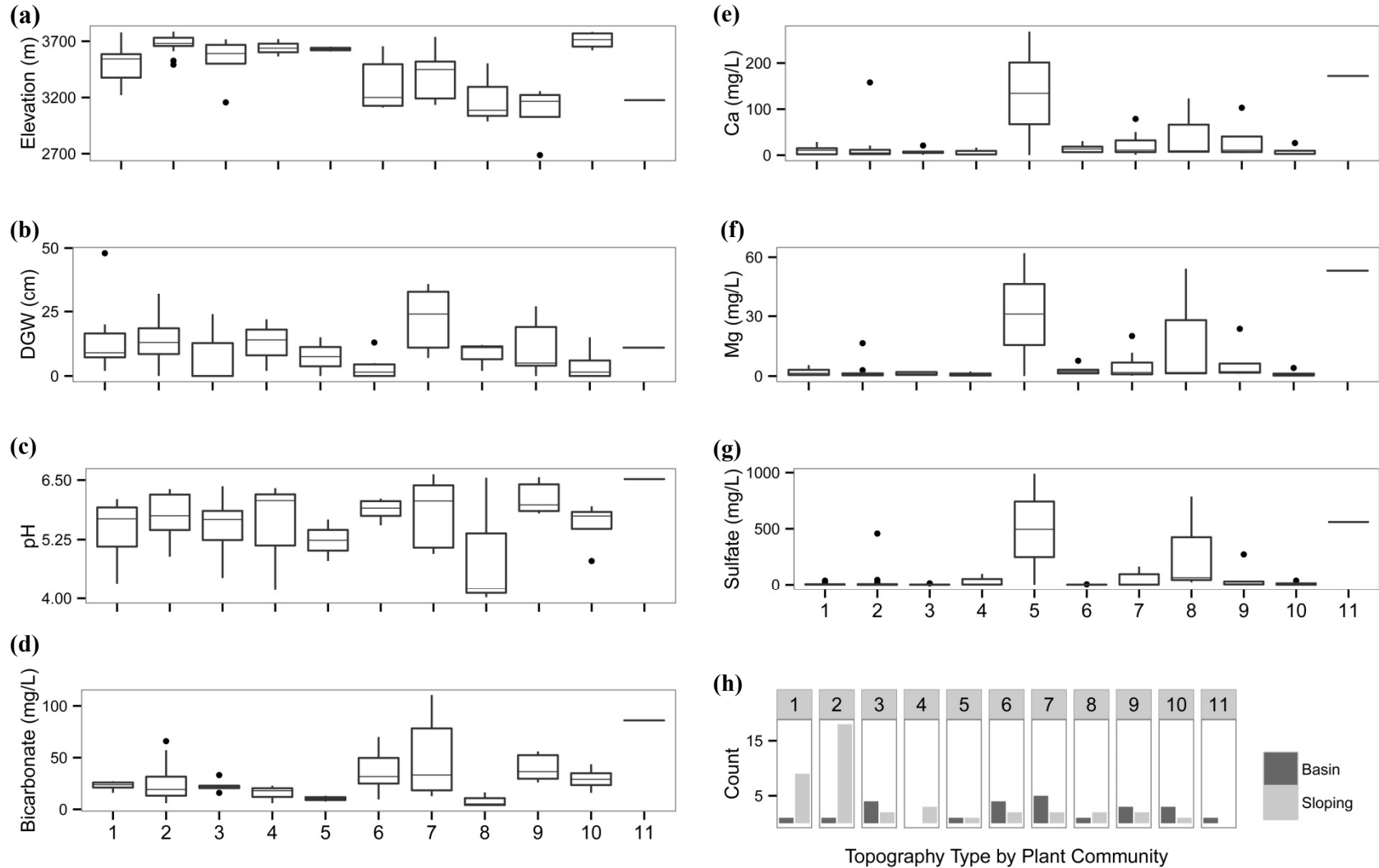
Figure 4. Continuous and categorical environmental variable values compared between classified plant communities. See Table 1 for classified plant community identities. (**a-g**) Boxplots showing environmental variable range between classified plant communities. Points reflect outliers, occurring past the 95th percentile denoted by the end of the whisker. The upper and lower boundary of the box represents the 75th and 25th quartile respectively. DGW is depth to ground water. (**h**) Distribution of topographic position categories between classified plant communities.
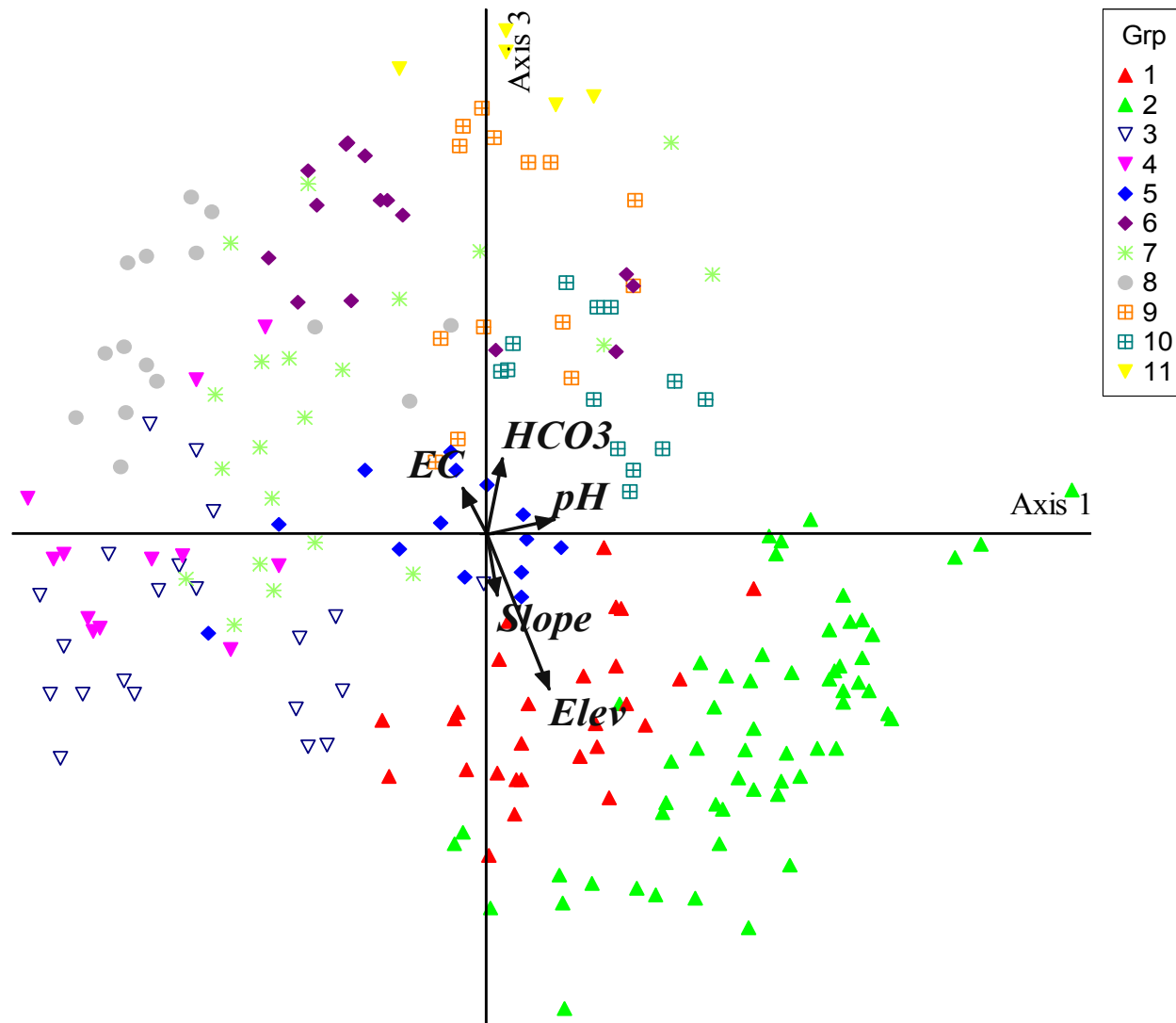
Figure 5. NMS diagram of all vegetation stands and environmental vectors with an r^2 cut off = 0.100. Vegetation stands in ordination are grouped by plant community type ("Grp" in key) as determined by hierarchical cluster analysis.   See Table 3 for group (Grp) identities. Arrows point in the direction of positive correlation.
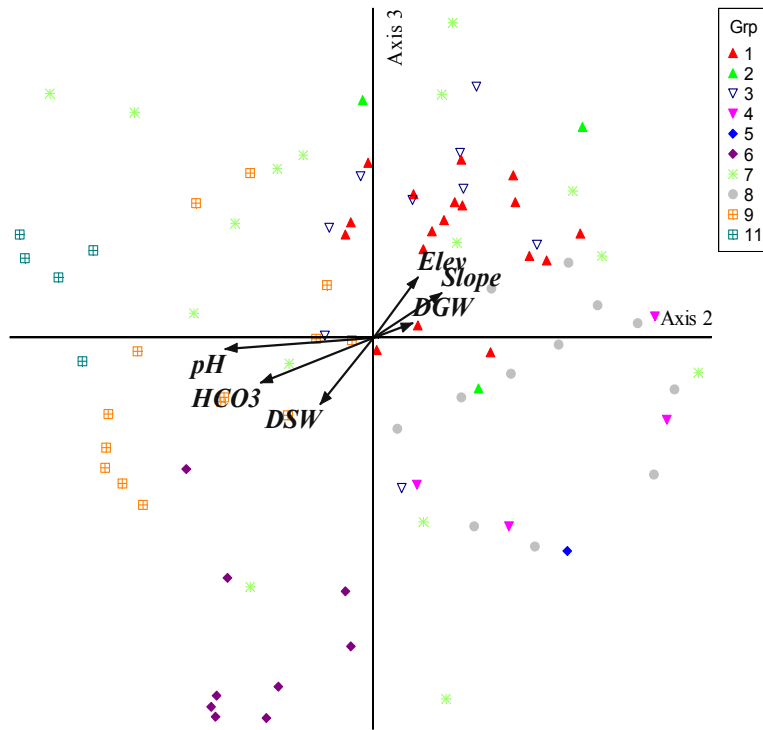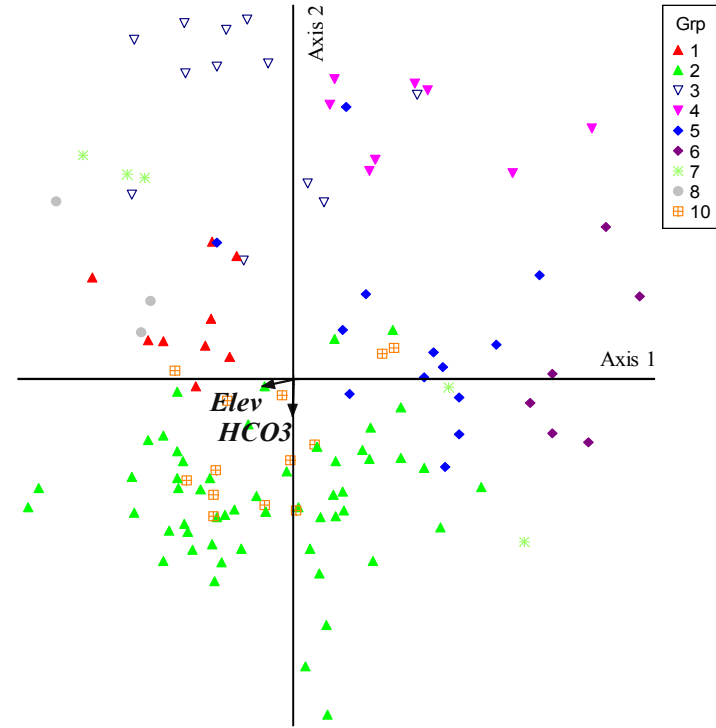
Figure 6. Joint plots of *(a)*subalpine and *(b)*alpine NMS ordinations and correlated environmental variables with an r^2 cutoff of 0.10 and 0.08 respectively. Vegetation stands in ordination are grouped by plant community type ("Grp" in key) as determined by hierarchical cluster analysis. See Table 3 for group identities. DGW=Depth to ground water. DSW= Surface water depth.

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Appendix A. Vascular plant and bryophyte species list from sampled stands.

Vascular Plants

Apiaceae
Conioselinum scopulorum
Oxypolis fendleri
Podistera eastwoodiae

Asteraceae
Achillea millefolium
Antennaria corymbosa
Arnica mollis
Artemisia scopulorum
Cirsium parryi
Erigeron lonchophyllus
Packera crocata
Senecio triangularis
Taraxacum officinale

Betulaceae
Alnus incana s. tenuifolia
Betula glandulosa

Boraginaceae
Mertensia ciliata
Mertensia franciscana
Mertensia lanceolata

Brassicaceae
Cardamine cordifolia
Descurainia incana
Galium brevipes
Rorippa curvipes v. curvipes

Caprifoliaceae
Lonicera involucrata v. involucrata

Caryophyllaceae
Cerastium fontanum s. vulgare
Stellaria borealis
Stellaria calycantha
Stellaria longifolia

Caryphyllaceae
Stellaria longipes s. longipes
Stellaria umbellata

Crassulaceae
Rhodiola rhodantha

Cyperaceae
Carex aquatilis
Carex atherodes
Carex aurea
Carex canescens
Carex diandra
Carex disperma
Carex ebenea
Carex illota
Carex microglochin
Carex microptera
Carex nelsonii
Carex nigricans
Carex norvegica
Carex nova
Carex praeceptorum
Carex saxatilis
Carex scopulorum
Carex siccata
Carex simulata
Carex utriculata
Carex vernacula
Eleocharis macrostachya
Eleocharis palustris
Eleocharis quinqueflora
Eriophorum altaicum
Eriophorum scheuchzeri

Equisetaceae
Equisetum arvense

Ericaceae
Vaccinium myrtillus

Fabaceae
Trifolium parryi
Trifolium repens

Gentianaceae
Gentiana fremontii
Gentiana prostrata
Gentianella amarella s. acuta
Gentianopsis barbellata
Gentianopsis detonsa v. elegans
Gentianopsis thermalis
Swertia perennis

Geraniaceae
Geranium richardsonii

Grossulariaceae
Ribes inerme

Hippuridaceae
Hippuris vulgaris

Juncaceae
Juncus albescens
Juncus arcticus s. littoralis
Juncus drummondii
Juncus ensifolius
Juncus mertensianus
Juncus nevadensis
Luzula parviflora
Luzula subcapitata

Juncaginaceae
Triglochin palustris

Liliaceae
Allium geyeri v. tenerum

Onagraceae
Chamerion angustifolium
Epilobium anagallidifolium
Epilobium ciliatum s. glandulosum
Epilobium halleanum
Epilobium hornemannii s. hornemannii
Epilobium leptophyllum
Epilobium oregonense
Epilobium saximontanum

Ophioglossaceae
Botrychium furculatum

Orchidaceae
Platanthera dilatata v. dilatata
Platanthera obtusata

Pinaceae
Picea engelmannii

Poaceae
Agrostis humilis
Agrostis idahoensis
Agrostis scabra
Agrostis thurberiana
Agrostis variabilis
Alopecurus aequalis
Calamagrostis canadensis
Deschampsia brevifolia
Deschampsia cespitosa
Elymus trachycaulus
Festuca brachyphylla s. coloradensis
Festuca minutiflora
Festuca saximontana
Hordeum brachyantherum
Muhlenbergia filiformis

Poaceae
Phleum alpinum
Poa alpina
Poa arctica s. arctica
Poa compressa
Poa leptocoma
Poa pratensis
Poa reflexa
Trisetum wolfii

Polemoniaceae
Polemonium occidentale s. occidentale

Polygonaceae
Bistorta viviparum
Polygonum bistortoides
Polygonum minimum

Pyrolaceae
Pyrola asarifolia
Pyrola minor

Ranunculaceae
Aconitum columbianum
Caltha leptosepala
Ranunculus inamoenus v. inamoenus
Thalictrum sparsiflorum

Rosaceae
Dasiphora fruticosa s. floribunda
Fragaria vesca
Fragaria virginiana
Geum macrophyllum
Geum rivale
Geum triflorum
Potentilla diversifolia
Rosa blanda

Salicaceae
Salix brachycarpa
Salix geyeriana
Salix monticola
Salix planifolia
Salix wolfii

Saxifragaceae
Saxifraga odontoloma

Scrophulariaceae
Castilleja rhexiifolia
Pedicularis groenlandica
Pedicularis sudetica s. scopulorum
Veronica americana
Veronica peregrina v. xalapensis
Veronica wormskjoldii

Sparganiaceae
Sparganium emersum

Violaceae
Viola adunca
Viola macloskeyi v. pallens

Bryophytes

Amblystegiaceae
Amblystegium serpens
Calliergon giganteum
Campylium protensum
Campylium stellatum
Cratoneuron filicinum
Drepanocladus aduncus
Palustriella falcata
Sanionia uncinata
Scorpidium cossonii
Straminergon stramineum
Warnstorfia exannulata
Warnstorfia fluitans

Aulacomniaceae
Aulacomnium palustre

Bartramiaceae
Philonotis fontana

Brachytheciaceae
Brachythecium erythrorhizon
Brachythecium salebrosum
Sciuro-hypnum latifolium
Tomentypnum nitens

Bryaceae
Pohlia cruda
Pohlia nutans
Ptychostomum pseudotriquetrum
Ptychostomum weigelii

Climaciaceae
Climacium dendroides

Dicranaceae
Dicranum bonjeanii
Oncophorus virens

Ditrichaceae
Ceratodon purpureus

Helodiaceae
Helodium blandowii

Hypnaceae
Breidleria pratensis
Hypnum lindbergii

Mniaceae
Plagiomnium ellipticum
Rhizomnium pseudopunctatum

Polytrichaceae
Polytrichastrum alpinum
Polytrichastrum longisetum

Pottiaceae
Desmatodon latifolius

Sphagnaceae
Sphagnum angustifolium
Sphagnum fimbriatum
Sphagnum russowii

Appendix B. Photos of classified plant communities.

Carex illota - Podistera eastwoodiae

Carex scopulorum - Palustriella falcata

Eleocharis quinqueflora - Warnstorfia exannulata

Triglochin palustris - Carex canescens

Salix planifolia - Climacium dendroides

Carex utriculata - Brachythecium salebrosum

Salix monticola/brachycarpa-Polemonium occidentale ssp. occidentale

Carex aquatilis - Caltha leptosepala

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Warnstorfia fluitans - Polytrichastrum longisetum

Calamagrostis canadensis - Carex aquatilis

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Appendix C. Table of mapped potential fen field determinations and unvisited potential fens by stratification group.

Group ID Number	Number of Potential fens on Public Land	Sampled Fens	Field verified, unsampled fens	Re-assessed with aerial imagery, not a fen.	Visited, not a fen.	Inaccessible	Total Visited, Re-assessed, and inaccessible fens
1	107	7	--	47	25	1	80
2	11	2	--	2	7	--	11
3	4	0	--	3	1	--	4
4	180	36	12	3	33	1	85
5	20	7	--	4	9	--	20
6	4	1	--	--	3	--	4
7	3	0	--	--	3	--	3
8	23	12	--	2	7	2	23
9	2	0	--	--	1	1	2
10	30	0	--	14	16	--	30
Total	384	65	12	75	105	5	262

Appendix D. UTM coordinates and elevations of all sampled stands in visited fens.

Fen ID	X	Y	Elevation (m)	Fen ID	X	Y	Elevation (m)	Fen ID	X	Y	Elevation (m)
UTM NAD 83 Zone 13N											
Alpen 1	273442	4207939	3707	Cinn 4	277980	4202232	3778	Funk 2	289222	4196503	3263
Alpen 2	273496	4207937	3705	Cinn 5	278110	4202242	3783	Funk 3	289235	4196490	3263
Alpen 3	273435	4207937	3717	Cinn 6	278094	4202250	3783	Funk 4	289298	4196476	3256
Alpen 4	273427	4207936	3721	Devil 1	306709	4219995	3661	Funk 5	289339	4196475	3257
Arti 1	272692	4209802	3672	Dolly 1	274616	4205838	3659	Funk 6	289256	4196494	3258
Arti 2	272745	4209773	3672	Dolly 2	274606	4205830	3640	Gold 1	300289	4209556	3134
Arti 3	272743	4209763	3691	Dolly 3	274602	4205829	3658	Gold 2	300270	4209526	3135
Aspen 1	312788	4225174	3222	Drag 1	300463	4209574	3166	Gold 3	300234	4209573	3134
Aspen 2	312821	4225267	3226	Drag 2	300438	4209570	3154	Gold 4	300221	4209574	3137
Aspen 3	312918	4225289	3206	Drag 3	300449	4209555	3153	Gold 5	300245	4209574	3135
Aspen 4	312924	4225272	3221	Drag 4	300455	4209563	3156	Gorp 1	308625	4222992	3548
Bella 1	284584	4204792	3498	Drag 5	300451	4209559	3158	Gorp 2	308651	4222960	3550
Bella 2	284581	4204781	3503	Drag 6	300448	4209577	3151	Grizz 1	281196	4200128	3616
Bella 3	284569	4204769	3499	Dusk 1	295063	4236010	3259	Grizz 2	281200	4200138	3663
Bert 1	278493	4202969	3704	Dusk 2	295034	4236032	3252	Grizz 3	281190	4200134	3669
Bert 2	278518	4202989	3710	Elep 1	273702	4209697	3761	Grizz 4	281178	4200147	3665
Bert 3	278509	4202977	3707	Elep 2	273725	4209689	3752	Grizz 5	281185	4200116	3664
Bird 1	312927	4224905	3137	Elep 3	273674	4209659	3741	Grizz 6	281185	4200123	3655
Bird 2	312936	4224893	3143	Elk 1	287648	4195871	3573	Hazy 1	288717	4196956	3263
Birt 1	278025	4202757	3732	Elk 2	287654	4195859	3573	Hidden 1	310686	4222323	3493
Birt 2	278022	4202761	3741	Elk 3	287634	4195894	3573	Hidden 2	310681	4222315	3497
Birt 3	278004	4202766	3742	Ernie 1	278452	4202928	3719	Hurr 1	275479	4205118	3644
Birt 4	278009	4202762	3735	Ernie 2	278466	4202943	3719	Hurr 2	275455	4205145	3652
Birt 5	277948	4202779	3734	Ernie 3	278499	4202956	3723	Hurr 3	275736	4205130	3648
Birt 6	277953	4202763	3738	Ernie 7	278437	4202928	3705	Hurr 4	275736	4205130	3648
Butt 1	293518	4237391	3154	Ernie 8	278437	4202928	3705	Hurr 5	275446	4205130	3627
Butt 2	293607	4237382	3157	Fairy 1	273922	4206863	3784	Hurr 6	275372	4205135	3647
Chedda 1	308405	4223249	3589	Fairy 2	273926	4206874	3773	Ipa 1	309242	4222312	3506
Chedda 2	308405	4223261	3594	Frozen 1	275372	4205235	3671	Ipa 2	209239	4224291	3515
Cinn 1	278070	4202205	3773	Frozen 2	275345	4205239	3728	Jaw 1	275190	4205156	3663
Cinn 2	278019	4202231	3791	Frozen 3	275345	4205239	3728	Jaw 2	275190	4205162	3663
Cinn 3	277992	4202228	3788	Funk 1	289212	4196517	3263	Lake 1	300688	4209630	3177

UTM NAD 83 Zone 13N											
Fen ID	X	Y	Elevation (m)	Fen ID	X	Y	Elevation (m)	Fen ID	X	Y	Elevation (m)
Lake 2	300680	4209627	3176	Powd 1	314309	4224627	2985	Shov 3	277901	4202231	3787
Lake 3	300687	4209638	3178	Powd 2	314339	4224616	3113	Shov 4	277879	4202221	3779
Lake 4	300699	4209614	3178	Powd 3	314350	4224541	3122	Slum 1	302228	4206787	3087
Land 1	300718	4207220	2990	Powd 4	314410	4224547	3123	Slum 2	302094	4206771	3087
Land 2	300728	4207266	2988	Powd 5	314300	4224710	3108	Slum 3	302088	4206780	3087
Land 3	300707	4207263	2988	Powd 6	314359	4224684	3122	Slum 4	302048	4206648	3087
Land 4	300704	4207261	2987	Powd 7	314242	4225063	3115	Slum 5	302038	4206678	3087
Last 1	321585	4219434	2688	Powd 8	314209	4225142	3110	Slum 6	302021	4206636	3092
Last 2	321597	4219428	2688	Purdy 1	285742	4205611	3611	Slum 7	301948	4206634	3086
Liquid 1	292312	4238610	3039	Rambo 1	302307	4201444	3492	Snare 1	279436	4196390	3632
Liquid 2	292284	4238603	3027	Rambo 2	302279	4201430	3492	Snare 2	279471	4196348	3622
Liquid 3	292322	4238603	3036	Rambo 3	302222	4201512	3492	Snare 3	279460	4196368	3650
Liquid 4	292280	4238583	3026	Rambo 4	302245	4201551	3368	Snow 1	273614	4207379	3765
Litt 1	282598	4199029	3053	Rambo 5	302123	4201720	3488	Snow 2	273628	4207384	3755
Magic 1	278349	4195864	3777	Rambo 6	302162	4201799	3492	Snow 3	273628	4207384	3755
Magic 2	278331	4195858	3776	Red 1	284943	4205297	3532	Star 1	309094	4223205	3527
Magic 3	278334	4195870	3790	Red c 1	274702	4205742	3633	Star 2	309100	4223169	3523
Magic 4	278343	4195837	3785	Red c 2	274811	4205802	3633	Star 3	309118	4223145	3537
Magic 5	278330	4195843	3792	Red c 3	274801	4205805	3627	Star 4	309107	4223125	3523
Magic 6	278342	4195840	3777	Red c 4	274785	4205877	3624	Star 5	309124	4223097	3525
Midn 1	275301	4205171	3654	Red c 5	274801	4205870	3627	Star 6	309134	4223106	3535
Mill 1	291255	4197291	3205	Red c 6	271775	4205784	3631	Sun 1	275277	4209773	3617
Mill 2	291332	4197272	3194	Rock 1	289049	4196850	3247	Sun 2	275297	4209796	3637
Mill 3	291342	4197276	3197	Salty 1	273109	4208042	3783	Sun 3	275229	4209783	3644
Mill 4	291357	4197258	3188	Salty 2	273124	4208044	3783	Sun 4	275229	4209783	3644
Perk 1	305132	4222504	3448	Scop 1	278144	4202803	3716	Sun 5	275228	4209765	3646
Perk 2	305127	4222518	3451	Scop 2	278136	4202820	3736	Sun 6	275209	4209787	3637
Phelps 1	313765	4223178	3327	Scop 3	278151	4202834	3733	Sun 7	275277	4209731	3638
Pidd 1	278157	4202047	3745	Scop 4	278133	4202840	3733	Sven 1	306503	4220673	3715
Pidd 2	278151	4202043	3744	Scop 5	278118	4202861	3732	Sven 2	306504	4220707	3716
Pocket 1	272801	4209822	3676	Shov 1	277903	4202218	3765	Sven 3	306467	4220677	3716
Pocket 2	272814	4209814	3680	Shov 2	277914	4202216	3778	Sven 4	306456	4220660	3712

UTM NAD 83 Zone 13N							
Fen ID	X	Y	Elevation (m)	Fen ID	X	Y	Elevation (m)
Tail 1	274100	4206522	3671	Zycon 1	285324	4205559	3553
Tail 2	274100	4206522	3671	Zycon 2	285351	4205571	3560
Tail 3	274091	4206530	3679	Zycon 3	285346	4205568	3565
Thun 1	274638	4208842	3673	Zycon 4	285434	4205580	3570
Thun 2	274631	4208840	3667				
Thun 3	274633	4208812	3673				
Thun 4	274633	4208814	3673				
Thun 5	274633	4208844	3670				
Tick 1	275308	4205270	3672				
Tick 2	275289	4205275	3658				
Tick 3	275301	4205279	3663				
Titan 1	275653	4210031	3609				
Titan 2	275636	4210018	3612				
Titan 3	275631	4210013	3655				
Titan 4	275636	4210026	3632				
Titan 5	275634	4210034	3621				
Trail 1	282957	4202528	3222				
Trail 2	282949	4202404	3239				
Trail 3	282934	4202632	3245				
Trail 4	282926	4202642	3245				
Trail 5	282971	4202526	3230				
Wild 1	275708	4210063	3622				
Wild 2	275725	4210097	3626				
Wild 3	275691	4210127	3625				
Wild 4	275744	4210176	3612				
Wild 5	275726	4210207	3619				
Wild 6	275645	4210201	3623				
Wild 7	275557	4210173	3627				
Wild 8	275538	4210167	3639				
Wild 9	275626	4210107	3631				
Wind 1	272690	4209889	3672				
Wind 2	272661	4209936	3677				