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Vegetation Geo-climatic Zonation in the Rocky Mountains, Northern Utah, USA

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Abstract: We developed a vegetation geo-climatic zonation incorporating the zonal concept, gradient and discriminant analysis in Wasatch Range, northern Utah, USA. Mountainous forest ecosystems were sampled and described by vegetation, physiographic features and soil properties. The Snowpack Telemetry and National Weather Service Cooperative Observer Program weather station networks were used to approximate the climate of sample plots. We analysed vegetation and environmental data using clustering, ordination, classification, and ANOVA techniques to reveal environmental gradients affecting a broad vegetation pattern and discriminate these gradients. The specific objective was to assess and classify the response of the complex vegetation to those environmental factors operating at a coarse-scale climatic level. Ordination revealed the dominant role of regional, altitude-based climate in the area. Based on vegetation physiognomy, represented by five tree species, climatic data and taxonomic classification of zonal soils, we identified two vegetation geo-climatic zones: (1) a montane zone, with Rocky Mountain juniper and Douglas-fir; and (2) a subalpine zone, with Engelmann spruce and subalpine fir as climatic climax species. Aspen was excluded from the zonation due to its great ecological amplitude. We found significant differences between the zones in regional climate and landform geomorphology/soils. Regional climate was represented by elevation, precipitation, and air and soil temperatures; and geomorphology by soil types. This coarse-scale vegetation geo-climatic zonation provides a framework for a comprehensive ecosystem survey, which is missing in the central Rocky Mountains of the United States. The vegetation-geo-climatic zonation represents a conceptual improvement on earlier classifications. This framework explicitly accounts for the influence of the physical environment on the distribution of vegetation within a complex landscape typical of the central Rocky Mountains and in mountain ranges elsewhere.

Keywords: Ecological classification; Ecosystem survey; Land classification; Zonal concept; Vegetation zone; Vegetation geo-climatic zone; Climate change

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Introduction

"Without classification there is no science of ecosystems and ecology. And indeed, no science" - V. J. Krajina.

Rocky Mountain ecosystems have complex vegetation patterns that are affected by climate, topography, and geology as well as factors such as disturbances and plant interactions.

Environmental gradients are steep (Long 2003) and the legacies of natural and anthropogenic disturbances are pervasive (e.g., Gannett 1882; Barnes et al. 1982; McCune et al. 2002; Shaw and Long 2007). These are diverse, complex landscapes, with small ecosystems nested within large ones (e.g., Rowe and Sheard 1989; Bailey 1998, 2002). Understanding such mountainous landscapes requires a system that accounts for the underlying complexity in important environmental drivers.

There are many land classification systems in use throughout Western North America. These classifications and their units were built on different principles (typically on vegetation and/or climate) in different spatial scales and ecosystem segments such as life zones (Merriam 1890; Holdridge 1967), forest types (Larsen 1930), vegetation zones (e.g., Shreve 1915; Viereck et al. 1992), vegetational zones (Daubenmire 1943), habitat types (Daubenmire 1952), biogeoclimatic zones (Krajina 1965; Pojar et al. 1987), potential natural vegetation (Küchler 1969), ecoregions (Omernik 1987; Bailey 1998). A goal of all these classifications was generally the same; to provide general information about a landscape and important conditions of its segments, i.e., units as homogeneous as possible depending on research questions and tasks (e.g., Nelson et al. 1978) closely related to spatial scale (e.g., Bailey 1998).

In all of these classifications, there is the overarching influence of regional/macro climate, driving broad vegetation distribution patterns or regional ecosystems on local topography/ mesoclimate (Major 1951; Klinka and Chourmouzis 1999; K. Klinka, University of British Columbia, personal communication 2009). Regional climate is suggestive of *the zonal (climatic climax) concept* (Pojar et al. 1987). Originally formulated in terms of soil zonality (Dokuchaev ca 1870), it expresses the relationship between climate, associated vegetation, and soils (e.g., White 1997). Late-seral or old growth (climatic climax), i.e., minimally disturbed plant communities with intermediate topography and edaphic conditions (relative to the extremes of a region) are presumed to best reflect the influence of regional climate (Hills 1952; Krajina 1965; Bailey 2002). Thus, local climatic, topographical and edaphic extremes such as those found on warm, south-facing slopes, cool, north-facing slopes, cold depressions or skeletal soils, are disregarded and only intermediate environmental conditions are considered in application of the zonal concept. The zonal concept rests on the critical assumptions that the regional climate signal is of primary importance in structuring ecosystems and that it expresses itself in minimally disturbed vegetation and soils on intermediate terrain. Recently disturbed vegetation and atypical sites are considered "noise" when applying the zonal concept. The original idea of zonality (based on zonality of soils *sensu* Dokuchaev) has been criticized as "static" (Johnson et al. 1990). This critique is principally associated with the historic discussion on the climax concept rejected by some ecologists and by the recent discussion of potential natural vs. existing vegetation (Chiarucci et al. 2010). While state and transition models for plant communities were introduced especially on rangelands, no advanced more "dynamic" classification design, i.e., classification including time component, has been introduced for forests in North America. But ecological thresholds discriminating rangeland plant communities are difficult to quantify due to extreme complexity of interacting ecological factors in space and time (e.g., Brown 1994; Briske et al. 2005). Additionally, all important land classification systems are based on the intuition of experts (Haeussler 2011). Quantification, based on contemporary techniques, of both vegetation and environment is missing (Chytrý et al. 2011). There is intellectual power and potential in the zonal concept which can serve as a framework for advanced ecological classifications (Cook 1996; Haeussler 2011).

The mountainous US Interior West is an extremely valuable part of the U.S. and has been the location of widespread habitat and community type classifications for 60 years (e.g., Daubenmire 1952; Mauk and Henderson 1984; Mueggler 1988; Muldavin et al. 1996). Systems based on habitat and community typing are the only "fine-scale" forest classification largely accepted and currently available in the central Rocky Mountains. Because they are entirely based on vegetation (Pfister 1976), an explicit link between vegetation and physical environment is missing. The applied zonal concept may be the key to further classification steps with potential application in other mountain regions of the world. An overarching intent in this study was to raise awareness of the zonal concept and ecosystem classification, despite the criticism, and advocate their power and benefits recently overlooked by general ecological, biogeographical and forestry audience (a gap in development of classifications from 1970-1980's). Our general objective was better understood broad vegetation patterns in a Rocky Mountain landscape. We examined the relationships between vegetation and environmental variables for *zonal sites* (*sensu* Krajina 1965; Bailey 2002); sites with mature vegetation, moderate topographic and intermediate soil characteristics (i.e., intermediate site conditions) (Pojar et al. 1987; Klinka and Chourmousis 1999). Our specific objective was to assess the response of the complex vegetation to those environmental factors operating at a coarse-scale level of regional climate.

1 Methods

1.1 Study area

The study area (41°45'57"- 42°04'02"N and 111°39'02" - 111°27'12" W) covered ~20,000 ha and consisted of three parts: Franklin Basin (FB) a montane-subalpine area, approximately 15,000 ha in size, situated between the Bear River Range and the Wasatch Range in the central Rocky Mountains on the Utah and Idaho border; the T.W. Daniel Experimental Forest (TWDEF), ca 1000 ha, situated on the high ridge plateau of the Wasatch Range (10 km to the southeast of FB); and the upper part of Logan Canyon, ca 1,000 ha.

The mean annual precipitation ranges from about 720 to 1250 mm and mean annual air temperature ranges from 2.4°C to 5.7°C for Temple Fork, Tony Grove Lake, Franklin Basin, and Utah State University (USU) Doc Daniel weather stations (http://www.wcc.nrcs.usda.gov/snow/).

The terrain is mountainous, rocky and steep with occasional flat to gently sloping high ridge-plateaus. The elevation ranges from 1590 to 3060 m across the three study sites. High areas of the Bear River Range (from ca 2000 m) were repeatedly glaciated during the Pleistocene as manifested by glacial geomorphologic features like moraines, U-shaped valleys, erratics, and irregular glacial deposits (Young 1939; Degraff 1976). The highest parts of the study area such as plateaus and upper slopes were glaciated entirely, lower positions (lower slopes, valleys) were affected partially by moving ice masses down the valleys. The study area is mostly built from calcareous sedimentary rocks (limestone, dolomite) with interlayered quartzite, and from Tertiary sediments (grit, conglomerate, and siltstone of Wasatch Formation) at the TWDEF site. The soils are formed in residuum, colluvium, alluvium, glacial till and outwash, and occur on diverse landforms such as cliffs, moraines, karst valleys, slopes, landslides, plains, valleys, depressions, ravines, and wetlands (Schoeneberger et al. 2002).

Approximately half of the study area is occupied by forest ecosystems including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and woodland ecosystems including mountain mahogany (*Cercocarpus ledifolius*) and Rocky Mountain juniper (*Juniperus scopulorum*). Subalpine tall forb meadows, sagebrush steppe, and talus and rocky sites represent tree-less ecosystems. Settlement-era timber cutting, livestock grazing, and post-settlement wildfire suppression are associated with changes in the structure and the age-class distribution of forest stands. In many places, 100-160-year-old stands are now predominant (Long 1994). Forests in the study area are thus characterized by mid- and late-seral stages where forest understory is usually well developed (Pfister and Arno 1980).

1.2 Data collection

Ecosystems and their components change along an altitudinal gradient (e.g., Gannett 1882; Daubenmire 1943; Whittaker and Niering 1965; Peet 2000; Shaw and Long 2007). We established 163 sample plots in the summers of 2006 and 2007 along the study elevation range in order to capture broad climatic variation e.g., in temperature and precipitation. For this analysis we selected only zonal sites i.e., mature forest stands (over 70 years old, Pfister and Arno 1980) with intermediate site characteristics such as mid-slope position, gentle to moderate slope (< 30%), loamy soils > 50 cm deep with coarse rock fragment content < 50% by volume and no growing-season water table (Damman 1979; Pojar et al. 1987). Thus, we avoided those slope position, gradient, aspect and shape conditions that may substantially modify overall climate, such as frost pockets, cold air drainages and on steep south/north-facing slopes. As “mature” we considered vegetation with relatively stable stand composition in which potential climax tree species are recognizable, and where a clear successional trajectory is discernible, e.g., from advance regeneration of climax species (Pfister and Arno 1980; Pojar et al. 1987). True zonal sites are rare in the central Rocky Mountains, Utah because: (1) of a rough, mountainous landscape (Barnes et al. 1982) and “accidents of topography” (Gannett 1882), can appear to be more important than absolute elevation (Shaw and Long 2007); and (2) many ecosystems never reach potential climax due to natural disturbances such as fire (e.g., Pojar et al. 1987; Cook 1996) and human-caused disturbances such as logging. Since zonal sites are scarce, a compromise was necessary in site selection during this study. Rather than restricting sampling exclusively to old growth, we included sites with mature, mid- to late-seral stands with well-developed understory reflecting an obvious successional trajectory (Pfister and Arno 1980; Pojar et al. 1987).

A stratified (based on vegetation physiognomy) fixed (subjective selection) sampling design was used with circular zonal plots of 1000 m^2 (Brohman and Bryant 2005). We described each sample plot by species abundances (cover percentage) and by environmental variables including relatively static or constant physiographic attributes (elevation, slope aspect, slope gradient, topographic position and slope shape, e.g., Lotspeich 1980); dynamic attributes such as O and A horizon thickness, humus form, pH, nutrient pools, describing relatively slow changes; and attributes such as nutrient supply rates describing relatively fast processes (Table 1). Parent material observed on the sites was verified against a geologic map (Dover 1995). One soil pit was dug in each plot to the unweathered parent material and described using the National Cooperative Soil Survey protocols (Schoeneberger et al. 2002; Soil Survey Staff 1999, 2006). Humus form was identified following Green et al. (1993).

One composite soil sample from 0-30 cm was collected from a pedon face in each plot, air dried and sieved (< 2 mm), and the fine fraction analyzed for texture classes (sandy, loamy, clayey) using the feel-method (Thien 1979). Samples were then analyzed for pH (1:1 soil in water, Corning pH analyzer) and total C and N (LECO CN analyzer, Leco Corp., St. Joseph, MI). Exchangeable cations [using a mechanical vacuum extractor (Holmgren et al. 1977) and an inductively coupled plasma spectrophotometer (ICP; Iris Advantage, Thermo Electron, Madison, WI) for extractant analysis], extractable P [Olsen P method (Olsen et al. 1954)] and mineralizable N [7-day anaerobic incubation (Keeney and Bremmer 1966) followed by NH_4 extraction and analysis (Lachat Quickchem 8000 Flow Injection Analyzer)] were determined as a static-absolute nutrient availability index (SNAI).

To determine a dynamic-relative nutrient availability index (DNAI) (Qian and Schoenau 2002), plant root simulators (PRS™-probes; Western Ag Innovations, Inc., Saskatoon, Canada), a combination of anion and cation exchange membranes, were buried vertically into the mineral soil at each site for six weeks (during September and November), then sent to Western Ag Innovations for extraction and chemical analysis including Ca, Mg, K, S, Fe, Mn, Zn, Cu, Pb, Al, NH_4 cations, and NO_3 and PO_4 anions (Table 1).

Climatic data such as air temperature, precipitation, soil temperature, and soil moisture for the northern Wasatch Range were obtained from nearby weather stations to approximate ambient and soil climate of the zonal sites. Both the NRCS Snowpack Telemetry (SNOTEL, http://www.wcc.nrcs.usda.gov/snow/); and National Weather Service Cooperative Observer Program (COOP, http://www.nws.noaa.gov/om/coop/) station networks provide long term observations for air temperatures and precipitation (>10 years). Soil temperature (50 cm depth) and moisture (20 cm and 50 cm depth) measured daily in an open area (no tree canopy) were available at the SNOTEL sites for six years (2003-2008, USU Doc Daniel for 2008-2009). In addition, there were two COOP stations with soil temperature measurements for the northern Wasatch Range (Utah Climate Center, http://climate.usurf.usu.edu/). The weather record is short and no soil property information is available for the monitoring sites; nevertheless, these data provided important information in this analysis (Appendix 1).

Table 1 Research variables. Dynamic nutrient availability index (DNAI) indicated by '*d*', static nutrient availability index (SNAI) indicated by '*s*' in abbreviations.

Variable	Abbrev.	Units/Values
Static/constant		
Elevation	elev	meters
Topographic position	topos	1-crest,shoulder, 2-back slope, 3-foot slope, 4-flat (<5%), 5-toeslope, 6-depression
Slope gradient	sl	%
Slope aspect	av	aspect values 0-1; 0 corresponds with 210 azimuth degrees, 1 with 30 degrees (Roberts and Cooper 1989)
Slope shape	shape	1-convex, 2-linear, 3-concave
Parent material	parmat	1-quartzite, 2-Wasatch formation, 3-glacial till, 4-limestone and/or dolomite, 5-colluvium, 6-alluvium
Dynamic - slow changes		
Soil O-horizon depth	Ohor	centimeters
Soil A-horizon depth	Ahor	centimeters
Humus form	hum	values 1-17; e.g., 1-fibrimor, 10-mormoder, 14-rhizomull, 17-no humus (Green et al. 1993)
Soil depth	sdepth	centimeters
Coarse rock fragment content	RF	% volumetric
Soil mottles	mottles	0-no mottles, 1-faint mottles>80 cm deep
Soil color value	cvalue	1-7 according to Munsell® notation
Soil texture	text	1-sandy, 2-loamy, 3-clayey
Soil pH	pH	1-14 pH scale
Total nitrogen	Nox	%
Total carbon	Cox	%
Carbon nitrogen ratio	C.N	not applicable
Mineralizable nitrogen SNAI	Nmin_s	mg/kg of soil
Ammonium SNAI	NH_4_s	mg/kg of soil
Calcium SNAI	Ca_s	mg/kg of soil
Magnesium SNAI	Mg_s	mg/kg of soil
Potassium SNAI	K_s	mg/kg of soil
Phosphorus SNAI	P_s	mg/kg of soil
Iron SNAI	Fe_s	mg/kg of soil
Manganese SNAI	Mn_s	mg/kg of soil
Zinc SNAI	Zn_s	mg/kg of soil
Sulphur SNAI	S_s	mg/kg of soil
Aluminum SNAI	Al_s	mg/kg of soil
Dynamic - fast changes		
Mineralizable nitrogen DNAI	Nmin_d	µg/10 cm^2/6 weeks
Nitrate DNAI	NO_3_d	µg/10 cm^2/6 weeks
Ammonium DNAI	NH_4_d	µg/10 cm^2/6 weeks
Calcium DNAI	Ca_d	µg/10 cm^2/6 weeks
Magnesium DNAI	Mg_d	µg/10 cm^2/6 weeks
Potassium DNAI	K_d	µg/10 cm^2/6 weeks
Phosphorus DNAI	P_d	µg/10 cm^2/6 weeks
Iron DNAI	Fe_d	µg/10 cm^2/6 weeks
Manganese DNAI	Mn_d	µg/10 cm^2/6 weeks
Zinc DNAI	Zn_d	µg/10 cm^2/6 weeks
Sulphur DNAI	S_d	µg/10 cm^2/6 weeks
Aluminum DNAI	Al_d	µg/10 cm^2/6 weeks

1.3 Concepts of vegetation zones

In earlier classifications, vegetation zones were named after overall physiognomy of a plant community, e.g., life or vegetation zones (Merriam 1890; Daubenmire 1943; Peet 2000 based on Whittaker and Niering 1965), altitudinal vegetation zones/tiers (Zlatník 1976) or biogeoclimatic zones (Pojar et al. 1987). Areas within a zone were assumed to have a similar biotic potential represented by dominant tree species as climax vegetation (Whittaker 1972; Zlatník 1976; Pfister and Arno 1980; Pojar et al. 1987; Long 1994) and thus their potential vegetation was used to (1) factor out the effect of disturbances, thus keeping historic (successional) processes relatively constant (Pfister 1976); and (2) indirectly characterize zones (McCune et al. 2002).

Within the elevation range of the study area (1400 m), juniper, Douglas-fir, Engelmann spruce and subalpine fir zones have been characterized based on dominant potential climax tree species in habitat type classifications, i.e., as series (Mauk and Henderson 1984; Steele et al. 1983; Youngblood and Mauk 1985). Within those relatively broad vegetation zones, environmental variation is large (Kusbach et al. 2012); therefore additional environmental stratification may be warranted.

Aspen-dominated communities cover extensive areas in the Western U.S. (e.g., Rogers et al. 2010) and aspen is an extremely important component of many Rocky Mountain landscapes. To better understand the role of aspen and its response to environmental factors, which might be influencing the distribution of conifer-dominated communities, aspen was included in this analysis. There is ongoing discussion about the character of aspen in the Western U.S.; aspen is considered a pioneer, shade-intolerant species that may create either stable (persistent, climax) or unstable (seral) stands (e.g., Mueggler 1985; Kay 1997; Kulakowski et al. 2004; Shepperd et al. 2006; Kashian et al. 2007; Rogers et al. 2010) or even old growth ancient forests (Peterson et al. 1995). Successional status of aspen communities, especially stable aspen, as well as the environmental conditions within the community is still ill-defined (Mueggler 1988). Because of its successional status as a pioneer tree species, aspen is not included within earlier vegetation zonations and has been classified separately (Mueggler 1988). In this study, we sampled both mature conifer sites (< 15% of aspen canopy cover) and aspen-dominated sites (> 85% canopy cover and little or no conifer regeneration) (e.g., Mueggler 1985; Rogers et al. 2010).

1.4 Data analysis

We performed the following analytical steps to examine broad vegetation-site relationships: (1) grouping of vegetation data; (2) ordination of the sample plots based on environmental data; (3) cluster analysis of the plots/vegetation groups based on important environmental variables; (4) discriminant analysis of clusters based on important environmental variables; (5) ANOVA of vegetation groups; and (6) classification of zonal soils based on climatic data. The dataset was comprised of 35 zonal sites, 41 environmental variables and 18 tree and shrub species.

Vegetation grouping was performed as unsupervised cluster analysis of species abundances represented by cover percentage [flexible beta with β = -0.25, Sorensen distance (Bray and Curtis 1957)]. Identification of the vegetation groups was based on species constancy/frequency and dominance (e.g., Brohman and Bryant 2005; Winthers et al. 2005; Jennings et al. 2008). Species covers were square root transformed to approximate a normal distribution.

We used principal components analysis (PCA) ordination to determine the relative importance of the environmental variables and interpret principal components (PC) associated with zonal sites. Orthogonal rotations and correlation type of a cross-products matrix were used to derive independent, mutually uncorrelated PCs (Lattin et al. 2003). Significance of PCs was tested using a Monte Carlo randomization (based on proportion-based *p*-values for each PC). In order to document the relationship of the variables with the PCs and interpret PCs, we calculated correlation coefficients (loadings) with each ordination axis, and the linear (parametric Pearson's *r*) and rank (nonparametric Kendall's *tau*) relationships between the ordination scores and the observed variables. Our use of *r* and *tau* is suggested to be, even in relatively small datasets, more conservative than *p*-values for the null hypothesis of no relationship between ordination scores and variables (McCune et al. 2002). We set the threshold for *r* and *tau* > 0.35.

To associate the vegetation groups with important environmental factors obtained in the PCA and to distinguish among them, we did cluster analysis. We used Ward's (1963) linkage method with Sorensen (Bray-Curtis coefficient) rather than Euclidean distance as suggested by McCune et al. (2002). We transformed the variables with $|\text{skewness}|>1$, standardized the data by adjustment to standard deviate (*z*-scores) and checked the dataset for outliers. A clustering dendrogram was scaled by a distance objective function (Wishart 1969) and number of clusters retained was verified by pseudo F function (Calinski and Harabasz 1974).

Random Forests analysis (Breiman 2001), a machine-learning bootstapping method, was used to identify the most important environmental variables associated with meaningful zonal site clustering to highlight cluster differences. Random Forests is accurate, combines many classification trees, and determines variable importance (e.g., Chen et al. 2004; Cutler et al. 2007).

Using the most important factors obtained from Random Forests classification and PCA, we assessed differences between the vegetation groups by 1-way ANOVA using Student-Newman-Keuls and Tukey's multiple comparison tests. The variables were transformed for normality by power or logarithmic transformation when necessary.

We used the climatic data (Appendix 1) as approximation of ambient and soil climate of the zonal sites to classify soils following the National Cooperative Soil Survey (Schoeneberger et al. 2002; Soil Survey Staff 1999, 2006). Based on daily soil temperature measurements at a depth of 50 cm from the soil surface, we calculated mean annual soil temperature (MAST), mean summer soil temperature (MSST) (June, July, and August in the Northern Hemisphere), and mean winter soil temperature (MWST) (December, January, February in the Northern Hemisphere) (Soil Survey Staff 2006). We used daily soil moisture measurements at a depth of 20 and 50 cm (consistent with conditions for the moisture control section extent) for calculation of the mean soil moisture, mean number of dry consecutive days in the 4 months following the summer solstice, and mean number of moist consecutive days in the 4 months following the winter solstice (Soil Survey Staff 2006). We considered volumetric soil moisture content of 12% as a general threshold between a dry and moist soil moisture control section for loamy soils (Brady and Weil 1999).

In the mountains of northern Utah, elevation is a good predictor of air temperature, soil temperature and also precipitation (Kusbach 2010). Despite the significant change of mean soil temperature with elevation, [except mean winter soil temperature (MWST) due to snowpack insulation, Van Miegroet et al. 2000], the SNOTEL and COOP climatic data (Kusbach 2010) cannot be used to estimate temperature regime of zonal soils because of: (1) absence of lower elevation climate station data; and (2) absence of tree cover type and O horizon information at the monitoring sites. Tree cover type may influence soil temperature regime by fundamentally modifying air temperature (Olsen and Van Miegroet 2010). We estimated soil temperature regime (Soil Survey Staff 2006) based on Munk's (1988) measurements of soil temperatures under different tree canopy types in Logan Canyon, northern Utah.

JUICE software, version 7.0.45. (Tichý 2002), R software, version 3.0.0. (http://www.r-project.org/), SAS 9.1.3 Service Pack 4 software (http://www.sas.com/software/sas9/), and PC-ORD 6 (McCune and Mefford 2011) were used in the analysis.

2 Results

2.1 Vegetation grouping

Cluster analysis of species abundances resulted in the identification of five major vegetation groups based on both the most constant and dominant species. These groups are: Engelmann spruce, subalpine fir, Douglas-fir, Rocky Mountain juniper and aspen (Appendix 2).

2.2 Environmental ordination

The first of two PCAs of environmental data (Table 1) included: all 35 sites (i.e., both conifer- and aspen-dominated sites); the second included only the 18 conifer-dominated sites. The most important principal component (PC1) in both PCA runs was associated with elevation and soil properties (A horizon thickness, humus form, rock fragment content, parent material, soil colour, pH and nutrients). PC1 was interpreted as a climate/geomorphology gradient for both PCA runs, driven by elevation as the surrogate for regional climate (Kusbach 2010) and by geomorphology, which is reflected by parent material (geology) and soil properties (e.g., rock fragment content, colour, pH and nutrients) (Tables 2 and 3). The climate/geomorphology

Table 2 Principal component summary. Significant principal components are marked by asterisk*.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Entire dataset (with aspen)										
Eigenvalue	10.03*	6.49*	4.43*	3.85*	2.19	1.73	1.56	1.47	1.18	1.03
Var. %	24.46*	15.82*	10.80*	9.39*	5.35	4.21	3.80	3.57	2.88	2.51
CV %	24.46*	40.28*	51.08*	60.47*	65.81	70.03	73.82	77.39	80.27	82.78
p- value	0.0002*	0.0002*	0.0002*	0.0002*	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Conifer dataset										
Eigenvalue	12.75*	6.29*	4.65*	3.65	2.69	2.12	1.74	1.29	1.22	1.16
Var. %	31.09*	15.34*	11.34*	8.90	6.65	5.17	4.24	3.14	2.98	2.83
CV %	31.09*	46.43*	57.77*	66.68	73.24	78.41	82.65	85.79	88.77	91.59
p- value	0.0002*	0.0002*	0.0439*	0.7752	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000

Notes: Var. % = % of variance; CV % = Cumulative % of variance.

gradient explained 24% of total variance in the entire dataset (with aspen) but explanatory power increased to 31% in the reduced dataset (conifers), suggesting that inclusion of aspen-dominated sites in the analysis somewhat masked the importance of this major gradient. When the aspen-dominated sites were excluded, there was a 62 and 46% (for *r* and *tau* respectively) increase in elevation loadings (Table 3). Therefore, the reduced conifer dataset results and 23 important environmental variables indicated by significant loadings in PC1 were used further to characterize the climate/geomorphology gradient.

The second principal component (PC2) in the reduced dataset (conifer) was associated with aspect value, organic horizon thickness, soil texture, and nutrients such as N, Ca, Mg, K, Al and P (Table 3). We interpreted this PC as indicative of microbial activity. This activity influences soil organic matter decomposition rate, reflected in organic horizon thickness as well as the nutrient/chemical environment. Warm south-facing slopes experienced enhanced nitrification as indicated by high nitrate DNAIs (Table 3).

2.3 Cluster analysis

Twenty-three environmental variables with significant loadings in PC1 were used in cluster analysis to identify environmentally similar sites and their associations into internally homogeneous and mutually different clusters. In both the entire and truncated conifer-only datasets, there was a clear two-cluster solution based on the distance objective function and information retained (stability of the two-cluster solution was indicated by the longest horizontal distances of clusters' branches) (Figure 1a and 1b), and confirmed by calculation of the Pseudo F function with the highest *pF* value for the two-cluster solution. Interestingly, in the entire dataset including aspen-dominated sites, clustering did not discriminate these aspen sites (Figure 1a). In the conifer clustering, this solution discriminated spruce-fir and juniper-Douglas-fir vegetation groups (Figure 1b).

2.4 Discriminant analysis

The previous clustering revealed two important, approximately balanced (similar number of observation) clusters/classes (Chen et al. 2004; Breiman and Cutler 2005) that were internally homogeneous and mutually different and represented distinct environments. Random Forests classification identified those environmental variables most strongly associated with this two-cluster solution. There was a distinct break between more important and less important variables. Four environmental variables were identified by Random Forests as the most important factors discriminating the clustering of sites. In order of importance, they were: Ca_s (5.90), K_s (5.85), elevation (3.25) and Mn_d (2.9) (Mean Decrease Accuracy in brackets). Except for elevation, all of these variables relate to soil nutrient status. Although the results may vary from run to run, the ranking of variable importance was quite stable for solutions with 5-20 variables randomly used at each split (*mtry* function in R), and 500-1500 trees used to grow a “forest” (*ntree* function in R, Liaw and Wiener 2002). “Out-of-bag”

Table 3 Principal components and loadings

	Entire dataset				Conifer dataset			
Variable	**PC1**		**PC2**		**PC1**		**PC2**	
	r	*tau*	*r*	*tau*	*r*	*tau*	*r*	*tau*
elev	-0.52*	-0.37*	-0.55*	-0.31	-0.84*	-0.54*	0.03	-0.09
topos	0.43*	0.38*	0.39*	0.30	0.34	0.30	-0.24	-0.19
sl	0.12	0.13	-0.29	-0.15	0.25	0.25	0.36*	0.29
av	-0.49*	-0.31	0.48*	0.28	-0.36*	-0.13	0.53*	0.46*
shape	0.28	0.25	0.15	0.11	0.07	0.02	0.08	0.07
Ohor	-0.67*	-0.46*	0.50*	0.32	-0.48*	-0.19	0.72*	0.64*
Ahor	0.76*	0.60*	-0.21	-0.19	0.62*	0.40*	-0.15	-0.05
hum	0.73*	0.49*	-0.43*	-0.20	0.65*	0.50*	-0.50*	-0.30
sdepth	0.25	0.18	0.50*	0.27	0.24	0.14	0.01	-0.06
RF	-0.55*	-0.40*	-0.43*	-0.28	-0.66*	-0.56*	-0.19	-0.17
parmat	0.68*	0.54*	0.20	0.04	0.56*	0.45*	0.12	0.12
mottles	0.33	0.22	-0.04	-0.07	0.60*	0.49*	0.14	0.11
cvalue	-0.73*	-0.57*	-0.05	-0.02	-0.67*	-0.58*	-0.14	-0.02
text	0.18	0.12	0.42*	0.37*	0.52*	0.43*	-0.56*	-0.43*
pH	0.56*	0.37*	0.42*	0.23	0.69*	0.48*	0.23	0.07
Nmin_d	0.31	0.24	-0.84*	-0.61*	-0.11	-0.11	-0.66*	-0.46*
Nox	0.85*	0.64*	-0.08	-0.10	0.68*	0.48*	0.30	0.22
NO_3_d	0.38*	0.30	-0.82*	-0.60*	0.08	0.04	-0.61*	-0.44*
NH_4_d	-0.43*	-0.34	0.07	0.09	-0.64*	-0.44*	-0.31	-0.19
Cox	0.69*	0.55*	-0.01	-0.13	0.62*	0.41*	0.38*	0.24
C/N	-0.62*	-0.38*	0.15	0.12	-0.62*	-0.39*	-0.11	-0.03
Ca_d	0.38*	0.26	-0.35*	-0.26	0.13	0.15	-0.72*	-0.46*
Mg_d	0.40*	0.32	-0.23	-0.16	0.07	0.02	-0.74*	-0.49*
K_d	-0.16	-0.10	-0.29	-0.24	-0.24	-0.16	0.63*	0.50*
P_d	0.25	0.19	-0.28	-0.24	0.03	-0.01	-0.16	-0.21
Fe_d	-0.01	0.01	-0.76*	-0.60*	-0.57*	-0.36*	-0.19	-0.08
Mn_d	-0.60*	-0.37*	-0.62*	-0.41*	-0.89*	-0.71*	-0.17	-0.20
Zn_d	0.34	0.22	-0.69*	-0.55*	-0.08	-0.16	-0.19	-0.14
S_d	-0.30	-0.19	-0.52*	-0.33	-0.67*	-0.56*	-0.03	-0.10
Al_d	0.00	0.06	-0.22	-0.15	-0.15	-0.14	-0.87*	-0.80*
Ca_s	0.82*	0.59*	0.29	0.21	0.95*	0.79*	0.10	0.07
Mg_s	0.73*	0.59*	0.32	0.23	0.77*	0.58*	-0.33	-0.16
K_s	0.35*	0.26	0.41*	0.26	0.89*	0.67*	0.20	0.14
NH_4_s	0.21	0.18	-0.45*	-0.34	-0.36*	-0.28	0.16	0.05
Nmin_s	0.72*	0.60*	-0.15	-0.12	0.73*	0.62*	0.21	0.22
P_s	0.36*	0.19	-0.06	-0.06	0.28	0.20	0.61*	0.45*
Al_s	-0.64*	-0.47*	-0.11	-0.08	-0.75*	-0.60*	-0.07	-0.08
Fe_s	-0.44*	-0.37*	0.11	0.04	-0.72*	-0.54*	0.31	0.26
S_s	0.33	0.20	-0.14	-0.13	-0.23	-0.23	0.59*	0.33
Mn_s	-0.05	-0.02	-0.50*	-0.30	-0.55*	-0.32	0.24	0.23
Zn_s	-0.44*	-0.30	-0.19	-0.16	-0.71*	-0.58*	-0.05	-0.06

Notes: Significant Pearson's (*r*), and Kendall's (*tau*) coefficients are marked by asterisk *. Both significant *r* and *tau* for the particular PC indicate a significant variable for this particular PC. Variables are defined in Table 1.

estimate of error rate as a measure of misclassification was 6%.

2.5 ANOVA

One-way ANOVA revealed overall significant differences among the conifer-dominated vegetation groups in the important variables identified by Random Forests (Ca SNAI: $F = 4.57$, $p = 0.0053$; K SNAI: $F = 7.02$, $p = 0.0006$; elevation: $F = 15.32$, $p < 0.0001$; Mn DNAI: $F = 6.53$, $p = 0.0007$). Based on Student-Newman-Keuls and Tukey's multiple comparison tests, the juniper and Douglas-fir groups were not significantly different in terms of the important variables; neither were the subalpine fir and Engelmann spruce groups (both $p < 0.05$).

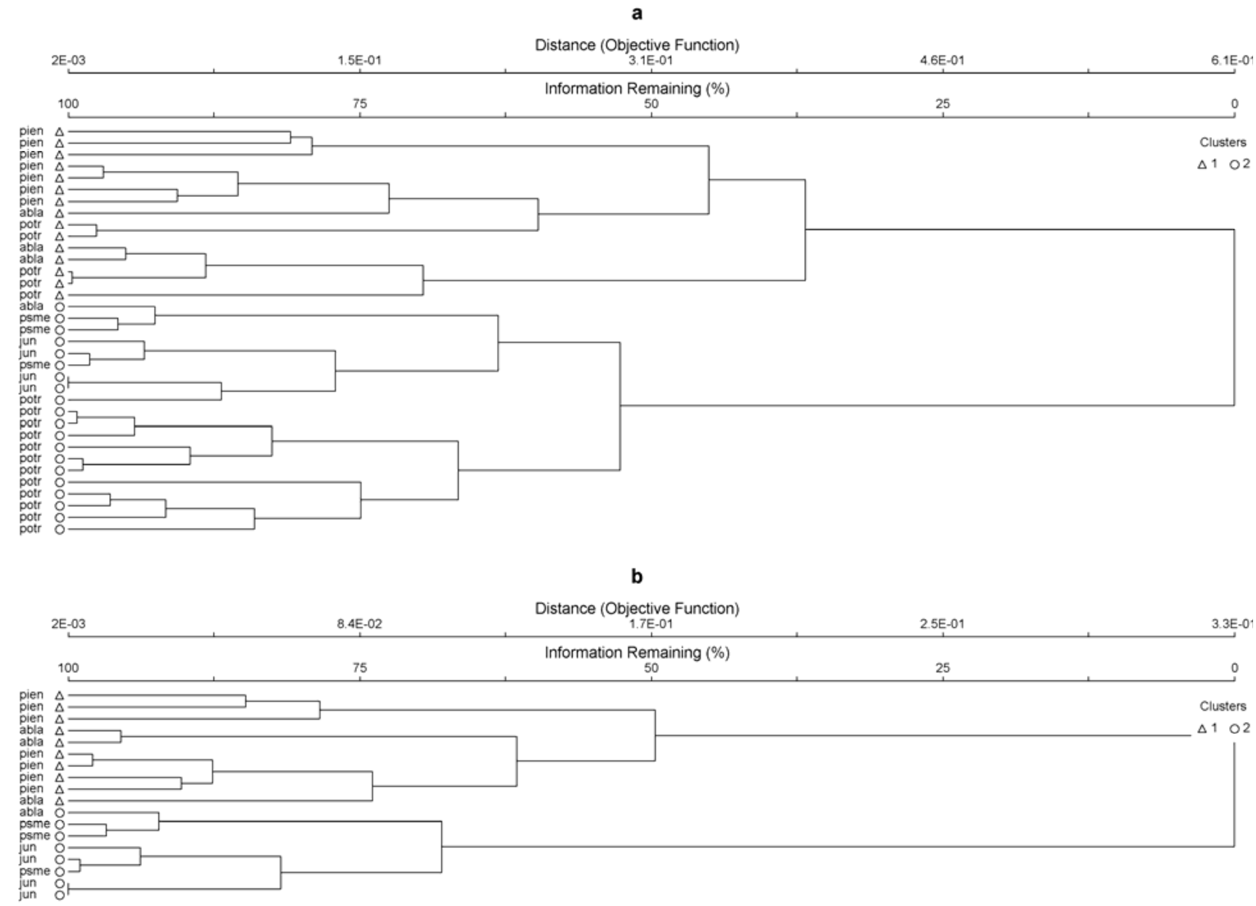

Figure 1 Cluster analysis dendrograms with the two cluster solution: a) the entire dataset included aspen-dominated sites; b) the conifer dataset. Rocky Mountain juniper (jun), Douglas fir (psme), aspen (potr), subalpine fir (abla), Engelmann spruce (pien) vegetation group.

The aspen group was not significantly different from the spruce and fir group (p < 0.01), but was different from the juniper and Douglas-fir group(aspen-dominated sites were absent in the lowest elevations) (Figure 2a, Table 4). Therefore, we combined the four conifer-dominated groups into two final physiognomic groups: the composite juniper/Douglas-fir group we referred to as *montane*; and the Engelmann spruce/subalpine fir group we referred to as *subalpine*. The two resulting physiognomic groups differed significantly from each other in all important environmental variables and Student-Newman-Keuls and Tukey's pairwise tests showed that the four important variables behaved consistently across the physiognomic groups (Ca SNAI: $F = 7.39$, $p = 0.0023$; K SNAI: $F = 9.99$, $p = 0.0005$; elevation: $F = 24.50$, $p < 0.0001$; Mn DNAI: $F = 9.19$, $p = 0.0007$; Figure 2b). Based on clustering, classification and ANOVA the montane and subalpine physiognomic groups differed from each other in terms of climate and geomorphology. Aspen-dominated sites did not differ from the subalpine physiognomic group but differed from the montane physiognomic group (Figure 2b, Table 4).

Microbial activity (PC2) was associated with pronounced nitrification on gently sloping, warm (i.e., south-facing) slopes. We focused on significant indicators of N availability i.e., mineralizable nitrogen and nitrate DNAI (Table 3). Once again, the vegetation groups were associated with distinctly different microbial activity (PC2) based on slope aspect, nitrogen DNAIs; (slope aspect: $F = 9.26$, $p = 0.0002$; Nmin DNAI: $F = 12.61$, $p < 0.0001$; NO_3 DNAI: $F = 14.36$, $p < 0.0001$). Student-Newman-Keuls pair-wise test showed significant differences between the Douglas-fir and juniper group in slope aspect, mineralizable nitrogen and nitrate DNAI ($\alpha = 0.05$). Tukey's pair-wise test showed significant difference between the Douglas-fir and juniper groups in nitrate DNAI (Table 4). These results implied that different aspects, even on mild slopes, may

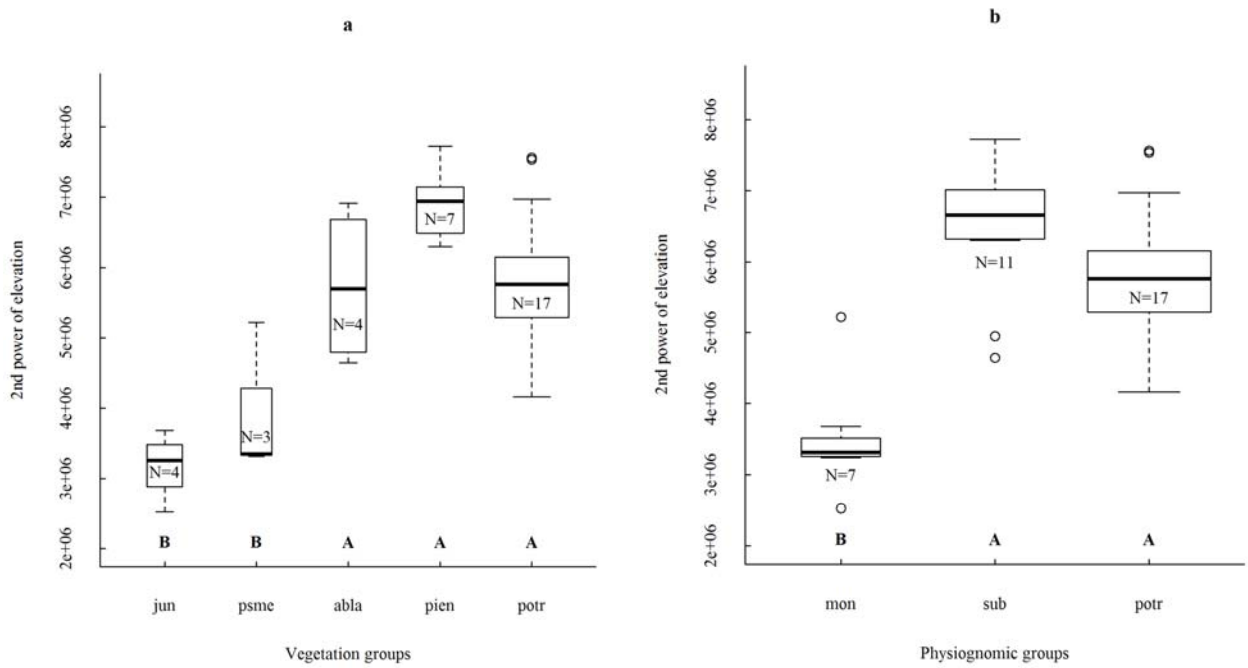

Figure 2 Vegetation groups (a) and physiognomic groups (b) and their relationship in elevation. The different letters represent significantly different groups (α = 0.05). Vegetation group abbreviations are defined in Figure 1b.

Table 4 Identification of the Vegetation Groups (VG)

VG	Elevation (m)	Ca_s (mg/kg of soil)	K_s (mg/kg of soil)	Mn_d (μg/10 cm²/6 weeks)	Nmin_d	NO_3_d
Juniper	1784B (1520, 2013)	3937A (2629, 5509)	41A (36, 48)	0.7BC (0.1, 5)	12.8B (7.1, 20.0)	12.0B (6.2, 19.8)
D_fir	1990B (1719, 2230)	4204A (2660, 6098)	44A (37, 51)	0.2C (0, 1.5)	4.8C (1.3, 10.4)	3.1C (0.4, 8.4)
S_fir	2396A (2207, 2571)	2627B (1582, 3935)	35B (29, 40)	4AB (0, 30)	9.5BC (6.5, 13.2)	7.2BC (4.3, 10.7)
ES	2625A (2497, 2748)	1528B (925, 2282)	27B (24, 31)	55A (13, 235)		
Aspen	2427A (2338, 2512)	3144B (2550, 3799)	35B (32, 38)	8AB (3, 21)	22.8A (18.8, 27.2)	22.1A (17.8, 26.8)

Notes: D_fir = Douglas-fir; S_fir = Subalpine fir; ES = Engelmann spruce.
Different upper case letters following variable mean values indicate significant differences between vegetation groups (α = 0.05). 95% confidence limits are in brackets. Variables are defined in Table 1.

contribute to differences in nitrification associated with differences in the occurrence of the Douglas-fir and juniper community.

2.6 Classification of zonal soils

We classified the soil temperature regime of soils under spruce-fir and aspen as *cryic*, and under Douglas-fir and Rocky Mountain juniper as *frigid* (Munk 1988). Soil moisture was not significantly related to either elevation or precipitation (Kusbach 2010); soil physical properties such as texture, depth, and coarse fragment content may be superimposed over the effect of overall climate represented by elevation. Because these soil physical properties were not available for the climate stations and calculation of the number of dry and moist consecutive days was inconclusive (Appendix 1), we used earlier measurements of soil moisture under different tree canopy types supported by the data of nearby weather stations again to estimate soil moisture regime. The soil moisture regime under spruce-fir and aspen was classified as *udic*, and under

Douglas-fir and Rocky Mountain juniper as *xeric* (Munk 1988; Soil Survey Staff 2006).

Soils in the montane group (juniper and Douglas-fir communities) were classified as Pachic and Typic Argixerolls in the soil order of *Mollisols*. The majority of soils in the subalpine group (subalpine fir and Engelmann spruce communities) were classified as Typic and Eutric Haplocryalfs in the soil order of *Alfisols* (Appendix 3) (Soil Survey Staff 2006). Soil classifications of both physiognomic groups were consistent with e.g., Erikson and Mortensen (1974) and Burns and Honkala (1990). The majority of soils under aspen community were classified as Pachic and Typic Palecryolls, Typic Argicryolls, and Typic Haplocryolls (Mollisols) (Table 5). As in the montane zone, Mollisols indicate formation of a thick A horizon, soil organic matter accumulation and large potential for C storage.

Table 5 **Identification of the vegetation geo-climatic zones**

<table>
<tr><th colspan="2">Zone</th><th colspan="2">Montane</th><th colspan="2">Subalpine</th><th colspan="3">Aspen</th></tr>
<tr><td colspan="2">Elevation</td><td colspan="2">1875B
(1590[a], 2285)</td><td colspan="2">2544A
(2070, 3060[b])</td><td colspan="3">2426A[c]
(1810, 2750)</td></tr>
<tr><td rowspan="5">MT</td><td>MAP</td><td colspan="2">794B
(735, 917)</td><td colspan="2">1021A
(847, 1137)</td><td colspan="3">971A[c]
(779, 1121)</td></tr>
<tr><td>Air</td><td colspan="2">6.9B
(5.1, 8.0)</td><td colspan="2">3.9A
(3.0, 6.1)</td><td colspan="3">4.5A[c]
(3.1, 7.2)</td></tr>
<tr><td>Soil (1)</td><td colspan="2">7.1B
(5.9, 7.8)</td><td colspan="2">5.0A
(4.2, 6.6)</td><td colspan="3">5.4A[c]
(4.3, 7.3)</td></tr>
<tr><td>Soil (2)</td><td colspan="2">13.6B
(11.6, 14.6)</td><td colspan="2">10.2A
(8.8, 12.7)</td><td colspan="3">10.9A[c]
(9.0, 13.8)</td></tr>
<tr><td>Soil (3)</td><td colspan="2">2.7A</td><td colspan="2">2.7A</td><td colspan="3">2.7A</td></tr>
<tr><td colspan="2">Ca_s</td><td colspan="2">4050A
(3009, 5247)</td><td colspan="2">1894B
(1332, 2553)</td><td colspan="3">4050A
(2543, 3808)</td></tr>
<tr><td colspan="2">K_s</td><td colspan="2">42A
(38, 47)</td><td colspan="2">30B
(27, 33)</td><td colspan="3">35B
(31, 38)</td></tr>
<tr><td colspan="2">Mn_d</td><td colspan="2">0.4B
(0.1, 2)</td><td colspan="2">22A
(7, 75)</td><td colspan="3">8A
(3, 22)</td></tr>
<tr><td colspan="2">PM</td><td colspan="2">FCD</td><td>GD</td><td>TS</td><td colspan="3">GD, FCD, TS, Q</td></tr>
<tr><td colspan="2">PST[d]</td><td>Pachic Arg.</td><td>Typic Arg.</td><td>Typic Hap.</td><td>Eutric Hap.</td><td>Pachic, Typic Pal.</td><td>Typic Arg.</td><td>Typic Hap.</td></tr>
</table>

Notes: MT = Mean temperature (°C); MAP = Mean annual precipitation (mm); PM = Parent material; PST = Prevailing soil type; FCD = Fluvio-colluvial deposits; GD = Glacial deposit; TS = Tertiary sediments; Q = Quartzite; Arg. = Argixerolls; Hap. = Haplocryalfs; Pal. = Palecryolls; Other variables and their units are defined in Table 1.
The mean temperature for Air, Soil (1), Soil (2), and Soil (3) are respectively the mean annual air temperature, the mean annual soil temperature, the mean summer soil temperature, and the mean winter soil temperature (°C).
Different upper case letters following variable values indicate significant differences between physiognomic groups/zones ($\alpha = 0.05$). 95% confidence limits are in brackets.
[a] Elevation of the lowest point of the research area; the montane zone can spread lower.
[b] Elevation of the highest point of the research area; the subalpine zone can spread higher.
[c] Significant difference from the montane zone because no aspen-dominated sites sampled in the lowest elevations.
[d] See Appendix 3.

Parent material of subalpine zonal soils was formed mostly by Pleistocene glacial deposits (moraine till) and Eocene sediments (grit, conglomerate, siltstone). Montane zonal soils are derived from late Pleistocene-Holocene fluvio-colluvial deposits of terrain benches derived from Ordovician and Cambrian calcareous sediments.

Significant differences between the physiognomic groups in elevation (Figure 2), together with strong relationships between elevation and climate suggested important climatic differences between these groups. These differences combined with divergence in geomorphology contributed to substantial soil differences among the physiognomic groups and distinguished zonal soils at the level of soil order (Table 5).

3 Discussion

Our analysis revealed a strong altitudinal pattern based on a broad ecological range of data (vegetation, climate, geomorphology/soil). We distinguished two firm vegetation geo-climatic zones: the montane or lower mountain and the subalpine or upper mountain zone. In general, these zones occur as stacked, broad, vertical belts with distinct climatic, geomorphologic and soil differences. However, when examined in detail, the boundary between these zones is not so abrupt because of local topography (topoclimate) which modifies vegetation (tree cover) at this mesoclimatic level.

The *montane zone* is characterized by Rocky Mountain juniper and Douglas-fir as the potential climatic climax species (Appendix 4). The zone is warmer and drier than the subalpine zone; fertile Mollisols, which are also younger than the subalpine zonal soils reflect these climatic properties together with different parent material and rich understory vegetation. Higher potential productivity of the montane Mollisols is indicated not just by a thick A horizon, but also by significantly higher concentrations of important macronutrients Ca and K contributing to higher soil alkalinity (Table 5). Because there was no significant difference between Douglas-fir and juniper communities in important environmental factors, and because there were relatively few zonal Douglas-fir-dominated stands (> ca 1000 m^2), we did not further separate a Douglas-fir vegetation geo-climatic zone in the northern Wasatch Range. Rocky Mountain juniper and Douglas-fir form mixed-species stands on zonal sites (Appendix 5). Floristic differences between Douglas-fir and juniper-dominated sites within the montane zone may result from: (1) different shade tolerance of these two species; and potentially (2) differences in N availability and form (either ammonium mineralization or nitrification). For example, increased insolation on non-zonal south-facing slopes may limit Douglas-fir reproduction via failed seed germination or low seedling survival (Bates 1923; Burns and Honkala 1990). The shade-tolerance and, indeed, the requirement for shade during establishment, of a species may be increased on warm dry sites (Krajina 1965; Klinka and Chourmousis 1999). Whereas Douglas-fir is intermediate in shade-tolerance compared to too many of its associates (Burns and Honkala 1990; Peet 2000), it may require more shade protection for establishment in semiarid conditions (Krajina 1965). Juniper, on the other hand, is a very shade-intolerant species (i.e., requires light exposure, particularly light from above) in the later life stages (e.g., Burns and Honkala 1990; West and Young 2000). If Douglas-fir is able to establish, it has the potential to overtop and outcompete juniper (e.g., in thicker secondary growth).

Generally, conifers such as spruce (*Picea*), fir (*Abies*) and pine (*Pinus*) are physiologically adapted to high ammonium levels in soils and take up ammonium preferentially (Olsthoorn et al. 1991; Bedell et al. 1999; Hangs et al. 2003; Yanai et al. 2009). For Douglas-fir in dry conditions of south-facing slopes, uptake of ammonium may be limited by its relative immobility (Gijsman 1991), albeit still preferred over nitrate (Kamminga-van Wijk and Prins 1993). Junipers appear to prefer nitrate to ammonium (Miller et al. 1991; Stark and Hart 1997) and may therefore be more competitive in high nitrification environments. In addition, allelopathic properties of Rocky Mountain juniper may inhibit establishment of other plants including Douglas-fir (e.g., Peterson 1972; Horman and Anderson 2003). Our ANOVA PC2 results are consistent with pronounced nitrification, and possibly low availability of ammonium, restricting Douglas-fir regeneration on south-facing slopes.

Engelmann spruce and subalpine fir are the climatic climax species for the subalpine zone at higher elevations (Appendix 5). The zone is cooler and moister than the montane zone. A major portion of the zone in the study area has a glacial history (Young 1939; Degraff 1976) and soils have experienced frequent climatic changes during the Pleistocene (Buol et al. 2003). Lower productivity and higher acidity of the subalpine Alfisols is indicated by significantly lower Ca and K concentrations and higher Mn supply rate (Table 5). The latter is associated with more humid subalpine conditions likely facilitating release of Mn from a parent material. Engelmann spruce and subalpine fir are both very shade-tolerant tree species. They are commonly found in mixtures with spruce dominance in old growth and late-seral stands (e.g., Aplet et al. 1988; Peet 2000). In lower, more accessible parts of the subalpine zone within the study area, subalpine fir tends to be more abundant than spruce, probably due to pioneer logging (i.e., late 1800s to early 1900s) which favoured removal of spruce. Because of the logging history, we suspect Engelmann spruce is still somewhat underrepresented in second-growth mid-seral stands.

The ecological amplitude of aspen is extremely broad compared to conifers. This amplitude is climatic, as represented by aspen's large elevation range, and geomorphologic, as indicated by its occurrence on diverse soil parent materials (Figure 2, Table 5). The wide range of climate and geomorphology/soil is associated with large differences in nutrient availability among soils in aspen-dominated sites. Aspen occurs on rich sites with surpluses of macronutrients such as N, K, Ca, and Mg. It also occurs on relatively poor sites where some secondary macronutrients may be deficient (Ca, Mg) and micronutrients such as Mn are in surplus. There is no single environmental factor, important at the level of regional climate that can discriminate aspen as a discrete vegetation geo-climatic zone; this confirms the exceptionally broad ecological amplitude (e.g., Mueggler 1988; Klinka et al. 1999; Mock et al. 2008).

There are no zonal sites in the highest elevations (over 3,000 m) in the study area and probably in the north Wasatch Range. Therefore, determination of the alpine vegetation geo-climatic zone, which would support real alpine vegetation is problematic. We suspect elevations are not high enough for the alpine zone.

Our vegetation geo-climatic zonation is explicitly framed by the regional, altitude-based climate and geomorphology/soil. There is general consistency in our approach with the earlier vegetation zonation of Merriam (1890) based on an idea of broad life zones depending on overall climate (Kusbach 2010). However, there is a substantial difference between our approach and the vegetation zonation of Daubenmire (1943) in that his approach is entirely based on vegetation without specific environmental information. Because there is a compensating influence on plants among environmental factors, the same climax vegetation may appear over a broad environmental range (Pojar et al. 1987; Meidinger and Pojar 1991). Whereas Daubenmire (1943) described spruce-fir, Douglas-fir, juniper and mountain mahogany communities as representatives of four different zones dependent on "ecologic criteria" represented by climate/elevation, our analyses indicate that these communities represent local topo-edaphic variations within a single vegetation geo-climatic zone. Large environmental variations (accompanied by environmental compensation) are thus reflected by floristic differences within a vegetation geo-climatic zone. It is apparent that Daubenmire's zonation combined the regional with the local (topography-moisture) levels. Peet's (2000) improved zonation explicitly differentiated two factors, represented by elevation and topography-moisture, and kept earlier vegetation zones *sensu* Daubenmire inside that framework.

Most existing land classifications are based almost entirely on vegetation, e.g., habitat type classifications in the US West (Steele et al. 1983; Mauk and Henderson 1984; Mueggler 1988), the biogeoclimatic ecosystem classification in British Columbia (Pojar et al. 1987) , the geobiocoenological system in central Europe (*sensu* Zlatník 1976). These largely intuitive classifications have both applied value and intellectual beauty (Haeussler 2011; K. Klinka, personal communication 2009). However, they can be substantially improved with the application of modern analytical techniques. Additionally, the vegetation geo-climatic zonation suggested here, should be expanded and tested on greater objective data sets, e.g., data coming from national inventories. Literature on vegetation zonation and especially land classifications from non-western and non-European countries is limited (but see Proctor et al. (2007) in West Africa, Rana et al. (2011) in northwest Himalaya and Jedrzejek et al. (2012) in Greenland). In regions without earlier, even intuitive, land classifications this approach has considerable potential for the development of ecologically sound classifications.

The zonal concept provides a solid framework for characterization of vegetation-geo-climatic zones in the complex environments of mountain landscapes. Within the framework of the regional/altitudinal climate, specifying floristic differences between the vegetation geo-climatic zones can explain many special cases in the distribution of forest vegetation, such as interfingering, telescoping, discontinuity and inversion of vegetation zones *sensu* Daubenmire (1943) that reflect local climate (i.e., topo-climate and available soil moisture, Kusbach 2010). This approach can contribute to "understanding of the discontinuity of the historical, environmentally broad vegetation zones" (Shaw and Long 2007). Our analysis also confirmed that soil properties, often used as indicators of forest site quality (Schoenholtz et al. 2000) and traditionally considered operating as fine-scale factors at a stand level, can be beneficial in coarse-scale land assessment (at a landscape level) (Table 5).

We suggest that ecosystem studies and management should be viewed in the context of a comprehensive ecosystem classification (e.g., Haeussler 2011). This general framework will facilitate detailed ecosystem structuring at lower ecosystem levels e.g., for a site (habitat) discrimination. The resulting classification should act as a reference platform for hot ecological issues such as global climate change, in connection with paleo-studies of the past (e.g., Abella and Denton 2009) and possible ecosystem changes in the future, related to biomass-carbon pools, fire risk, shifts of plant communities (Buček and Vlčková 2009) and species diversity and distribution changes (Schulz et al. 2009). An effective ecosystem classification also represents an important communication tool within and between ecosystem research and management (e.g., Report of the Intermountain Regional Forum 2006). It also provides a framework for practical interpretations and decisions such as resource treatments, collecting, organizing and reporting ecological information, e.g., in wildlife, timber, soil and water management, biodiversity assessment, restoration and conservation (e.g., Kotar 1988; Brownell and Larson 1995; Pregitzer et al. 2001; Sharik et al. 2010; Zenner et al. 2010).

4 Summary and Conclusions

We identified two vegetation geo-climatic zones as areas with the same overstorey composition in climatic climax in the study area. These zones were: *montane* with juniper/Douglas-fir; and *subalpine* with Engelmann spruce/subalpine fir as climatic climax species. We characterized these zones based on regional physical environment (i.e., climate and landform geomorphology/soils); with regional climate represented by elevation, precipitation and air and soil temperatures; and geomorphology by soil types. Aspen was excluded from the zonation due to its great ecological amplitude.

The vegetation geo-climatic zonation outlined in this paper is a conceptual improvement on earlier approaches to vegetation zonation in the region. It provides a framework for building comprehensive ecosystem classification, which is missing in the central Rocky Mountains of the United States and can be applied elsewhere. As a part of this classification, the vegetation geo-climatic zonation should act as an information platform and reference for current ecological issues such as global climate change.

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