THESIS

PATTERNS OF FLORISTIC DIVERSITY IN WET MEADOWS AND FENS OF THE SOUTHERN SIERRA NEVADA, CALIFORNIA, USA

Submitted by

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ABSTRACT

PATTERNS OF FLORISTIC DIVERSITY IN WET MEADOWS AND FENS OF THE SOUTHERN SIERRA NEVADA, CALIFORNIA, USA

Wetlands are often described as important contributors to species diversity, but this contribution has seldom been quantified. In mountain regions, wetlands often occur as geographically isolated habitats in a matrix of forest, shrub, or dry meadow communities, providing important ecosystem services and increased habitat heterogeneity. The goal of this study was to quantify the contribution of wet meadows and fens to the floristic species richness of Sequoia and Kings Canyon National Parks in California, USA, and assess variables that influence species richness and composition in wetlands and broad vegetation assemblages.

Park-wide inventory data were used from 687 samples to identify broad-scale vegetation assemblages and compare species richness values among assemblages. Data were grouped using an iterative clustering procedure able to handle highly heterogeneous data ranging from alpine talus to montane meadows. Species richness in vegetation assemblages were compared using a series of complementary methods including: Shannon's and Simpson's Indices, Coleman Rarefaction curves, and 'Chao 2' non-parametric species richness estimator curves. Classification and regression trees (CART) were used to describe the variables influencing species richness and composition in vegetation assemblages. A combination of ordination and classification was used to interpret vegetation pattern in wet meadows and fens.

Cluster analysis identified 10 broad vegetation assemblages. Species richness indices and estimator curves revealed that Montane Wet Meadows, Subalpine Wet Meadows, and Lower Montane Woodlands and Chaparral were the most species rich assemblages. Combined Montane and Subalpine Wet Meadows had the highest species richness values of all groups, even though they occupied only 2% of the almost 350,000 hectare survey area. Wet Meadows were found to be important to species richness across the study area as well as being highly complementary to other vegetation assemblages in the park. Lower Montane Woodlands and Chaparral also make important contributions to species richness and occupy 6.5% of the survey area. CART models indicated that elevation, topographic wetness, and slope were important to species richness and vegetation assembly.

This study suggests that a simple series of complementary methods can be used to analyze inventory data to assess patterns of species richness at landscape scales. These findings can inform future monitoring efforts and the protection of diverse habitats in montane regions.

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1. INTRODUCTION

Organisms are unevenly distributed on the landscape due to site history and local, regional, and global scale abiotic and biotic factors and processes (Barbour 1999). Species diversity is a basic attribute of ecological communities used to describe both the distribution and abundance of organisms. Patterns of species diversity have been related to latitude, climate, biological productivity, habitat heterogeneity and complexity, disturbance, patch dynamics, environmental stresses, altitude, and age of substrate (Ricklefs and Schluter 1993, Stohlgren 2007). Determining the factors that influence species diversity in ecological communities, continues to be a prominent question in community ecology (Morin 1999).

Understanding global patterns of diversity requires knowledge of continental, regional, and local scale environmental gradients and their influences on species distributions (Myers et al. 2000). North America contains a wide range of climates, latitude, lithology, and topographic variability. Although temperate zones are typically less diverse than tropical zones, North America supports one floristically unique region, the California Floristic Province (Flora of North America Editorial Committee 1993, Hickman 1993, Myers et al. 2000). California includes 11 terrestrial ecoregions, supporting more than 5,800 native and naturalized vascular plant species (Hickman 1993). Landscape heterogeneity, history, climate, geology, hydrology, and soils all contribute to the number of vascular plants found in California (Vasey and Holl 2007).

The Mediterranean climate regime in portions of California is one important factor influencing species richness. Mediterranean regions of the world support high proportions of endemic species, harbor unique species assemblages, and are considered global diversity hotspots (Stebbins and Major 1965, Cole 1979, Huston 1994, Cowling et al. 1996, Myers et al. 2000, Dirzo and Raven 2003). The California Floristic Province contains over 50 endemic genera of vascular plants, while by comparison the Rocky Mountain Floristic Province of North America contains only 5 endemic genera (Flora of North America Editorial Committee 1993). Approximately 24% of California's vascular plants are endemic, 17.7% of plant species in the Sierra Nevada are endemic (Stebbins and Major 1965, Hickman 1993). One protected area in the southern Sierra Nevada, Sequoia and Kings Canyon National Parks (SEKI), supports 146 vascular plants that are endemic, rare, threatened, or endangered at the park, state, or federal level (Stokes 2003, Haultain 2011).

Interactions between regional and local scale processes determine the spatial variability of species. Though variables such as climate drive broad vegetation patterns at global to landscape scales, variables including landscape context, soil moisture, and water table depth are important to vegetation patterns at local scales (Ratliff 1982, Huston 1994). Seasonally and perennially flooded and saturated sites are thought to be floristically less diverse, supporting primarily obligate wetland plants, but can also harbor unique bryophytes, vascular plant assemblages, and invertebrates (Tiner 1993, Vitt et al. 1995, Bedford and Godwin 2003, Locky and Bayley 2010). Wetlands with seasonally variable water tables often support both obligate and facultative plant species with broader ranges of wetland occurrence probabilities (Rolon et al. 2008, Nygaard and Ejrnaes 2009). Geomorphic features and geologic discontinuities influence the formation of hydrologically variable habitats in mountainous regions (Allen-Diaz 1991). Wetlands in the Sierra Nevada have formed along complex soil moisture gradients that range from perennial to periodic saturation regimes. In SEKI, wetlands also vary based on soil type, elevation, slope, water source, geology, annual precipitation, aspect, landscape context, and size. This variability provides unique habitats for a wide range of plant species.

Two important wetland types in the Sierra Nevada are wet meadows and fens. They are supported largely by groundwater, having vegetation dominated by species in the *Cyperaceae*, *Poaceae*, and dicotyledonous annual and perennial herbs (Ratliff 1985, Loheide et al. 2009). These wetlands increase patch heterogeneity in a landscape dominated by mixed coniferous forests (Ratliff 1982, Allen-Diaz 1991, Miller et al. 2003). They also provide an array of ecological functions including water quality improvement and flood attenuation storage, while creating vital habitat for biota (Erman and Erman 1975, Morefield 1992, Owen and Otton 1995, Lindquist et al. 2000, Mitsch and Gosselink 2000). Wet meadows and fens are distinguished by their hydrologic regime, landscape context and soils (Cooper and Wolf 2006). Fens have perennially saturated soils maintained at low temperatures by perennial ground water inflow, which slows organic matter decomposition and allows peat accumulation (Moore and Bellamy 1974, Bartolome et al. 1990, Bedford and Godwin 2003). Wet meadows, as defined here, have mineral, seasonally saturated soils with little or no peat accumulation.

Previous research has indicated that wetlands are species rich and make important contributions to local and regional scale diversity, but this has rarely been quantified (Bedford and Godwin 2003, Tiner 2003, Williams et al. 2004, Chong and Stohlgren 2007, Flinn et al. 2008, Loheide et al. 2009, Morley and Calhoun 2009). Even fewer studies have considered the species contribution of wet meadows and fens in mountain regions of North America (Morefield 1992, Warner and Asada 2006, Naqinezhad et al. 2009).

Sampling that addresses resources at landscape scales and the availability of data in geographic information systems (GIS) allow plant species composition and relation to physical variables to be assessed at large scales. Wetlands have been targeted by long-term monitoring protocols in North American National Parks as important physical and biological indicators of anthropogenic stresses and climate change (Mutch et al. 2008, Gage 2009, Schweiger 2010). In this study, landscape scale vegetation composition data were used to assess the cumulative contribution of wet meadows and fens to the floristic diversity of Sequoia and Kings Canyon National Parks. The objectives of this research were to: 1) assess and compare the contributions of broad-scale vegetation assemblages to vascular plant species richness across SEKI using species richness indices and estimators, 2) using available GIS data, identify the physical variables that influence species assemblages and richness, and 3) assess plant species composition and diversity in wet meadows and fens.

2. SITE DESCRIPTION

SEKI are located in the southern Sierra Nevada of California (Figure 1). The Sierra Nevada geomorphic province is the highest and longest mountain range in the conterminous United States, bordered to the east by the Great Basin and to the west by the Central Valley of California (Hill 2006). SEKI encompass 349,581 hectares, ranging from 412 m to 4417 m in elevation. Plant distributions, diversity, and endemism in the Sierra Nevada have been attributed to high variability in climate, topography, elevation, soils, soil moisture, and geology at local and landscape scales (Hickman 1993, Sierra Nevada Ecosystem Project 1996, Kraft et al. 2010). The Sierra Nevada was formed by tectonic uplift of the Sierra Nevada Batholith, a tilted fault block, creating an asymmetrical-shaped range, rising gradually along the western slope and abruptly dropping along the steep eastern escarpment (Matthes 1960, Huber 1987). The Batholith consists of Mesozoic age plutons of granites, overlain by persistent remnants of variously metamorphosed volcanic and sedimentary rocks. Parent material and prevailing climate have created soils that are relatively nutrient poor and undeveloped in most areas (SNEP 1996).

The climate is a Mediterranean pattern with cool, wet winters and warm, dry summers (Stephenson 1988, SNEP 1996). Elevations above 2100 m experience an alpine climate pattern with average temperatures below -3°C during the coldest winter months (Mutch 2008). Average annual precipitation ranges from 430 to 1200 mm, with the majority falling as snow in montane and subalpine zones (900-1200 mm annually), decreasing with increasing elevation to a much drier alpine zone (430-650 mm) (Luzio 2007). Precipitation and elevation are two important, interacting physical drivers that control vegetation patterns in the Sierra Nevada (Stephenson 1990, SNEP 1996). Biotic zones vary with latitude, microtopography, and other local-scale variables, but generally follow these groups: foothill (300-900 m), lower montane (900-2100 m), upper montane (2100-2700 m), subalpine (2700-3200 m), and alpine (>3200 m) (Storer et al. 2004). SEKI encompass a large portion of this elevation gradient and supports approximately 1200 of the 5800 vascular plants of California and approximately 140 vegetation associations (NPS 2008, USGS 2010).

3. MATERIALS AND METHODS

3.1 SAMPLE AND RESPONSE DESIGN

Data used in this study were collected as part of two park-wide inventory programs, the Natural Resource Inventory (NRI) and the Wetland Ecological Integrity Protocol (WEI) (Figure 2). NRI data were collected from 1985 to 1991 to provide a comprehensive, systematically sampled dataset of park vegetation (Graber et al. 1993). Vegetation and environmental variables were analyzed in 0.1 ha circular plots, at 1 km UTM grid intersections. Density and basal area were collected for each tree species. An estimate of tree species importance was generating using an index based on values of density and basal area as an approximation of cover (Haultain 1993). Herbaceous plant species cover was surveyed in 4, 1 m^2 quadrats, and shrub cover was surveyed along 2, 17.8 m long transects.

WEI data were collected during the 2008 and 2009 summer field seasons. Survey sites for the WEI protocol were selected using a modified two-stage, spatially balanced, probability-based survey design at the watershed and site level (Stevens and Olsen 2004). This design disperses sample sites randomly, helping to minimize field effort while retaining the ability to make inference to the target population of fens and wet meadows at the desired spatial extent. The first stage of the design consisted of a stratified random selection of watersheds based on physical drivers that influence wetland abundance and type, including mean annual precipitation, elevation, slope, and bedrock geology. The sample frame consisted of all wet meadows and fens mapped in selected watersheds. The second stage consisted of a random, site-level selection from this sample frame of wetland complexes. All selections were made using the ‘grts’ (Generalized Random-

Tessellation Stratified) function in the ‘spsurvey’ package in R (Stevens and Olsen 2004, Kincaid et al. 2008, R Development Core Team 2010). Cover data for vascular plants in the WEI protocol were collected in 4, 1 m^2 quadrats. The final combined dataset included 687 plots, 592 from the NRI protocol and 94 from the WEI protocol. Presence data were collected at larger scales for both protocols, because these scales varied between designs, those data were not included in comparative analyses. Presence data at the 100 m^2 scale in WEI sites was used in analysis of wetland composition.

3.2 STATISTICAL ANALYSIS

3.2.1 Vegetation Groups

Cover data for both the NRI and WEI datasets were averaged across quadrats and transects to produce an absolute cover value for each species per sample location in the dataset. Data were square root transformed to moderate the influence of dominant species and increase the significance of uncommon species (Jongman 1995). Monotonic transformations are often used with ecological data when there is extreme variation in cover values because they do not alter the ranking of cover, but do moderate cover values (McCune and Grace 2002). Cluster analysis to group samples into vegetation assemblages was performed using the Isopam (clustering) function in the ‘isopam’ package in R (Schmidtlein et al. 2010, R Development Core Team 2010). The function ordinates species data based on isometric feature mapping, and then optimizes clusters based on ordination scores and indicator species. Indicator species are tested in the ‘isopam’ function using Fisher’s F test to maximize the quality and quantity of species fidelity in groups.

NRI survey sites consist of large, systematically placed plots that often crossed steep environmental gradients, including more than one habitat. Because outliers can greatly affect multivariate analyses and some samples appeared to fall into inappropriate groups, strict criteria and a series of objective methods were used to detect outliers in groups resulting from the cluster analysis (McCune and Grace 2002). Outliers were initially assessed as isolated groups in the Isopam cluster analysis. Cluster groups that separated in the first split with very few plots or as single plots were removed from further analysis. Within cluster analysis groups, single outliers were detected in ordination space using Detrended Correspondence Analysis (DCA) and outlier analysis in PC-ORD (McCune and Mefford 2006). Potential outliers were inspected and compared to other samples in the cluster before being removed from further analysis. Samples were removed only if they were markedly different from the majority of other samples in the group, for example if they had only a few species, considerably more species than other samples, or if they shared no species with other plots in the group.

3.2.2 Species Richness Estimation

Quantifying species richness provides a simple approach for comparing species contributions between assemblages in a survey area (Gotelli and Colwell 2001). Though simple species richness is a useful and easily attained value in sample-based surveys, it is greatly influenced by sampling effort, sample unit size, and is biased if used to compare diversity between groups with a different number of samples (Magurran 2004). Instead, a series of complimentary measures were used to assess floristic diversity between groups derived from the cluster analysis. Diversity indices rank communities differently depending on the index’s emphasis on richness versus evenness in the data (Hill 1973).

Two indices with varying degrees of emphasis on richness versus evenness were used, Simpson's and Shannon's. Simpson's index uses an unbiased estimator and is effective at ranking communities with variable and small sample sizes (Lande et al. 2000). Shannon's index, though biased with small sample sizes due to its dependence on the true value of species richness, emphasizes species richness over evenness and was used as an additional diversity measure to compare vegetation assemblages (Lande 1996, Magurran 2004).

Nonparametric species richness estimators are another approach for comparing vegetation assemblages. These measures were used to estimate total species richness of a group of relatively homogenous sample units with unknown species abundance distributions (Colwell and Coddington 1994, Magurran 2004). Nonparametric estimators were used instead of species accumulation curves or parametric methods due to the difficulty in fitting a common species abundance model to the highly variable vegetation assemblages in the study area.

'Chao' estimators can be used to produce a reasonable estimate of minimum richness even when curves are non-asymptotic (Longino et al. 2002, Magurran 2004). The 'Chao 2' estimator was used to develop estimates of species richness based on species presence/absence between samples and was more appropriate in this case because frequency data were not collected (Magurran 2004). 'Chao 2' richness estimator curves with log-linear 95% confidence intervals were generated for the cluster analysis groups (Gotelli and Colwell 2001). Coleman's Rarefaction curves were also used to provide a visual comparison of observed species accumulation per assemblage. Curves were computed with 500 randomizations without replacement in EstimateS software (Colwell 2005).

The vegetation map of Sequoia and Kings Canyon National Parks was used to approximate the area covered by groups derived from the cluster analysis (National Park Service 2007). The vegetation map is 80% accurate at the plant association level and 86% accurate at the plant alliance level (Grossman et al. 1998, National Park Service 2007).

Complementarity or beta (β) diversity was used to measure the biological distinctness of cluster analysis assemblages based on a distance matrix (Colwell and Coddington 1994, Magurran 2004). Similarities between assemblages were calculated using the Classic Sørensen (Bray-Curtis) Index which assesses occurrences of species between groups (Magurran 2004). Values range from 0 to 1, with a value of 1 indicating complete similarity and 0 indicating no similarity. Complementarity was calculated in EstimateS using presence/absence data (Colwell 2005).

3.2.3 Classification and Regression Trees

Classification and regression trees were used to explore the influence of environmental response variables on species richness and vegetation assemblages (De'ath and Fabricius 2000). A classification tree was used to describe the variation in cluster analysis groups and a regression tree was used to describe the variation in species richness per sample. Environmental variables available for all samples were used as the independent or predictor variables in partitioning. Predictor variables included elevation (m), precipitation, UTM coordinates, slope, aspect, topographic position index, topographic wetness index, and geology (Theobald 2007, PRISM Climate Group

2007)(Table 1). Slope, aspect, and topographic position were derived from the SEKI, 10 m digital elevation (DEM) model in ArcMap 9.3 (ESRI 2008). Trees were pruned for the final solution based on minimum cross-validation rates which provide an error estimate for each tree size (Breiman et al. 1984). Classification trees were constructed using the recursive partitioning and regression trees package, ‘rpart’ in R (Therneau and Atkinson 1997, R Development Core Team 2010).

3.2.4 Wetland Composition and Diversity

A combination of hierarchical cluster analysis, Nonmetric Multidimensional Scaling (NMS) ordination, and Mantel test was used to interpret and visualize patterns in wetland composition. Cluster analysis was performed using the Isopam (clustering) function in the ‘isopam’ package in R using both vascular and non-vascular plants (Schmidtlein et al. 2010, R Development Core Team 2010). The NMS ordination was run in PC-ORD using the Sørensen (Bray-Curtis) distance measure on all vascular and non-vascular plants encountered in greater than three samples (McCune and Mefford 2006). Square root transformed values of average cover across 4, 1m^2 plots were used for NMS ordination and ‘isopam’ clustering.

A simple Mantel test computes the correlation between two distance matrices, in this case, sample floristic composition and environmental variables and was used to determine whether environmentally similar samples have similar species composition and whether environmentally different samples have dissimilar composition (Goslee and Urban 2007). Including UTM coordinates in the environmental variable distance matrix allows an assessment of the underlying geographic spatial structure in the data (Urban et al. 2002). Mantel’s test was run on presence of species occurring in more than one plot at the 100 m^2 scale and 12 physical variables, elevation, topographic position index, topographic wetness index, slope, aspect, depth to water, soil saturation, soil temperature, peat thickness, cover of bare ground, and cover of water using 10,000 permutations in PC-ORD (McCune and Mefford 2006). Jaccard distance was used for the vegetation matrix and Euclidean distance for the matrix of environmental variables (Legendre 1983, McCune and Grace 2002).

Complementarity was assessed between wet meadow groups by computing shared species statistics in EstimateS using presence data from 100m^2 WEI plots (Colwell 2005). All complementarity measures were based on Sørensen (Bray-Curtis) distances.

4. RESULTS

4.1. VEGETATION GROUPS AND SPECIES RICHNESS

Approximately 1,561 vascular plant species are known to occur in Sequoia and Kings Canyon National parks. Of these species, 750 were recorded in NRI and WEI plots at the 1 m^2 scale and 945 were recorded at the 100 m^2 scale in WEI plots and the 1,000 m^2 scale in NRI plots combined.

Cluster analysis of the combined NRI and WEI vegetation data was used to identify 10 broad-scale assemblages (Table 2). Names for assemblages were derived from the standardized National Vegetation Classification System (NVCS) proposed for the U.S. Geological Survey and National Park Service (USGS/NPS) Vegetation Mapping Program and the California Wildlife Habitat Relationships (CWHR) System (Mayer and Laudenslayer 1988, The Nature Conservancy 1994, Environmental Systems Research Institute 2007). NVCS names are based on indicator species and physiognomic classes including Forest (60-100% canopy cover), Woodland (25-60% canopy cover), and Chaparral, which refers to evergreen, sclerophyllous shrublands of Mediterranean climates in California (Westman 1991, The Nature Conservancy 1994). For those groups including a broad range of vegetation alliances, such as Montane Coniferous Forests, CWHR names, elevation, and physiognomic groups were used (Mayer and Laudenslayer 1988).

Diversity indices and species richness estimators that allow for variance in sample sizes were used to make comparisons between assemblages (Lande et al. 2000, Gotelli and Colwell 2001). The Rock and Sparsely Vegetated (Simpson's Index = 31.3, Shannon's Index = 4.2), Alpine Meadows (29.1, 4.0), Montane Wet Meadows (28.6, 3.9), Subalpine Wet Meadows (28.0, 3.9), and Lower Montane Woodlands and Chaparral (27.3, 4.1) had the highest Simpson's and Shannon's indices (Table 1). Combined Montane and Subalpine Wet Meadows had the highest values for these indices (43.6, 4.3). Values for both Simpson's and Shannon's indices were lowest in the subalpine forest types *Pinus contorta* var. *murrayana* Forests and Woodlands (3.3, 2.5) and *Pinus balfouriana* ssp. *austrina* Woodlands (2.1, 1.5).

Montane and Subalpine Wet Meadows make significant contributions to species diversity and cover the smallest area of the parks vegetation assemblages (Table 2). These two Wet Meadow types occupy approximately 2.0% of the area in SEKI (National Park Service 2007). In the 0.018 hectares of Montane Wet Meadows surveyed 157 species occurred. In 0.022 hectare of Subalpine Wet Meadows surveyed, 151 species occurred. Combined, all surveyed wet meadows contributed 220 species in 0.04 hectares of the 355,000 hectare survey extent.

The ‘Chao 2’ classic richness estimator was asymptotic for the majority of groups, more stable than other estimators, and did not overestimate diversity in most groups. Local scale sampling, such as the 4 m^2 scale used here, is reported to miss many locally rare species (Barnett and Stohlgren 2003). The ‘Chao 2’ estimator is based on the number of species found in only one and two samples, so the scale of sampling likely aided in the stability of this estimator. Incidence and abundance coverage-based estimator curves (ACE, ICE) were rising for most vegetation types when all samples were added and tended to give much higher estimates of diversity for the majority of assemblages.

The Coleman Rarefaction and ‘Chao 2’ species richness estimator curves for the 10 vegetation types showed a similar trend as the Simpson’s and Shannon’s indices with the same vegetation types having high estimates of species richness (Figure 3Figure 4). For the Montane Wet Meadows, 157 species were observed, and 234 species were projected by the ‘Chao 2’ species richness estimator in 45 samples. In Subalpine Wet Meadows, 151 species were observed, and 210 species were projected by the ‘Chao 2’ species richness estimator in 56 samples. In the combined Montane and Subalpine Wet Meadows, 220 species were observed, and 275 species were estimated in 101 samples. In the Alpine Meadows 177 species were observed and 299 species were estimated. In the Rock and Sparsely Vegetated type, 306 species were estimated. This type includes samples from SEKI vegetation map associations covering 27.9% of the area in the park and estimates were based on 117 samples, more samples than were include in other estimates. The Lower Montane Woodlands and Chaparral type was also species rich, with an estimated 339 species in only 57 samples, covering 0.029 hectare. The Alpine

Meadows, Lower Montane Woodlands and Chaparral, Montane Mixed Conifer, Montane Wet Meadows, and Rock and Sparsely Vegetated type produced non-asymptotic curves. All of these assemblages were sampled from a broad range of vegetation types which likely contributed to high richness estimates. For the forest and woodland types, small sample sizes per type and the 4 m^2 sampling area used likely contributed to higher richness estimates. The two subalpine Forested types, *Pinus contorta* var. *murrayana* and *Pinus balfouriana* ssp. *austrina* Forests and Woodlands had asymptotic curves well below 200 estimated species when all samples were added. These vegetation types typically inhabit middle and upper elevations, dry slopes and cover approximately 15.6% of the area in the park.

Complementarity assessment revealed compositional similarity in vegetation types of similar elevations and environmental conditions. Highly complementary assemblages had a Sørensen Quantitative (Bray-Curtis) Index greater than 0.3 (Table 3). The Subalpine Woodland and Forest types including Upper Montane Mixed Conifer Forests, *Pinus contorta* var. *murrayana* Forest and Woodlands, and *Pinus balfouriana* ssp. *austrina* Woodlands were complimentary, with the latter two types being very similar (0.37 SQI). Lower Montane Mixed Coniferous Forests and Montane Mixed Coniferous Forests were highly complementary (0.40 SQI). Alpine Meadows were complementary to both *Pinus contorta* var. *murrayana* Forests and Rock and Sparsely Vegetated sites (SQI 0.35, 0.53). Montane Wet Meadows were complementary to Subalpine Wet Meadows (SQI 0.38), but were distinct, having very few shared species with any other groups (SQI 0.01-0.09). Subalpine Wet Meadows also had low similarity to other groups (SQI 0.00-0.14) and moderate similarity to Alpine Meadows because this group contained a number of alpine wet meadows as well as dry meadows (SQI 0.28).

4.2 CLASSIFICATION AND REGRESSION TREES

Classification and regression trees were used to explore the relationship between species richness and vegetation assemblages with environmental variables at landscape scales. Species composition differed significantly between the 10 vegetation types (MRPP, $P < 0.001$, $A = 0.18$). Univariate regression tree analysis of species richness per sample data resulted in a tree with six terminal nodes (Figure 5). Elevation was an important variable in the final solution, and reduced the sum of squares more than other variables at three splits in the tree. Topographic wetness index and slope were both the best predictors at the remaining three splits. 23.8% of the variability was explained by the model with a six node solution.

Classification tree analysis based on the 10 vegetation assemblages from the cluster analysis resulted in a 16 node solution with a 35.4% misclassification rate (Figure 6). Elevation was the most important variable separating the 10 vegetation groups. Slope, precipitation, and topographic wetness were also retained in the final model. Geology, aspect, and topographic position were not retained in the final solution.

4.3 WETLAND COMPOSITION AND DIVERSITY

The National Wetland Plant List provides wetland affinities for each species based on a cooperative rating by a panel of regional experts (Lichvar and Kartesz 2009). These ratings were used to assess the percentage of species in the parks that are likely to be found in wetlands. Obligate (OBL) and Facultative Wetland (FACW) species have an estimated probability of occurring in wetlands greater than 67% of the time. Facultative

(FAC) species are estimated to occur in wetlands 34-66% of the time. The national status of each species was used only if a regional status was not assigned. Approximately 330 or 21% of plant species recorded in SEKI are OBL or FACW and approximately 31% of plants observed in the park are found in wetlands greater than 34% of the time (Lichvar and Kartesz 2009).

Nonmetric Multidimensional Scaling ordination based on Sørensen distance resulted in a 2 dimensional plot that represented 69% of the variation in vascular plant composition in wet meadows and fens (McCune and Grace 2002). Axis 1 was strongly correlated ($r^2 = 0.50$) with the landscape scale variables elevation, precipitation, and easting (Figure 7). Axis 2 was moderately correlated ($r^2 = 0.19$) with the local scale variables peat thickness and water table depth and the landscape scale variable northing (Figure 7). A Mantel test indicated that a significant correlation existed between matrices for vegetation and geographic position (northing and easting; $r = 0.39$, $p < 0.0001$) and environmental variables ($r = 0.66$, $p < 0.0001$). The test significance indicates a high degree of spatial autocorrelation in the data.

Ordination was coupled with a hierarchical cluster analysis of samples to provide a model of vegetation composition and a visual assessment of wet meadow groups along environmental gradients (Figure 7). Clustering resulted in three groups, Montane Wet Meadows and Fens, Subalpine Fens and Saturated Wet Meadows, and Subalpine and Alpine Wet Meadows with a 0.56 - 0.64 within group average Sørensen distance.

Three subgroups were evident in the Montane Wet Meadows and Fens group based on species composition, hydrology and soils. The first subgroup is characterized by OBL wetland species including *Oxypolis occidentalis, Galium trifidum* L. ssp.

columbianum, Eleocharis decumbens, Scirpus microcarpus, and Ptychostomum pacificum (Spence 2006). Water tables were close to the ground surface and peat thickness was greater than 25 cm at most sites, although a few sites had no peat yet similar vegetation. The second subgroup is characterized by FACW to OBL wetland species including *Mimulus guttatus*, *Veratrum californicum*, *Epilobium ciliatum* ssp. *ciliatum, Senecio triangularis*, *Stachys albens, Glyceria striata*, and *Amblystegium varium.* The only species with high fidelity to the third subgroup were drier habitat species including *Achillea millefolium* and *Danthonia californica* var. *americana*. This group was characterized by seasonally wet soils that likely dry out at some point during the summer season and higher soil temperatures.

Subalpine Fens and Saturated Wet Meadows supported both OBL and FACW species including *Vaccinium uliginosum, Carex fissuricola, Agrostis idahoensis,* and *Allium validum, Trifolium monanthum* ssp. *monanthum* and *Eleocharis suksdorfiana.* Water tables at these sites were predominantly close to the soil surface, and most sites had peat soils.

Wet meadows in the Subalpine and Alpine zones were characterized by *Eleocharis quinqueflora, Carex scopulorum* var. *bracteosa*, and *Oreostemma alpigenum* var. *andersonii.* These sites were characterized by deeper water tables during the late summer, soils saturated for part of the growing season and peat soils in only a few sites. Species with high fidelity to this group ranged from upland species to OBL wetland species included *Gentiana newberryi* var. *tiogana, Calamagrostis breweri, Polytrichum juniperinum, Vaccinium cespitosum, Botrychium simplex, Trichophorum clementis, Juncus mertensianus, Carex nigricans,* and *Carex spectabilis.*

Complementarity between the three wetland groups for vascular and nonvascular plant species revealed a similar pattern to that seen in the broad-scale vegetation groups, higher floristic similarity in groups with overlapping elevation ranges (Table 4). The montane and subalpine groups were similar, Montane Wet Meadows/Fens and Subalpine Fens/Saturated Wet Meadows (Sørensen Quantitative Index = 0.46) and the subalpine and alpine groups, Subalpine Fens/Saturated Wet Meadows and Subalpine/Alpine Wet Meadows (SQI 0.44) were similar. Montane Wet Meadows and Fens and Subalpine and Alpine Wet Meadows had much lower floristic similarity (SQI 0.22) with limited elevation and spatial overlap.

5. DISCUSSION

5.1 CONTRIBUTIONS TO SPECIES RICHNESS

This study found that wet meadows and fens make important contributions to the floristic diversity in Sequoia and Kings Canyon National Parks. These wetland types have both high site diversity and beta diversity compared to other habitats. These findings support the assertion that meadows not only provide necessary and valuable ecosystem functions, but also support an important component of the regional flora. Wet meadows and fens provide these important biotic contributions while inhabiting the very small portion of the study area where groundwater discharges or collects due to geomorphic or geologic features. These wetlands often occur as isolated patches, increasing patch and species diversity across the landscape (Figure 8). Wet meadows and fens, particularly Montane Wet Meadows, support a flora distinct from upland Woodland, Forest, and Shrubland habitats that constitute the area (65%) in SEKI. A similar trend has been reported for wet meadows in the Rocky Mountains of Colorado and wetlands in the White Mountains of California and Nevada (Morefield 1992, Chong and Stohlgren 2007). Species richness in wet meadows and fens is sustained by the highly variable hydrologic regimes and soil moisture, complex landscape patterns, and the presence of these wetland types throughout the entire survey extent from lower montane to alpine elevations.

Wetlands such as species poor *Spartina* marshes have been described as global diversity "coldspots", that provide critical ecosystem services (Kareiva and Marvier 2003). In other regions of the world, particularly in arid and semi-arid regions, wetlands provide diverse and necessary ecosystem services, and make important contributions to species diversity (Erman and Erman 1975, Chong and Stohlgren 2007, Flinn et al. 2008, Naqinezhad et al. 2009). Isolated wetlands have been shown to be particularly important in comparison to surrounding uplands (Morefield 1992, Haukos and Smith 1994, Bedford and Godwin 2003, Tiner 2003). This study provides evidence of a similar pattern of diversity in isolated wetlands in a predominantly forested upland matrix in the Southern Sierra Nevada.

Lower Montane Woodlands and Chaparral were also rich in vascular plant species. This may be attributed to local scale habitat heterogeneity and high topographic variability. The vegetation types sampled in this group included a wide range of species associations occurring in steep, topographically variable terrain below 1800 meters elevation in the western portions of SEKI and in the Kings and Kern River Valleys. Topographic positions ranged from ridges to valley bottoms and sampled areas comprise a highly variable matrix with small patches of grassy openings, dense shrubs, and woodlands. Other montane regions of North America exhibit a similar trend of increasing species diversity from forest-dominated montane to subalpine zones, to more open, drier, low elevations with high woody species diversity (Whittaker and Niering 1975).

Montane and Subalpine Forests and Woodlands also conformed to this trend being the least diverse habitats sampled. These sites comprise approximately 36% of the area in SEKI and are dominated by *Pinus contorta* var. *murrayana* and *Pinus balfouriana* ssp. *austrina* and Montane Mixed Coniferous Forests dominated by *Abies concolor*, *Abies magnifica*, *Pinus jeffreyi*, *Pinus lambertiana*, and openings of *Chrysolepis sempervirens* and *Arctostaphylos patula*. Upper Montane Mixed Coniferous Forests occur in the zone of highest snow accumulation in the Sierra Nevada, experience a short growing season, have nutrient poor soils, a relatively closed canopy, and a species-poor understory (Barbour et al. 1991). *Pinus contorta* var. *murrayana* and *Pinus balfouriana* ssp. *austrina* are poor competitors for light and dominate the harsh environments of upper subalpine slopes with poorly developed soils above the high snowpack zone (DeClerck et al. 2005, Eckert 2006).

Although the available data were not specifically collected for assessing species richness, they provide a robust park-wide estimate of species richness by habitat. The use of random sampling at the park scale and standard sized sampling plots (1 m^2) allowed the combination of samples from different designs for analysis. This scale has been shown to be appropriate in wetlands dominated by herbaceous species (Kaeser and Kirkman 2009). In all 1 m^2 WEI samples, 212 species were recorded, while only 45 more species were recorded when sampled area was increased to 100 m^2, an increase of almost 9800 m^2. The use of 4 m^2 data from 4, 1 m^2 plots may not be appropriate for sampling species richness in forest, woodland, or shrubland habitats where locally rare species are likely to be missed (Keeley and Fotheringham 2005, Stohlgren 2007, Kaeser and Kirkman 2009). However, no other data span the entire park area allowing the comparison of such disparate groups.

Inventory and monitoring programs implemented at landscape scales provide the data necessary for studying both common and rare habitats. Inventory data sets were effectively used in this study to assess the species richness contributions of broad vegetation assemblages at regional scales. Though systematic sampling has been used in many large-scale vegetation inventories because of its simplicity and spatial balance, it can often result in patchy responses in large, heterogeneous landscapes and when sampling spatially structured resources (Larsen et al. 2008). The NRI systematic sample design included 26 wetlands in 591 samples and 28 portions of wetlands. The coverage of this survey provided a sufficient evaluation of dominant vegetation types for the study extent. The addition of a targeted survey of wet meadows and fens allowed a more intensive assessment of this resource at larger scales.

5.2 ENVIRONMENTAL INFLUENCE ON SPECIES PATTERNS

Classification and regression trees are increasingly being used to assess environmental influences on species richness and composition (De'ath and Fabricius 2000, Urban et al. 2002, Johnston et al. 2009, He et al. 2010, Poulos and Camp 2010). In the CART models used in this study, elevation was the most important variable to both vegetation assemblages and species richness. Elevation in the regression tree model exhibited a unimodal pattern with the highest elevation sites (>3685m) having the lowest species richness values and low elevation sites (<1385) having the highest species richness. Elevation was also an important variable in the classification tree model, driving six of the ten breaks in the tree.

Mountain regions typically exhibit vegetation zonation that creates high spatial variability of habitat, species density, and species richness. Although vegetation assembly cannot be explained by any single process, elevation has often been studied as a primary influencing factor (Billings 1952, Whittaker and Niering 1975, Barbour et al. 1991). Elevation serves as a proxy for several correlated and biologically meaningful environmental gradients such as precipitation and temperature, and is an easily acquired and useful variable when assessing vegetation composition (Lookingbill and Urban 2005).

Topographic wetness was another important variable in the classification and regression tree models and has been shown to be an important variable in species composition and species richness in many studies (Whittaker and Niering 1975, Peet 1978, Poulos and Camp 2010). Topographic wetness defined the split between Subalpine Wet Meadows and three much drier groups, *Pinus contorta* var. *murrayana* and *Pinus balfouriana* ssp. *austrina* Forests and Woodlands and Rock and Sparsely vegetated sites. Rock and Sparsely vegetated sites had the lowest topographic wetness as well as many samples with the lowest species richness, containing only one to five species. Sites with higher species richness also had higher topographic wetness.

Slope defined the split between *Pinus contorta* var. *murrayana* and *Pinus balfouriana* ssp. *austrina* Woodlands and Forests and between Montane Wet Meadows and Upper Montane Mixed Coniferous Forests. *Pinus* species are relegated to the driest and most harsh conditions in the survey area. *Pinus balfouriana* is a poor competitor for resources compared to *Pinus contorta*, forming monocultures on steep, exposed slopes (Eckert 2006).

5.3 WETLAND COMPOSITION

In surveyed wetlands, species composition was correlated with elevation, precipitation, peat thickness, depth to water and spatial location. Soil temperature, slope, aspect, and topographic position of study sites were not correlated with species composition. Soil temperature was likely not correlated because warm summer temperatures may be moderated by cool night time soil temperatures in all sites. The affect of slope, aspect, and topographic position are likely moderated by the influence that groundwater has on species composition in wetlands.

Wetlands including wet meadows, seeps, riparian areas, forested wetlands and other wetland types cover approximately 4.7% of SEKI (National Park Service 2007). Wetland species are a prominent component of the park flora, and wetlands support a large number of species with special or endemic status. Twelve percent of species with special status were found in the 1.0 hectare sampled for the WEI protocol. The list of special status species in SEKI indicates that approximately 27.3% of the listed species occur in wetlands (Haultain 2011).

6. CONCLUSION

Wet meadows and fens are important ecological components of mountain regions, providing habitat for unique biota, while performing essential ecosystem functions. These wetlands occupy a very small proportion of SEKI and occupy headwater positions where they provide invaluable water quality maintenance for the health of three large California rivers, the Kings, Kaweah, and Kern. Wet meadows and fens in the Sierra Nevada are threatened by anthropogenic disturbances including visitor use and grazing by pack stock. These wetlands are also susceptible to changes in climate that may alter temperature, snowpack, and groundwater (Ababneh and Woolfenden 2010). California has lost approximately 91% of its wetland area, making the task of understanding and managing these resources imperative (Dahl and Johnson 1991, Brinson and Malvarez 2002).

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Table 1 Variables used in CART analysis.

Variable	Definition
Elevation	Elevation above sealevel based on 10 m NED (National Elevation Dataset)
Precipitation	Mean annual precipitation from PRISM group (Oregon State University, NRCS)
UTM Coordinates	Position coordinates acquired using handheld GPS unit during data collection
Slope	Slope calculated from 10 m NED (National Elevation Dataset), using Spatial Analyst in ArcGIS 9.3
Aspect	Aspect calculated from 10 m NED (National Elevation Dataset), using Spatial Analyst in ArcGIS 9.3
Topographic Position Index	Topographic Position Index in Geodatabase tools in ArcGIS 9.3
Topographic Wetness Index	Landscape Connectivity and Pattern (LCaP) metrics tools (Theobald 2007)
Geology	Geology values for Sequoia and Kings Canyon were derived from incomplete geology layers of the park

Table 2 Richness and area data for each vegetation type and combined Montane and Subalpine Wet Meadows.

Ecological System	Average Elevation (m)	Area (hectare)	% of Park	Average Number of Species Per Plot	Simpson's Index	Shannon's Index
Alpine Meadows	3400	33132	9.4	11.9	29.1	4.0
Lower Montane Mixed Coniferous Forest	1800	18808	5.3	8.5	7.6	2.6
Lower Montane Woodlands and Chaparral	1000	22921	6.5	16.3	27.3	4.1
Montane and Subalpine Wet Meadows	2800	7190	2.0	17.3	43.6	4.3
Montane Mixed Coniferous Forest	2100	31237	8.8	7.3	5.8	2.8
Montane Wet Meadows	2400	3414	1.0	18.2	28.6	3.9
Pinus balfouriana Woodlands	3200	24470	6.9	4.6	2.1	1.5
Pinus contorta Forests and Woodlands	3000	30730	8.7	6.6	3.3	2.5
Rock and Sparsely Vegetated	3400	98911	27.9	7.2	31.3	4.2
Subalpine Wet Meadows	3000	3776	1.1	16.6	28.0	3.9
Upper Montane Mixed Conifer Forests	2500	40171	11.3	7.0	7.7	2.8

Table 3 Complementarity of vegetation assemblages based on the Sørensen Quantitative Index (SQI).

	Lower Montane Mixed Coniferous Forest	Lower Montane Woodlands and Chaparral	Montane Mixed Coniferous Forest	Montane Wet Meadows	Pinus balfouriana Woodlands	Pinus contorta Forests and Woodlands	Rock and Sparsely Vegetated	Subalpine Wet Meadows	Upper Montane Mixed Conifer Forests
Alpine Meadows	0.018	0.013	0.052	0.085	0.162	0.351	0.534	0.279	0.124
Lower Montane Mixed Coniferous Forest		0.17	0.399	0.008	0.017	0.047	0.033	0.003	0.275
Lower Montane Woodlands and Chaparral			0.074	0.014	0.005	0.026	0.02	0.001	0.094
Montane Mixed Coniferous Forest				0.073	0.065	0.128	0.062	0.027	0.396
Montane Wet Meadows					0.022	0.096	0.04	0.383	0.077
Pinus balfouriana Woodlands						0.372	0.208	0.058	0.191
Pinus contorta Forests and Woodlands							0.376	0.141	0.303
Rock and Sparsely Vegetated								0.108	0.153
Subalpine Wet Meadows									0.053

Table 4 Complementarity of wetland groups based on the Sørensen Quantitative Index (SQI).

Group1	Group2	SQI
Montane Wet Meadows and Fens	Subalpine Fens and Saturated Wet Meadows	0.459
Montane Wet Meadows and Fens	Subalpine and Alpine Wet Meadows	0.223
Subalpine Fens and Saturated Wet Meadows	Subalpine and Alpine Wet Meadows	0.438

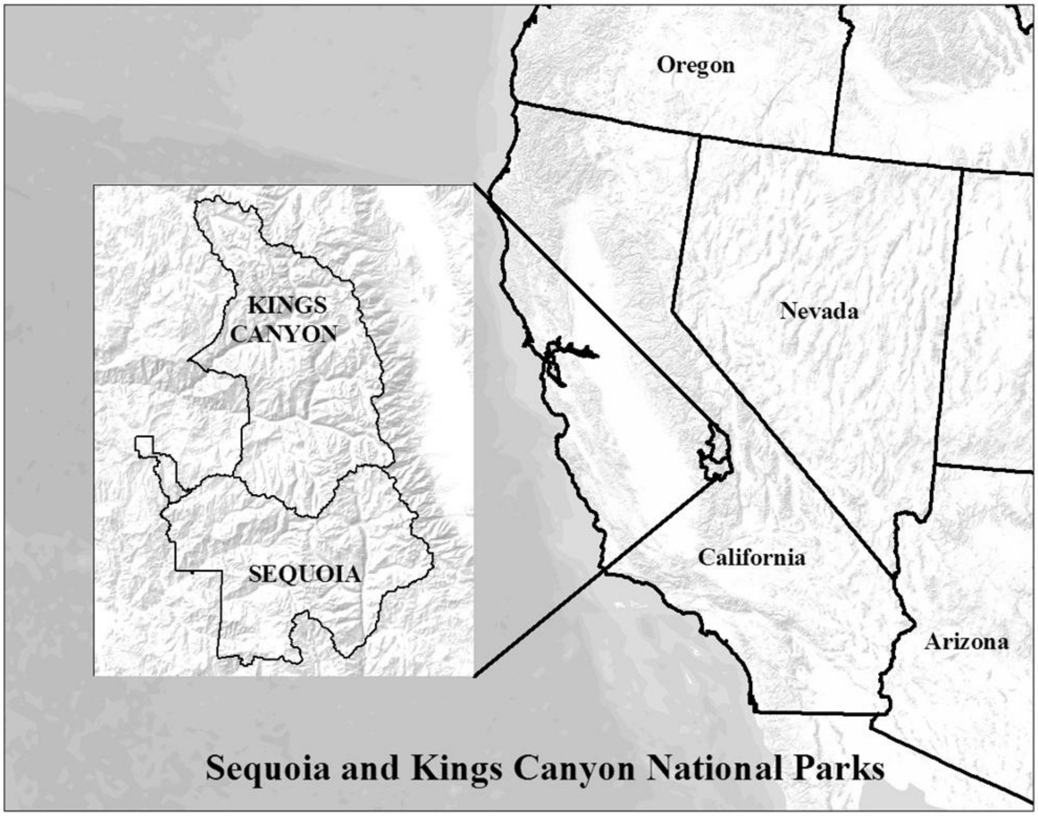

Figure 1 Sequoia and Kings Canyon National Parks, California, United States.

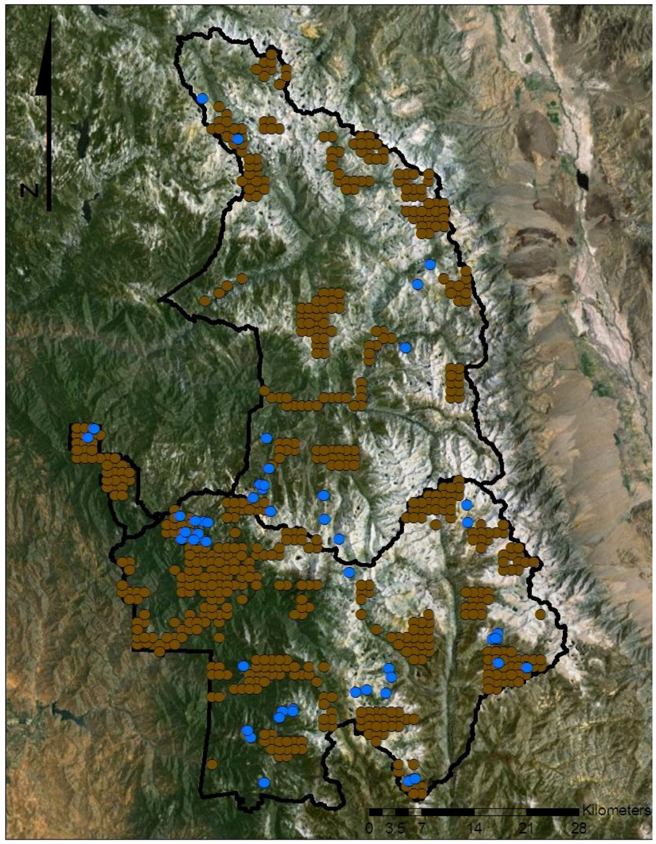

Figure 2 Map of Natural Resource Inventory (brown circles) and Wetland Ecological Integrity (blue circles) survey sites in Sequoia and Kings Canyon National Parks.

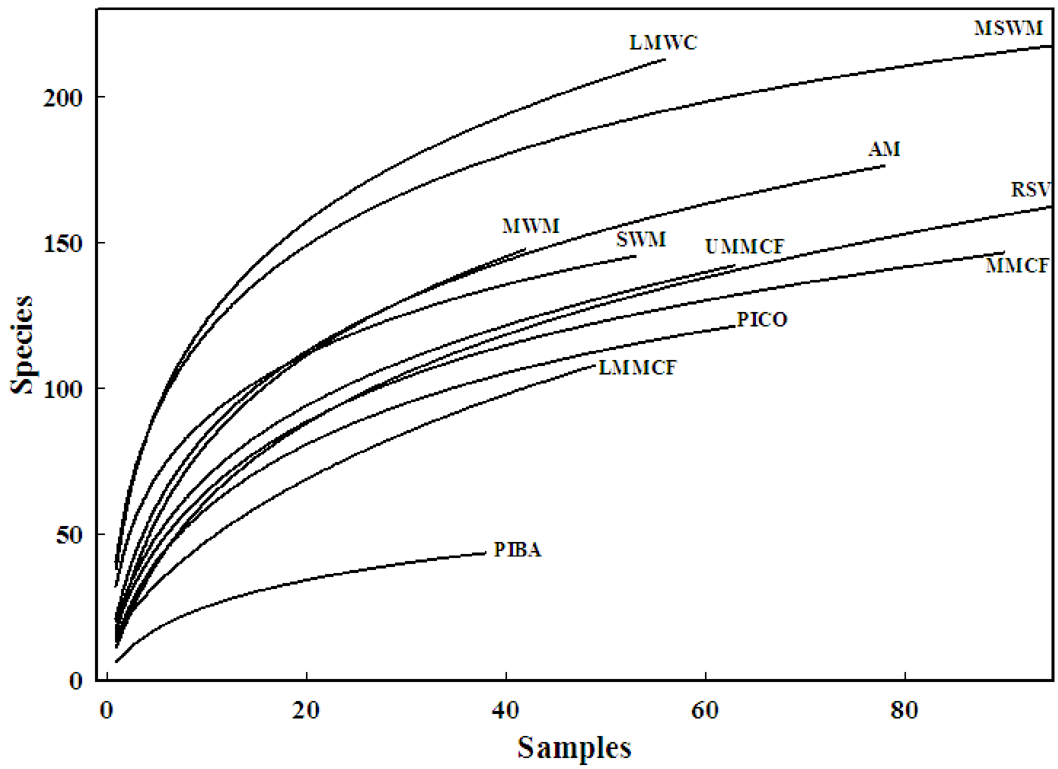

Figure 3 Coleman rarefaction curves for vegetation assemblages and combined Montane and Subalpine Wet Meadows. AM = Alpine Meadows, LMMCF = Lower Montane Mixed Coniferous Forest, LMWC = Lower Montane Woodlands and Chaparral, MSWM = Montane and Subalpine Wet Meadows, MMCF = Montane Mixed Coniferous Forest, MWM = Montane Wet Meadows, PIBA = Pinus balfouriana Woodlands, PICO = Pinus contorta Forests and Woodlands, RSV = Rock and Sparsely Vegetated, SWM = Subalpine Wet Meadows, UMMCF = Upper Montane Mixed Conifer Forests.

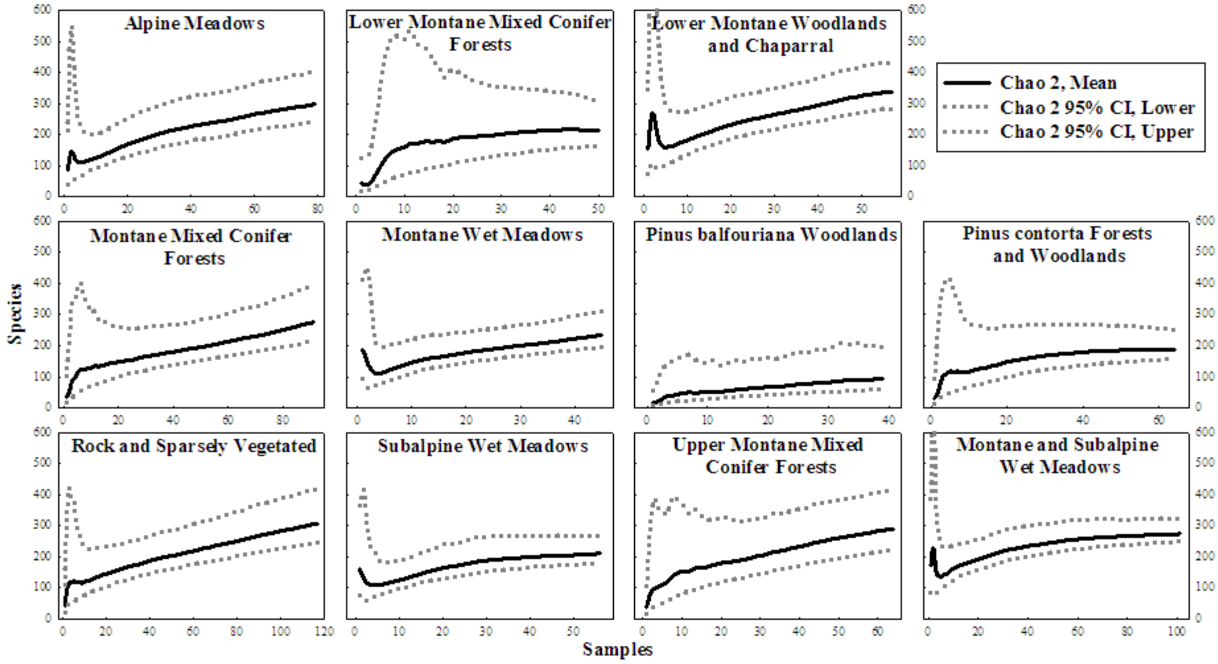

Figure 4 Chao2 species richness estimator curves for vegetation assemblages and combined Montane and Subalpine Wet Meadows. The solid line represents the mean Chao 2 richness estimator. Dotted lines represent the upper and lower 95% confidence intervals.

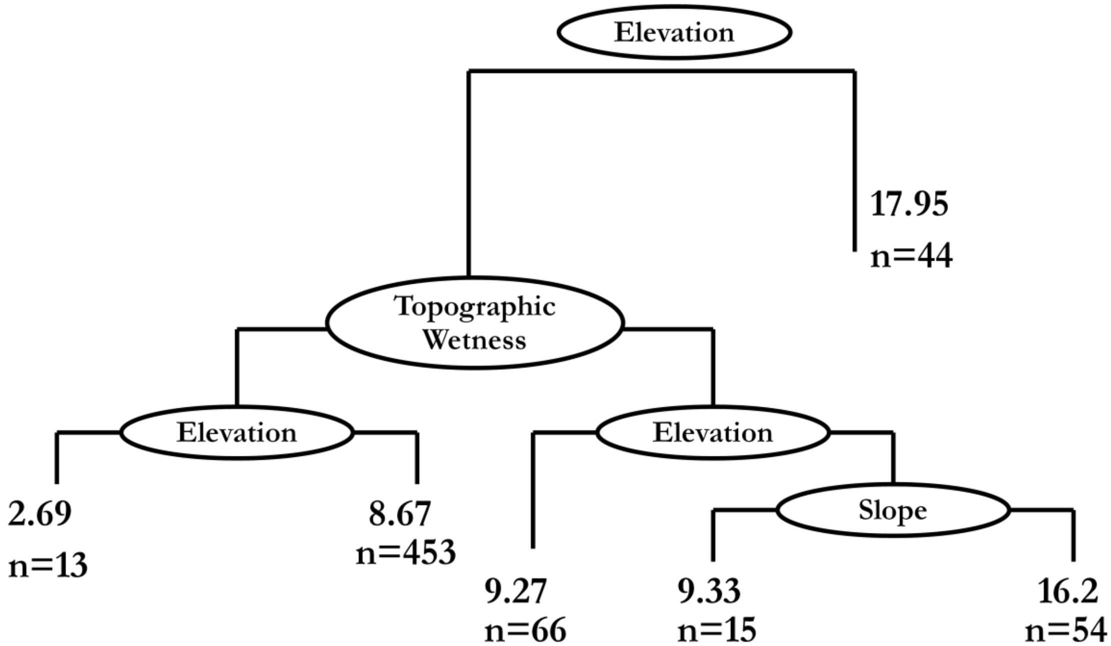

Figure 5 Pruned regression tree for species richness. Values at each terminal node represent the mean species richness value for that node. N represents the number of samples remaining in each terminal node.

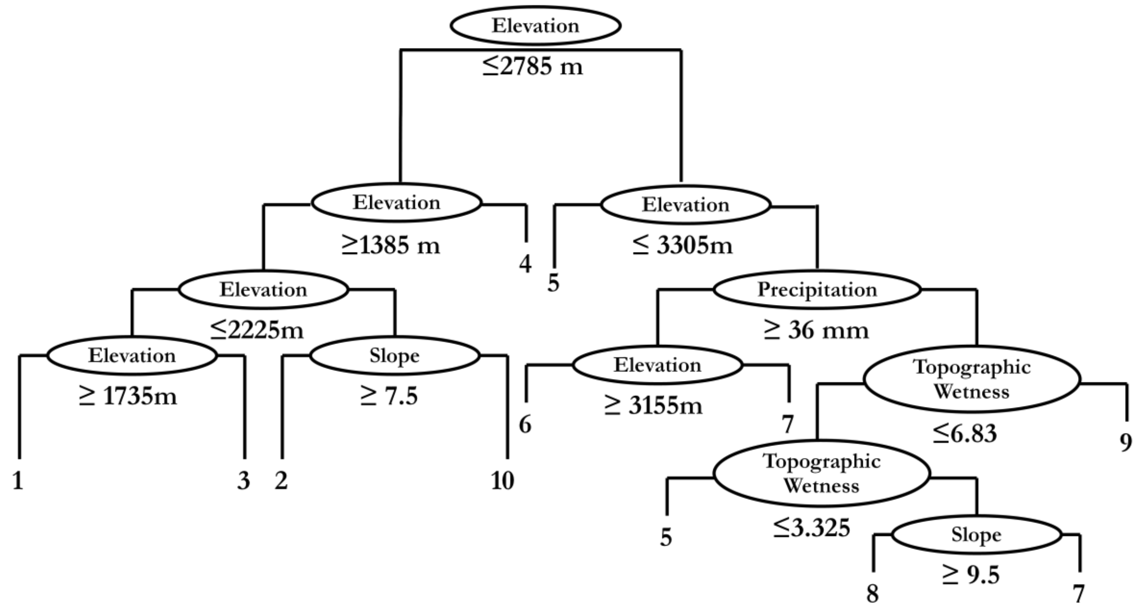

Figure 6 Pruned classification tree for vegetation assemblages. The numbers at terminal nodes represent the vegetation assemblages. 1 = Montane Mixed Coniferous Forest, 2 = Upper Montane Mixed Conifer Forests, 3 = Lower Montane Mixed Coniferous Forest, 4 = Lower Montane Woodlands and Chaparral, 5 = Rock and Sparsely Vegetated, 6 = Alpine Meadows, 7 = Pinus contorta Forests and Woodlands, 8 = Pinus balfouriana Woodlands, 9 = Subalpine Wet Meadows, 10 = Montane Wet Meadows

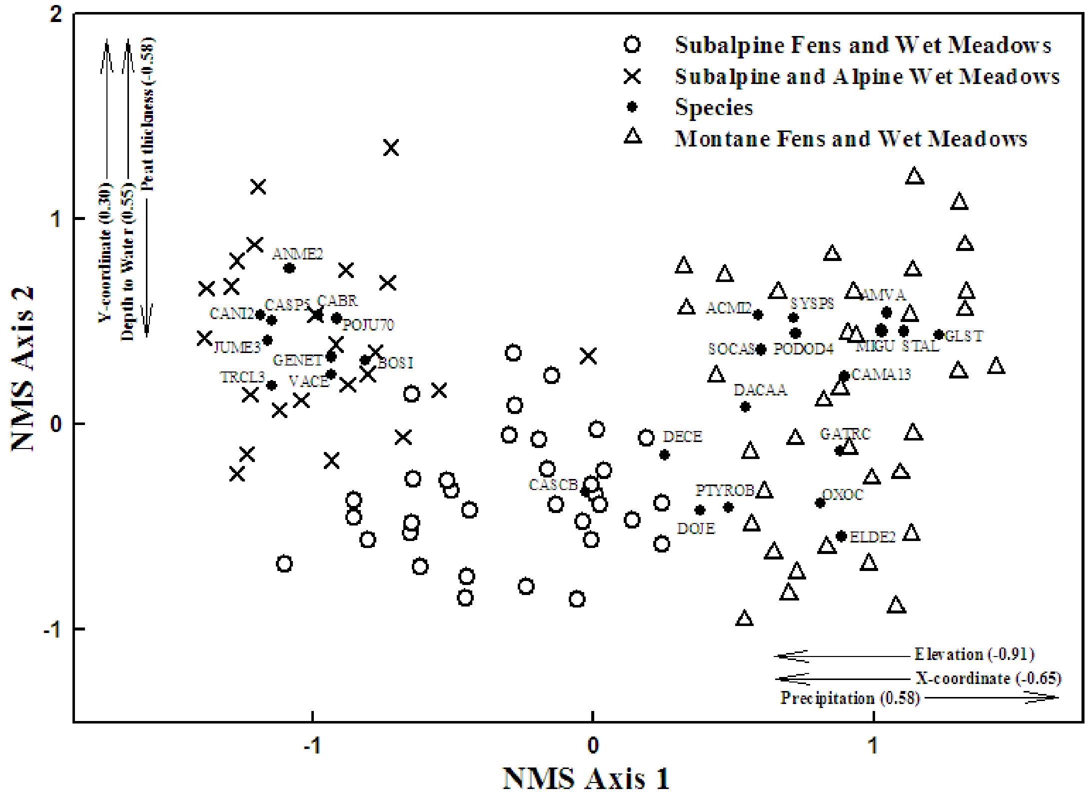

Figure 7 Nonmetric Multidimensional Scaling ordination based on vascular plants in WEI samples. ACMI2 = *Achillea millefolium*, AMVA = *Amblystegium varium*, ANME2 = *Antennaria media*, BOSI = *Botrychium simplex*, CABR = *Calamagrostis breweri*, CAMA13 = *Carex mariposana*, CANI2 = *Carex nigricans*, CASCB = *Carex scopulorum* var. *bracteosa*, CASP5 = *Carex spectabilis*, DACAA = *Danthonia californica* var. *americana*, DECE = *Deschampsia cespitosa*, DOJE = *Dodecatheon jeffreyi*, ELDE2 = *Eleocharis decumbens*, GATRC = *Galium trifidum* ssp. *columbianum*, GENET = *Gentiana newberryi* var. *tiogana*, GLST = *Glyceria striata*, JUME3 = *Juncus mertensianus*, MIGU = *Mimulus guttatus*, OXOC = *Oxypolis occidentalis*, POJU70 = *Polytrichum juniperinum*, PTROB = *Ptychostomum pacificum*, PODOD4 = *Polygonum douglasii* ssp. *douglasii*, SOCAS = *Solidago canadensis*, STAL = *Stachys albens*, SYSPS = *Symphyotrichum spathulatum* var. *spathulatum*, TRCL3 = *Trichophorum clementis*, and VACE = *Vaccinium cespitosum*.

Figure 8 Images of wet meadows and fens in SEKI. A. Montane Wet Meadow. B. Large fen. C. Fen edge contrasted with adjacent upland forest. D. *Pinus balfouriana* habitat with large wetland complex in distance. E. Sloping wet meadow with sparse, *Pinus* dominated uplands. F. Alpine meadow with Mount Whitney in the background.