

Fens of the Sierra Nevada, California, USA: patterns of distribution and vegetation

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SUMMARY

A broad sample of 79 montane fens in the Sierra Nevada revealed that underlying geology and topography exert strong control over the distribution and vegetation of these ecosystems. Distinct granodiorite, metamorphic, volcanic, carbonate and serpentine bedrock geology resulted in very different water chemistry, which had significant effects on the particular plant species found at each site. Wide-ranging values of pH (4.28–8.00) and dissolved cation concentrations (1.6–62.0 mg L⁻¹) spanned the categories of transitional poor-rich to extremely rich fens. The vegetation of a pair of fens on carbonate bedrock and two floating mat fens was markedly different from the vegetation recorded at any other study sites. Once these outlier fens were removed from the analyses, the environmental variables that correlated most closely with the vegetation data were pH, altitude, presence of volcanic bedrock and fen slope. The measured environmental parameters explained 9.7 % of the variability in the vegetation data. Species richness was primarily (and negatively) correlated with altitude. Peat thickness (15–253 cm) was constrained in smaller catchments and on steeper slopes, and was positively correlated with soil organic matter content (16–92 %). Of the four typical fen landforms (bedrock contact, slope, spring mound and basin), sloping fens were the most common (63 % of the 79-fen sample).

KEY WORDS: bedrock, geomorphology, peatland, species richness, water chemistry

INTRODUCTION

Peatland formation requires a specific combination of physical and biological processes that most commonly occur in low-relief tropical and boreal regions of the world. Perennial soil saturation, very low mineral soil deposition and erosion rates, and net storage of soil carbon resulting from plant productivity must coexist for centuries or millennia to form peat soils (Moore & Bellamy 1974). Suitable conditions for peatland formation are of limited occurrence in mountain landscapes (Cooper *et al.* 2012). For example, peatlands occupy 1.0 % of the land surface area in the Beartooth Mountains of Wyoming, USA (Heidel & Rodemaker 2008), 1.0 % of the San Juan Mountains in Colorado, USA (Chimner *et al.* 2010), 2.5 % of the Snowy Mountains in New South Wales, Australia (Hope *et al.* 2012) and 0.4 % of the autonomous region of Galicia in northwest Spain (Pontervedra-Pombal *et al.* 2006). Preliminary measurements in the Sierra Nevada, from Sequoia and Kings Canyon National Parks (California, USA), indicate that peatlands cover approximately 0.2 % of the land area (Hopkinson *et al.* 2013).

Mountain ranges are highly variable landscapes created by glaciers, hillslope erosional processes and geological forces such as faulting and uplift. Uplift

and erosion expose highly variable bedrock types so that water (surface and groundwater) flowing through mountain systems acquires different chemical characteristics depending on the local lithology. Water chemistry profoundly influences peatland vegetation (Cooper & Andrus 1994, Lemly & Cooper 2011). Steep mountain topography also promotes drainage and, thus, rapid drying of soils, high soil erosion rates on slopes and high mineral sediment deposition rates in valleys and basins (Patterson & Cooper 2007).

The distinctive characteristics of mountains include large altitudinal and climatic ranges, complex migratory pathways for biota, large floras with diverse biogeographical connections and histories (Weber 2003, Cooper *et al.* 2012), and high species and community-level biodiversity (Bedford & Godwin 2003). As a small areal component of the landscape, mountain peatlands support a disproportionate diversity of plant species (Jones 2011, Sekulová *et al.* 2013) and provide important habitat for insects (Holmquist *et al.* 2011) and many other organisms (Bedford & Godwin 2003). In addition to their importance for flora and fauna, many mountain peatlands have accumulated organic carbon for millennia (Wood 1975), allowing prehistoric climate and vegetation to be reconstructed (Anderson & Smith 1994). While the quantity of

stored carbon in some mountain peatlands is minor with respect to the global carbon budget, the preserved record of climate and vegetation over the past several thousand years is invaluable. Because of their relative scarcity, their value for biodiversity and wildlife, and their importance as records of past ecological conditions, mountain peatlands have become priority research and conservation targets for land management organisations around the world (Bragg *et al.* 2003, Michael Succow Foundation 2014, Wetlands International 2014) and in the western USA (Chadde *et al.* 1998, Sikes *et al.* 2013). Mountain peatlands exist within a highly variable physical template, making them diverse and challenging to understand. Specifically, it is unclear what physical factors control mountain peatland distribution and plant biodiversity.

The Sierra Nevada of California is one of the largest and most continuous high mountain ranges in North America. A few mountain vistas (e.g. Yosemite Valley) are world-famous icons and the majestic conifer forest vegetation has been well studied (Ratliff 1985, Barbour 1988, Fites-Kaufman *et al.* 2007). However, relatively little is known about the diversity of wetlands in the Sierra Nevada. One of the first peatlands described in the western USA is in California (Rigg 1933, Baker 1972, Erman *et al.* 1977), but there have been relatively few studies of peatlands since then (Beguin & Major 1975, Burke 1991, Bartolome *et al.* 1990, Allen-Diaz 1991).

The goal of this study is to characterise the flora, vegetation, soils, geochemistry, physical setting and landforms of representative peatlands in the Sierra Nevada, southern Cascade Range and nearby Klamath Mountains in California, focusing primarily on the Sierra Nevada. We specifically addressed the following questions: (1) are peatlands present in all regions of the study area? (2) are the abundance, distribution and development of peatlands influenced by landscape-scale factors? and (3) how do physical site characteristics influence peatland vegetation and floristic biodiversity?

STUDY AREA

The Sierra Nevada mountain range runs north–south for 640 km in the east of the state of California, USA. The highest peak is Mount Whitney (4,421 m). To the north and north-west are the Cascade Range and the Klamath Mountains, which are regarded by earth scientists as contiguous but distinct geomorphic provinces (Figure 1). Our goal was to sample peatlands in each National Forest (NF) throughout the Sierra Nevada, with limited sampling in the National Parks (NP) and southern parts of the

Cascade Range and Klamath Mountains, to cover a broad range of mountain peatland occurrences throughout California.

The dominant bedrock type varies across this large study area. Granodiorite (a quartz-rich crystalline intrusive rock similar to granite) dominates the central and southern Sierra Nevada, while volcanic rocks form the Cascade Range. Metamorphic belts are exposed in the northern Sierra Nevada and on its west- and east-facing slopes, as well as in the Klamath Mountains. Very localised exposures of carbonate metasedimentary rocks such as marble, and ultramafic metavolcanics like serpentine, occur within the metamorphic belts.

There is a strong north–south precipitation gradient (see Figure 1), with annual precipitation ranging from > 200 cm in the north and west to < 65 cm in the south and east. The climate of the Sierra Nevada is characterised by wet winters with abundant snowfall above approximately 1,600 m altitude (snowfall is 70–90 % of annual precipitation) and dry summers with only 10–30 % of annual precipitation falling between June and October (Fites-Kaufman *et al.* 2007). Therefore, peatlands must be kept saturated through the four-month growing season (July–October) by groundwater discharge with minor supplementation by direct rainfall. During the spring of each year, the melting snowpack recharges the aquifers that supply the groundwater discharge in summer (Cooper *et al.* 2015). Because all peatlands in the Sierra Nevada must rely primarily on groundwater to remain saturated they are classified as minerotrophic peatlands, or fens (Rydin & Jeglum 2013), as opposed to ombrotrophic (rain-supported) bogs.

METHODS

Site visits

Potential fens were initially identified using natural colour air photos and topographic maps. Sites for field visits were chosen to represent the range of altitudes and habitats occurring within the mountain ranges, and for ease of accessibility. A total of 79 fens were visited: 2 in the Klamath Mountains (Shasta-Trinity NF), 11 in the Cascade Range (Lassen NF and Lassen NP), and 66 in the Sierra Nevada (Plumas, Tahoe, Eldorado, Stanislaus, Inyo, Sierra and Sequoia National Forests, and Yosemite NP; see Appendix). We delineated each fen's catchment area and determined its altitude, predominant catchment bedrock type (granodiorite, metamorphic, volcanic, carbonate or serpentine) and average annual precipitation using topographic maps and geospatial data layers (State of California 2015) in a GIS

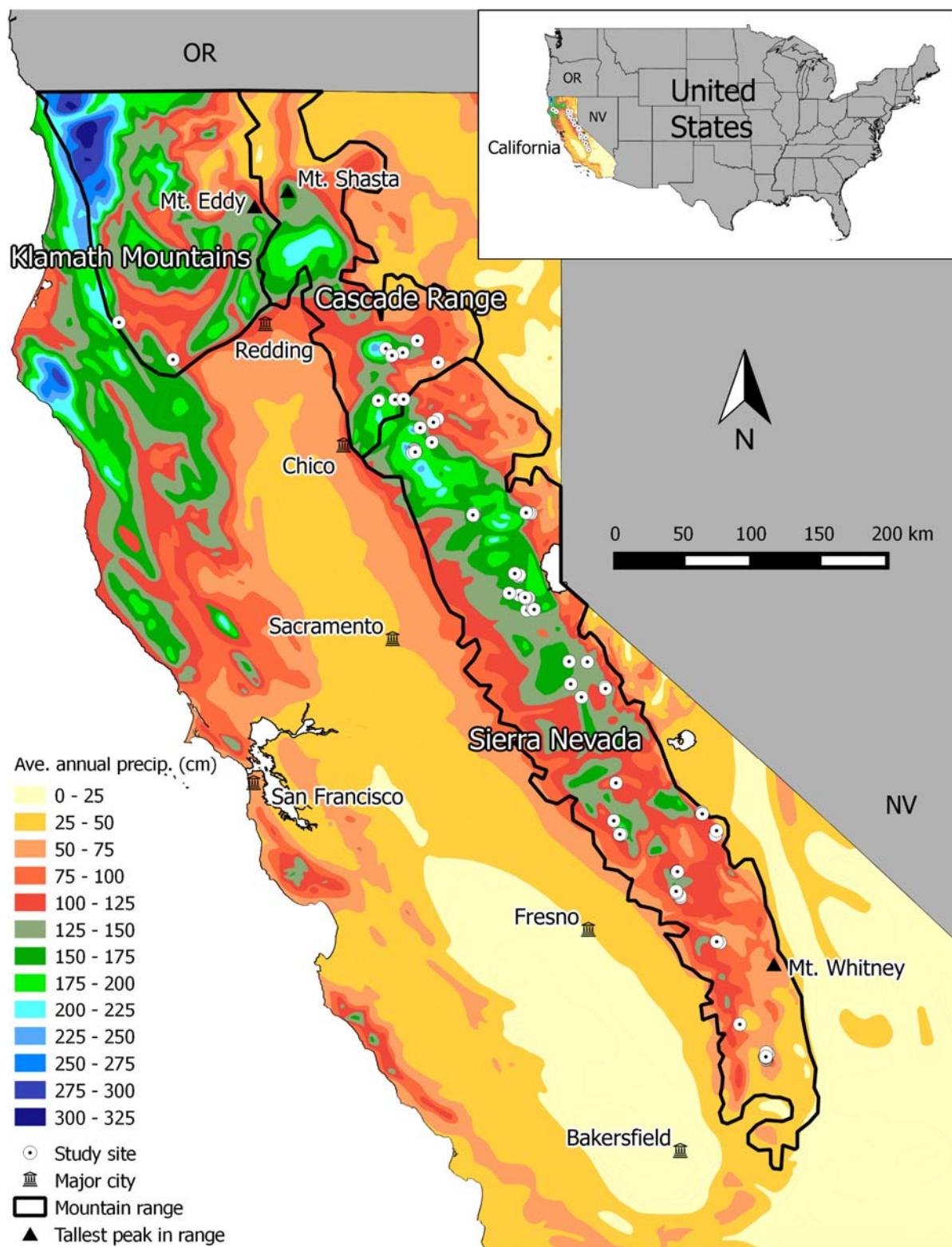


Figure 1. Locations of the 79 study fens in California. Colour scale illustrates average annual precipitation (cm). The Klamath Mountains, Cascade Range, and Sierra Nevada geomorphic provinces, and each of their highest peaks, are indicated.

environment (QGIS Development Team 2014). All 79 sites were visited between 09 July and 21 September 2003. During the field visits we assigned each fen to a landform type, observed aspect azimuth using a compass, and measured the fen surface slope using a clinometer.

Water

In the field we measured the pH of groundwater that filled a shallow hand-dug open well. The hole was bailed and allowed to refill several times to ensure an uncontaminated sample of groundwater. Sampling groundwater (as opposed to surface water or water held in living moss tissue) has been found to yield the most consistent measurements of environmentally-controlled site pH in fens (Tahvanainen & Tuomaala 2003). We measured pH *in situ* using an Orion model 250A portable pH meter with combination electrode, which was calibrated daily with fresh pH standards. In each fen (not each vegetation relevé) we made one pH measurement and collected one water sample that was sealed immediately and frozen until analysis. The water samples were analysed for electrical conductance and concentrations of Ca^{2+} , Mg^{2+} , K^+ , Na^+ , HCO_3^- , CO_3^{2-} , Cl^- , SO_4^{2-} , hardness, alkalinity and total dissolved solids at the Colorado State University Soil and Water Testing Laboratory.

The field data collection was spread out across an entire growing season, and we expected that water table depth measurements would not be comparable between sites measured early *versus* late in the summer. However, water tables were within 20 cm of the surface at all sites when visited, even during the driest period of late summer 2003. Because small differences in hydrology can affect fen functioning, it must be noted that we did not make fine-scale hydrological measurements and, therefore, draw no conclusion about the effect of site hydrology on the study fens.

Soils

In each fen we analysed soils in a hand-dug pit and measured peat thickness by pushing a steel probe vertically through the soil until rock or mineral sediment was contacted. It has been demonstrated that probing is an effective method for measuring peat thickness (Parsekian *et al.* 2012, Chimner *et al.* 2014). We collected one soil sample from 30–40 cm depth and determined percent organic matter content using loss on ignition (LOI) (Schulte & Hopkins 1996). For the purpose of classifying soils as organic we used the established estimate that approximately half of the soil organic matter is organic carbon (Ball 1964, Chimner *et al.* 2014). Although we did not directly measure clay content, all soils were hand-tested in the field and none formed ribbons that would

indicate clay content greater than 20 %. Therefore, we conservatively assumed that all soils contained 20 % clay. At this clay content soils require 14 % ($12 + [20 * 0.1]$) organic carbon, or 28 % organic matter as determined by LOI, to be considered organic soils according to the US Department of Agriculture definition of organic soils (Soil Survey Staff 1999). While this definition may suffice for soil taxonomic purposes, there are no scientific criteria or thresholds for organic content or organic horizon thickness that are known to influence the functioning of a site as a peatland (Driver 2010).

Vegetation

We sampled 1–7 homogenous relevés within each fen, recording a total of 290 relevés within the 79 fens. Relevés were 4–20 m² in area, depending upon the size of the largest plants, the smallest relevés being used for moss-dominated stands and the largest for those with shrubs and stunted trees (Mueller-Dombois & Ellenberg 1974). Within each relevé a complete list of the plant species present was made and the percent canopy cover of each species was visually estimated by the same experienced observer.

Nomenclature for vascular plants is consistent with the *Jepson Manual: Vascular Plants of California* (Baldwin *et al.* 2012), and for non-vascular plants (mosses) with the *Jepson California Moss eFlora* (Wilson 2015) and the *Flora of North America* (Flora of North America Editorial Committee 2015).

Data analysis

The Shannon diversity index (Hill 1973) was calculated for each vegetation relevé but, since diversity relies on relative abundances, we could not scale up the data to calculate fen-level diversity because the percent cover data are only relevant within each relevé. Instead, we calculated fen-level species richness, which is a simple count of the total number of species present within all of the relevés at a single fen. The logarithmic relationship between fen-level species richness and fen area was evaluated to determine the degree to which the species-area relationship contributes to observed species richness (Gleason 1922).

Statistical differences in water chemistry, peat thickness and species richness between fens with different categories of bedrock geology and landforms were determined using ANOVA with Tukey's HSD multiple comparison test (R Core Team 2014).

We evaluated the ability of 13 continuous environmental variables to predict peat thickness and species richness using multi-model selection. When evaluating model fit, all possible combinations of

explanatory environmental variables were ranked by AICc (Akaike's Information Criterion, corrected for small sample size) using the *glmulti* and *AICmodavg* packages in R (R Core Team 2014). All models within two points of the minimum AICc model were exhaustively cross-validated (using the leave-one-out technique) to determine their predictive power using mean-squared-error (*cv.glm* routine in the "boot" R package).

Variables were then systematically removed and models cross-validated to evaluate whether simpler models would provide equivalent predictive error. For estimating peat thickness or species richness on the basis of the measured environmental parameters, the model with the smallest number of parameters that provided equivalent predictive error to the minimum AICc model was identified as the model of choice. This was because the datasets for some fens were not complete and, under these circumstances, inclusion of more parameters in the models could influence the effective sample size by excluding the fens with missing data. Therefore, we experimented with removing parameters from the minimum AICc model to maximise sample size while including the most important predictive variables.

We used Detrended Correspondence Analysis (DCA), which is an indirect ordination technique, to identify the overall structure of the floristic gradients within the 290-relevé vegetation data set. The structure in the vegetation data was analysed for correlations with environmental variables in a canonical correspondence analysis (CCA). Because the environmental data were collected at the fen level, each relevé within a fen was associated with the same set of environmental variables. To determine whether the observed CCA correlations between species and environmental data could have arisen by chance, we conducted Monte Carlo simulations. The environmental data were randomly reassigned to fens, the CCA was re-run 100 times, and correlations and eigenvalues were calculated for each randomised run. The observed values were compared with the Monte Carlo output to determine the probability that the observed correlation between the environmental matrix and the vegetation data could have arisen by chance, reported as a p-value. The program PC-Ord, version 4.37, was used to perform all ordination analyses (McCune & Mefford 1999).

The 13 continuous environmental variables used to model peat thickness were: altitude, fen slope, fen aspect azimuth (sine transformed: $\sin(\text{azm.} + 90) + 1$), soil organic matter, fen area, catchment area, average annual precipitation, soil-water pH, soil-water electrical conductivity (EC), calcium concentration (Ca), magnesium concentration (Mg), north latitude and species richness.

These same 13 variables, with species richness substituted by peat thickness, were used to model species richness and to generate the CCA ordination. In addition, the categorical variables of catchment bedrock geology (five categories) and geomorphic landform (four categories) were converted to binary variables for use in the CCA. The five binary geology variables created were: granodiorite, metamorphic, volcanic, serpentine and carbonate. The four binary landform variables created were: (bedrock) contact, slope, (spring) mound and basin (see Results). Each fen was assigned to one geological type and one landform type, and values of unity were assigned to the corresponding binary variables (e.g. for a sloping fen in a granodiorite catchment: slope = 1, all other landform variables = 0; granodiorite = 1, all other geology variables = 0).

RESULTS

Site characteristics

Fens were found throughout the Sierra Nevada, the southern Cascade Range and southern Klamath Mountains (Figure 1). The areas of the 79 fens we visited ranged from 45 m² to 200,000 m² (median 1,713 m²) and their altitudes ranged from 1,207 m to 3,233 m a.s.l. (median 2,094 m). Fens occurred at lower altitudes in the Cascade Range, Klamath Mountains and northern Sierra Nevada than in the southern Sierra Nevada, which is the highest-altitude section of the range with relatively low annual precipitation (see Appendix).

These fens had formed in four major geomorphic settings, namely: at geological bedrock contacts, on slopes, as spring mounds, and in basins (Figure 2). Multiple landform types can occur within a single fen site. For example, a sloping fen may be adjacent to and connected with a basin fen, and spring mounds can occur at the heads of sloping fens or within larger basin fens. When multiple landform types occurred within a single fen complex, we observed which mechanism was most important for maintaining the hydrological regime of the fen and classified it accordingly.

At bedrock contacts, more permeable rock (an aquifer) overlies less permeable rock, forcing water out of the ground along the contact zone. This often occurs where one lava flow lies on top of another, and the lower flow's upper surface has been sealed by contact with the later flow. Snowmelt water moves laterally on the impermeable surface created by the discontinuity and discharges on hillslopes where the contact is exposed. These spring complexes may be large and produce perennial flows of water, forming fens on steep slopes that nonetheless have thick peat

bodies and well-developed fen vegetation. Eleven (14 %) of the 79 studied fens were classified as bedrock contact fens.

Fifty (63 %) of the 79 study fens had formed on hillslopes where groundwater discharges to the surface from glacial moraines, talus, alluvium and hillslope-exposed bedrock fractures. Slopes range from gentle to steep (Figure 3), and although small pools may occur, large areas of open water are never present. Sloping fens require constant inflow of groundwater to maintain soil saturation because downhill drainage is relatively rapid.

Spring mounds form at localised points of groundwater discharge that can often support only small fens. Many spring mound fens are only tens of metres in diameter, but they are morphologically and ecologically distinct. Spring mound fens may occur at locations with strong upward groundwater discharge within a sloping fen complex. Five (6 %) of the 79 fens were characterised as spring mounds with upwelling groundwater.

The remaining 13 (16 %) of the 79 fens were in basins. Basin fens probably originated as lakes or

ponds that infilled with partially decomposed plant remains. They are typically flat and may enclose ponds with floating mats of peat-forming vegetation that rise and fall with the water level, thus maintaining contact between the peat and water surfaces. This fen type is widespread and includes the largest fens in the Sierra Nevada region. *Sphagnum teres* and *Sphagnum subsecundum* are common species, along with the vascular plants *Carex limosa*, *Menyanthes trifoliata*, *Carex lasiocarpa* and *Dulichium arundinaceum*.

Water chemistry

The 79 study fens spanned a broad range of water chemistry. The multi-year, multi-season, volume-adjusted field-measured pH of precipitation across a series of measurement locations spanning the north-south range of the Sierra Nevada is 5.26 (National Atmospheric Deposition Program 2014). Only the five most acidic of the 79 study fens had pH values below 5.26, indicating the predominance of groundwater processes that raise the pH of rainwater as it moves through an aquifer. Using the well-

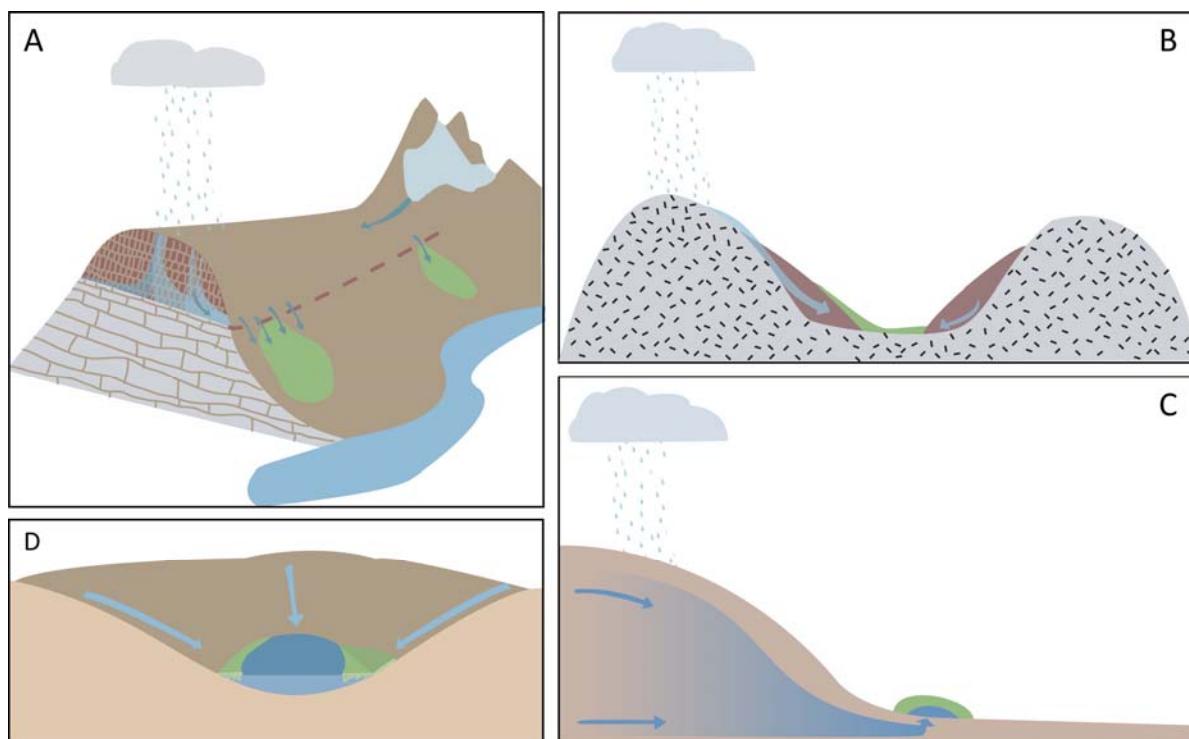


Figure 2. The four major landform types identified amongst the Sierra Nevada fens. A = bedrock contact (fed by seepage from the contact zone between an aquifer and an underlying layer of less permeable rock), B = slope, C = spring mound (formed at a groundwater discharge site), and D = basin. The arrows indicate directions of groundwater and/or surface water flow.



Figure 3. Four fens in the study region:

(top left) gently sloping fen dominated by the spike-sedge *Eleocharis quinqueflora*;

(top right) fen with high cover of *Pinus contorta* and shrubs;



(bottom left) steeply sloping fen with the pitcher plant *Darlingtonia californica* in the foreground;

(bottom right) Convict Creek basin, which is the only region with limestone/marble in the Sierra Nevada, showing fen dominated by the sedge *Kobresia myosuroides*.

established poor-rich gradient terminology (Sjörs 1950, Cooper & Andrus 1994, Lemly & Cooper 2011), the fens in the study area ranged from transitional (intermediate between poor and rich) to extremely rich, based on their pH and cation concentrations (Figure 4). Of the 27 transitional fens, four had metamorphic bedrock, one had volcanic bedrock, and 22 were in catchments dominated by granodiorite. The lowest pH value (4.3) was found at a floating mat in Willow Lake, within a volcanic bedrock catchment. Low concentrations of dissolved ions in the Willow Lake sample, along with high *Sphagnum* moss cover, suggest that the acidity is generated by the moss rather than by geochemical weathering by-products. The highest pH values (7.5 and 8.0) were found at two fens in the Convict Creek basin (Figure 3), where carbonate rocks (primarily marble, and some calcareous hornfels) are exposed (Major & Bamberg 1963). High concentrations of calcium and carbonate in water at the Convict Creek sites confirms that the high pH is a result of geochemical weathering of the marble and hornfels

bedrock.

Bedrock lithology strongly influenced fen water chemistry. Fens on granodiorite and undifferentiated metamorphic bedrock (metamorphics other than serpentine and carbonate marble) had significantly lower concentrations of calcium, lower EC, and were more acidic than fens on other rock types (Figure 5). The two carbonate fens had significantly higher EC and levels of calcium, and were more basic than other fens. The one serpentine fen we visited contained groundwater with markedly elevated levels of magnesium.

Peat

The peat layer in sampled fens averaged 83 cm thick, ranging from as thin as 15 cm to a maximum of 253 cm. The fens with the largest catchment areas typically contained the thickest peat, but this relationship included considerable scatter in larger catchments, where peat ranged from thick to thin (Figure 6A). The positive linear correlation between peat thickness and catchment area was statistically

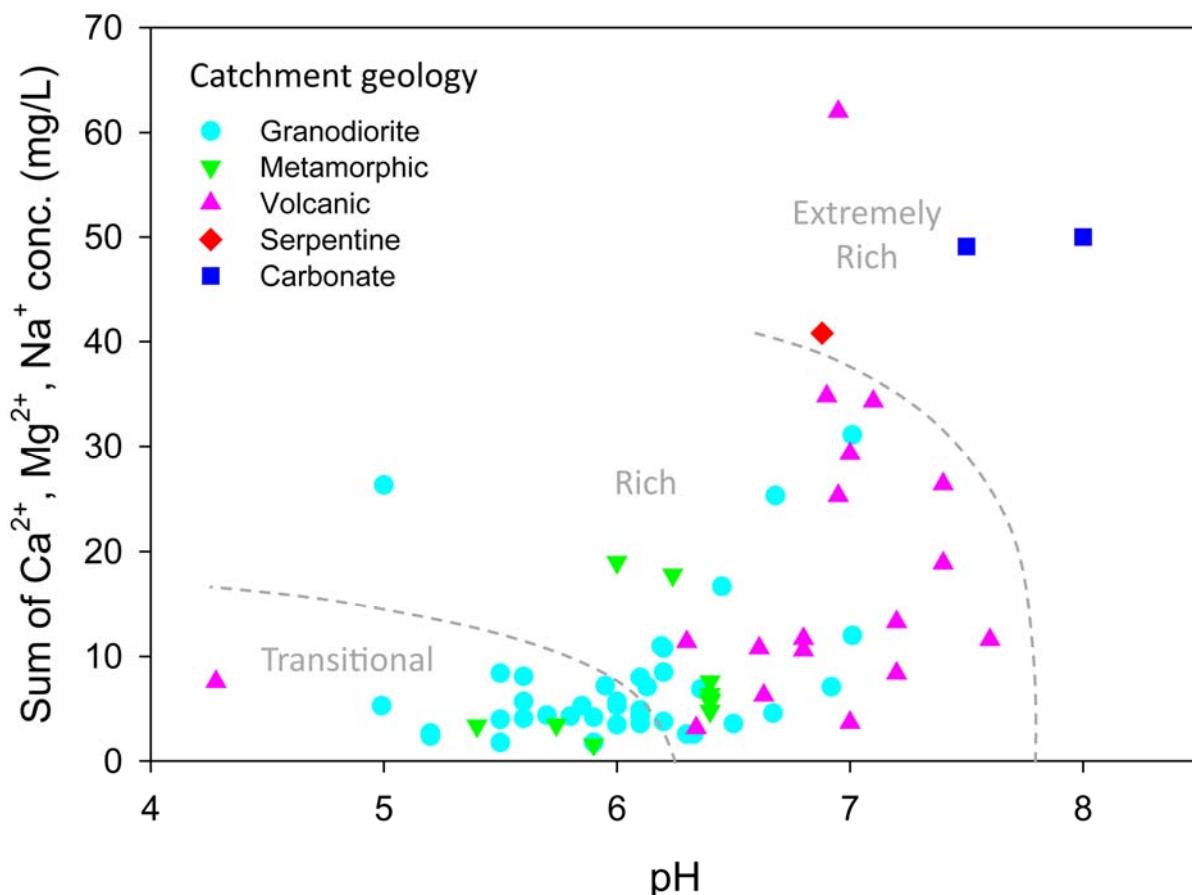


Figure 4. Classification of fens by pH and cation concentration. The bedrock geology of each fen's catchment is indicated by symbol shape and colour.

significant ($p = 0.0163$) but explained only 7 % of the variation in the data ($R^2_{adj} = 0.06652$). The regression was less significant ($p = 0.0818$) when catchment area was log transformed and compared to peat thickness, but the log-transformation allows for better visual assessment of the pattern of increasing maximum peat thickness in larger catchments (see dashed line in Figure 6A).

Peat thickness was negatively correlated with fen slope; fens on steeper slopes generally had thinner peat layers (Figure 6B). Although this was a statistically significant regression ($P = 0.0134$), fen slope only explained about 7 % of the variation in peat thickness ($R^2_{adj} = 0.0711$). Peat thickness varied widely in gently sloping fens, whereas its range was restricted to relatively low values in more steeply sloping fens. As with the relationship between peat

thickness and catchment area, an increase in slope reduced the maximum peat thickness attained (see dashed line in Figure 6B).

The organic matter content of the sampled peat averaged 57 % and was above the 28 % organic matter threshold for organic soils (see Methods) in 91 % of the samples. Twenty-two percent of the samples contained more than 80 % organic matter. The fens with the thickest peat tended to have the highest organic matter content ($P = 0.0015$), and this correlation accounted for 14 % ($R^2_{adj} = 0.1381$) of the variation in peat organic matter content (Figure 6C).

The evaluation of 13 environmental variables in models of peat thickness produced a minimum AICc model involving six environmental variables, namely percent soil organic matter (OM), catchment area, fen area, aspect (sine transformed), pH and EC. Cross

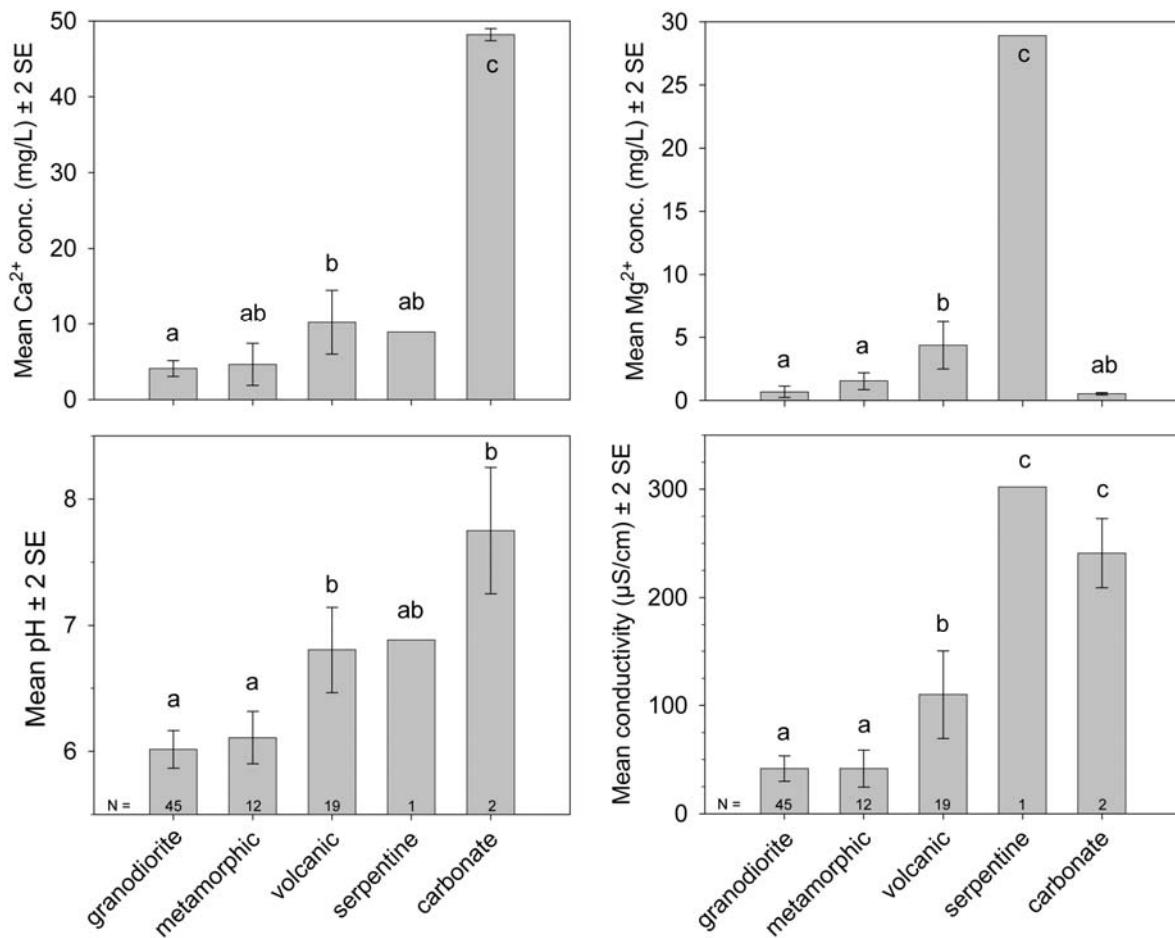


Figure 5. The pH, electrical conductivity, calcium and magnesium concentrations of groundwater in fen catchments dominated by granodiorite, metamorphic, volcanic, serpentine and carbonate rocks. N = number of fens in each category. Letters indicate significant differences determined by ANOVA with Tukey's HSD multiple comparison test.

validation of the six-parameter minimum AICc model indicated a prediction error of ± 49.8 cm of peat. By evaluating nearly-equivalent models and testing variable-removal effects on prediction error, we arrived at a three-parameter model using OM (%), catchment area (ha) and fen area (ha) which had a

peat-thickness prediction error of ± 44.9 cm. The peat-thickness prediction interval for this three-parameter model was 90 cm, and slightly more than one-third of the total observed peat thickness range of 238 cm. The three-parameter model, with $R^2_{adj} = 0.2991$, is:

$$(peat thickness, cm) = 0.8523*(OM) + 0.1190*(\text{catchment area}) + 5.3076*(\text{fen area}) + 21.6950 \quad [1]$$

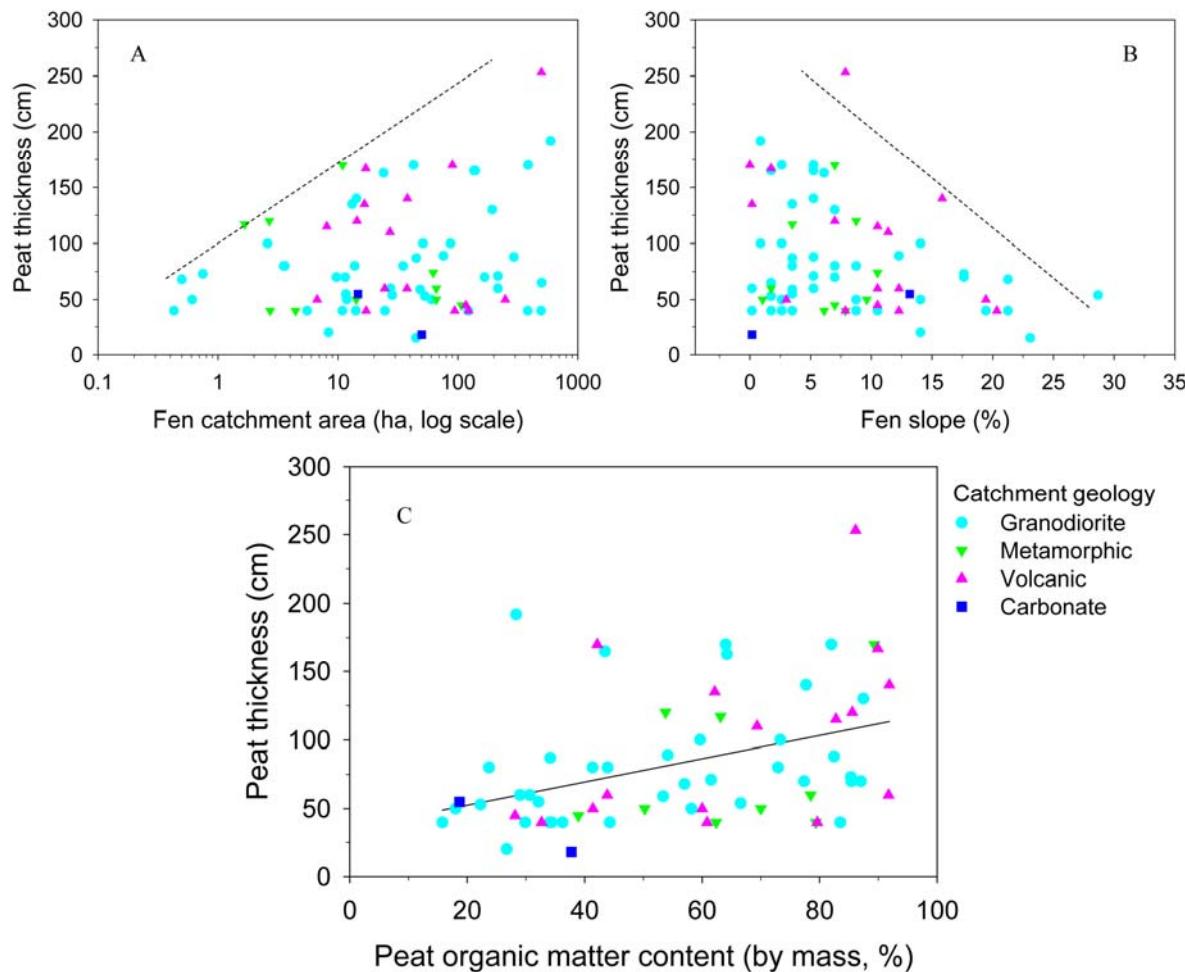


Figure 6. The relationships of peat thickness with catchment area, fen slope and soil organic content. Panel A shows peat thickness as a function of fen catchment area (note log scale). Catchment area has been log transformed to highlight (with a visually fitted dashed line) the increase in maximum peat thickness as catchment area increases. Panel B shows peat thickness *versus* slope. The thickest peat bodies occur on the gentlest slopes, and few peat bodies exceed 1 m thickness on slopes steeper than 15 %. A visually-fitted line (dashed) shows maximum peat thickness decreasing as slope increases. Panel C illustrates that thicker peat bodies have higher organic matter content. The linear regression line is shown ($P = 0.0015$) and explains 14 % of the variation in the data ($y = 0.8461x + 36.1937$, $R^2_{adj} = 0.1381$). The bedrock geology of each fen's catchment is indicated by symbol shape and colour. The single serpentine site is not shown because it is missing peat thickness data.

Vegetation

In total, 170 vascular plant and bryophyte species were identified in the 290 relevés recorded at the 79 study fens. The relevé-level Shannon diversity index ranged from zero (one species) to 2.443 (20 species) across 290 relevés. Relevé-level richness ranged from one to 23 species. Scaled up to the fen level, species richness ranged from two to 42 species. The relationship between \log_{10} (fen area) and species richness had a p-value of 0.0542 and fen area explained about 4 % ($R^2_{adj} = 0.03839$) of the variation in species richness. Altitude alone explained approximately 29 % ($R^2_{adj} = 0.2894$) of the variation in species richness between fens (Figure 7).

The single-parameter altitude model had an AICc of 501 and a cross-validated prediction error of ± 6.47 species. Therefore, using altitude alone, the

prediction window for fen species richness is 12.94 species wide, which is 32 % of the entire 40-species range in richness. This model has an $R^2_{adj} = 0.2894$ and is able to predict which one-third of the species richness (SR) range a given fen will fall into, based on altitude only. Multi-parameter model selection using the full set of 13 environmental variables arrived at an optimal four-parameter model with an AICc of 407. The four variables selected were altitude (m), fen slope (%), peat thickness (cm) and OM (%). This four-parameter model has a cross-validated prediction error of ± 5.78 species, yielding a prediction window 11.56 species wide. The window spans 29 % of the entire 40-species range in richness, a 3 % improvement over the altitude-only model. The four-parameter model has $R^2_{adj} = 0.5121$, and is as follows:

$$SR = -0.0072 * (\text{altitude}) + 0.3488 * (\text{fen slope}) + 0.1041 * (\text{OM}) + 0.0399 * (\text{peat thickness}) + 22.7314 \quad [2]$$

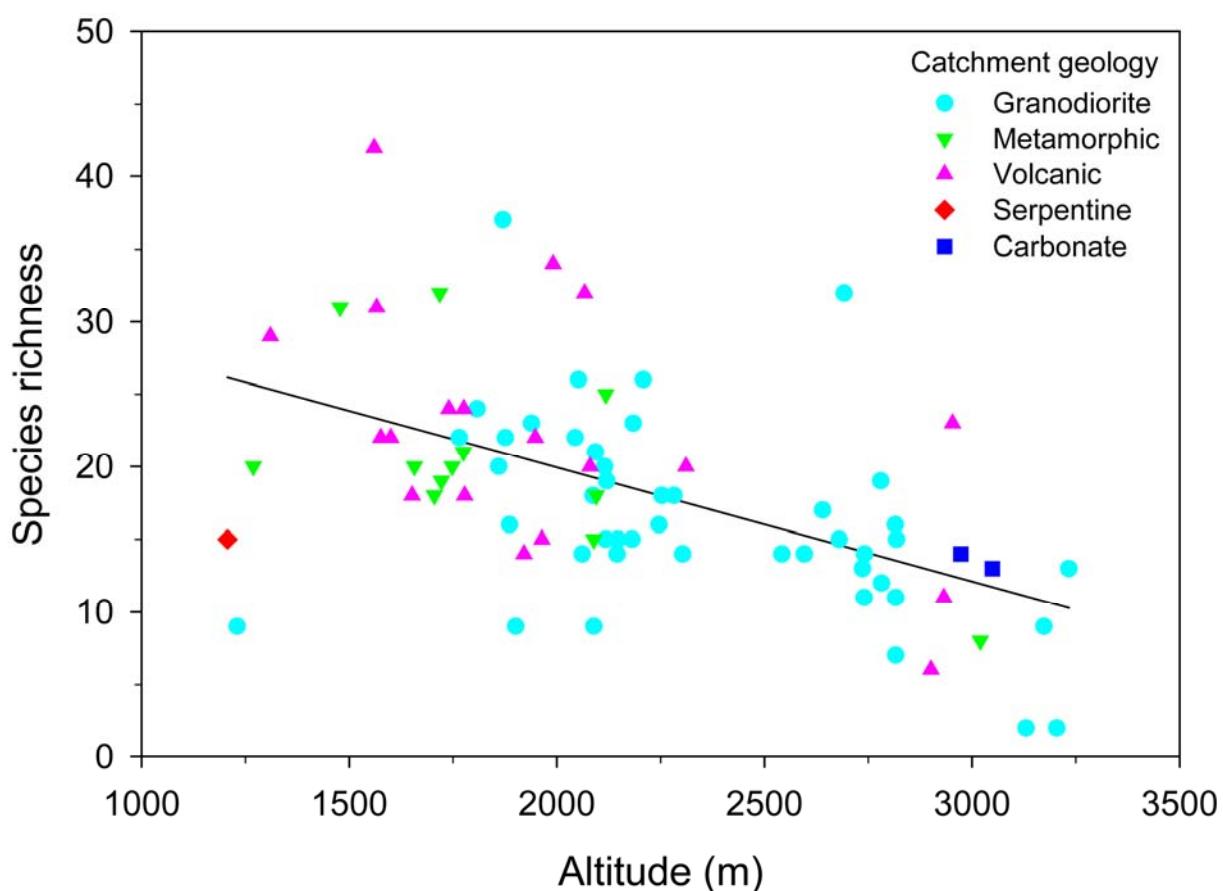


Figure 7. The relationship between species richness and altitude. Each fen's catchment bedrock geology is indicated by symbol shape and colour. Fen plant species richness decreases with altitude ($p << 0.0001$). The equation of the plotted regression line is $y = -0.0078x + 35.5917$, $R^2_{adj} = 0.2894$.

Indirect ordination using DCA (Figure 8) illustrates the complex floristic gradients in the vegetation dataset. The two primary ordination axes shown are scaled in standard deviation (SD) units. A 4-SD distance between relevés along either axis represents almost no overlap in species composition (McCune & Mefford 1999). The DCA of all 290 relevés (inset, Figure 8) is roughly separated into three distinct vegetation groups. Relevés from two volcanic bedrock fens in the Lassen National Forest (Willow Lake and Domingo Lake) occur on the right side of Axis 1, about 3–4 SD units from a vertically-oriented mass containing most of the relevés. These are basin fens with floating mats dominated by *Carex lasiocarpa*, *Carex vesicaria*, *Dulichium arundinaceum*, *Menyanthes trifoliata* and *Utricularia macrorhiza*. The vegetation from the relevés in two extremely rich carbonate bedrock fens in the Inyo National Forest (Hanging Fen and Mildred Lake) is made up of *Trichophorum pumilum*, *Kobresia myosuroides*, *Thalictrum alpinum* and others. These species occur about 0.5 SD units left-of-centre of the central mass of relevés. In other words, the primary (Axis 1, Figure 8 inset) pattern in the vegetation data is driven by the distinct flora of the outlier fens, with the two volcanic sites to the right and the two carbonate sites to the left.

Removing the 17 outlier relevés that represent the two carbonate and two volcanic fens allowed an analysis of the vegetation patterns in the absence of the sites with unique vegetation that dominate the DCA. The 273-relevé DCA with outliers removed (Figure 8, main panel) shows a fairly continuous vegetation gradient within the main group of relevés. The environmental variable that correlated most strongly with the purely vegetation-derived patterns in the DCA was pH, with an R^2 of 0.2079 with respect to Axis 1. All other environmental variables had $R^2 < 0.1110$. At the extreme right of Axis 1 are fens dominated by trees, shrubs and *Sphagnum* (*Pinus contorta*, *Rhododendron columbianum*, *Lonicera caerulea*, *Kalmia polifolia*, *Vaccinium uliginosum*, *Rhynchospora alba*, *Sphagnum teres* and *Sphagnum subsecundum*) (Figure 3). At the opposite (left) end of Axis 1, correlated with basic pH conditions, are relevés dominated by several species of *Carex*, *Scirpus microcarpus* and *Calamagrostis canadensis* with the brown mosses *Drepanocladus sordidus*, *Drepanocladus longifolius* and *Meesia triquetra*.

The explicit inclusion of the environmental data into the ordination of vegetation data at the fen level, in a CCA, highlights the unique flora at the carbonate sites. In the CCA of all 79 fens, by far the strongest gradient along Axis 1 is membership of the carbonate bedrock class, followed by calcium concentration. The segregation of the carbonate fens from the rest of

the sites by 8 SD units (Figure 9, inset) is the main pattern in the combined vegetation-environment CCA ordination. To further explore the environmental gradients within the main group of data, the two carbonate fens were removed because their distinct flora, structured by a unique rock type and water with very high calcium content, overshadowed the influence of other variables on the rest of the data.

Leaving out the two carbonate fens and running a CCA ordination on the remaining 77 sites produced a much more even spread of data in the ordination space (Figure 9, main panel). The sites that had been the farthest outliers in the DCA (vegetation data only), Willow Lake and Domingo Lake with unique occurrences of *Dulichium arundinaceum* and *Scheuchzeria palustris*, plot in the lower middle of the ordination space but are contiguous with the rest of the data. Four environmental variables were correlated ($R^2 > 0.24$) with the structure in the 77-fen ordination, namely pH, altitude, fen slope and membership of the volcanic bedrock class. The orientations of these correlations are indicated by the red arrows on the CCA (Figure 9).

The main pattern in the vegetation data, along Axis 1, is a separation of species by the dominant rock type in the catchment and the pH of the fen water. Species and fens associated with volcanic bedrock and higher pH are to the left of the ordination, granodiorite and mid-pH species and fens are central, and metamorphic and acidic plants and sites lie to the right. Although the lone serpentine fen is classified as extremely rich due to its high pH and cation concentration (Figure 4), its vegetation is most similar to that of acidic metamorphic sites with species like *Rhododendron columbianum*, *Narthecium californicum*, *Darlingtonia californica* and *Carex echinata*. The *Sphagnum* moss species plot in the middle-right, in the moderately acidic region dominated by granodiorite sites.

A secondary pattern in the CCA, along Axis 2, is the separation of species on steeply sloping sites from those in flat valleys and basins. The major outlier species in the vegetation-only DCA (Figure 8, inset), which are unique to the Willow Lake and Domingo Lake fens, occur in basin fens with no slope and plot at the bottom of the ordination. None of the measured environmental variables show a major difference between the Willow and Domingo fens and the rest of the dataset; they fit in with the broader trends of the CCA gradients, albeit at the edge. This is in sharp contrast to the carbonate sites, whose distinct vegetation is correlated with unique bedrock geology and extreme water chemistry values. A significant altitude gradient is correlated with both axes, with high-altitude sites plotting in the upper left and low-

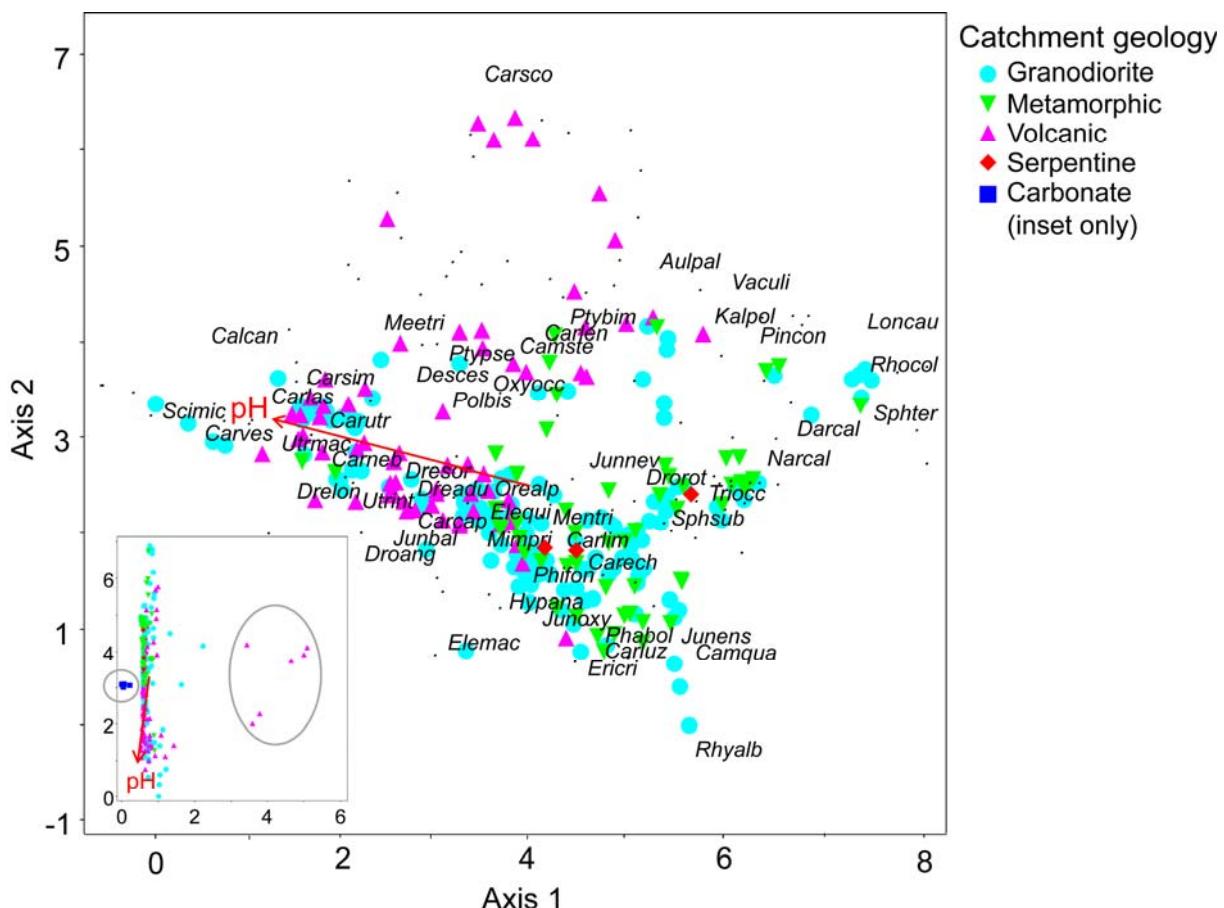


Figure 8. Detrended correspondence analysis (DCA) of the vegetation at 273 fen relevés. The DCA of all 290 relevés is shown inset, and indicates that the relevés from the two carbonate fens (blue squares, circled on left) and two volcanic fens (pink triangles, circled on right) are outliers that dominate the structure of the full dataset. Species names show relative species positions (unlabelled species appear as small black dots); coloured shapes show relative relevé positions, coded by catchment geology. Axes are scaled in standard deviation (SD) units. Complete species turnover occurs at a distance of ~4 SD. Axis 1 is a vegetation gradient that correlates with pH (overlaid red arrow indicates direction of increasing pH, $R^2 = 0.21$). Selected species abbreviations are: Aulpal = *Aulacomnium palustre*; Calcan = *Calamagrostis canadensis*; Camqua = *Camassia quamash*; Camste = *Campylium stellatum*; Carcap = *Carex capitata*; Carech = *Carex echinata*; Carlas = *Carex lasiocarpa*; Carlen = *Carex lenticularis*; Carlim = *Carex limosa*; Carluz = *Carex luzulina*; Carneb = *Carex nebrascensis*; Carpel = *Carex pellita*; Carsco = *Carex scopulorum*; Carsim = *Carex simulata*; Carutr = *Carex utriculata*; Carves = *Carex vesicaria*; Darcal = *Darlingtonia californica*; Desces = *Deschampsia cespitosa*; Dreadu = *Drepanocladus aduncus*; Drelon = *Drepanocladus longifolius*; Dresor = *Drepanocladus sordidus*; Droang = *Drosera anglica*; Drorot = *Drosera rotundifolia*; Elemac = *Eleocharis macrostachya*; Elequi = *Eleocharis quinqueflora*; Ericri = *Eriophorum criniger*; Hypana = *Hypericum anagalloides*; Junbal = *Juncus balticus*; Junens = *Juncus ensifolius*; Junnev = *Juncus nevadensis*; Junoxy = *Juncus oxymeris*; Kalpol = *Kalmia polifolia*; Loncau = *Lonicera cauriana*; Meetri = *Meesia triquetra*; Menti = *Menyanthes trifoliata*; Mimpri = *Mimulus primuloides*; Narcal = *Narthecium californicum*; Orealp = *Oreostemma alpigenum*; Oxyocc = *Oxypolis occidentalis*; Phabol = *Phalacroseris bolanderi*; Phifon = *Philonotis fontana*; Pincon = *Pinus contorta*; Polbis = *Polygonum bistortoides*; Ptybim = *Ptychosotomum bimum*; Ptypse = *Ptychosotomum pseudotriquetra*; Rhocol = *Rhododendron columbianum*; Rhyalb = *Rhynchospora alba*; Scimic = *Scirpus microcarpus*; Sphsub = *Sphagnum subsecundum*; Sphter = *Sphagnum teres*; Triocc = *Triantha occidentalis* subsp. *occidentalis*; Utrint = *Utricularia intermedia*; Utrmac = *Utricularia macrorhiza*; Vaculi = *Vaccinium uliginosum*.

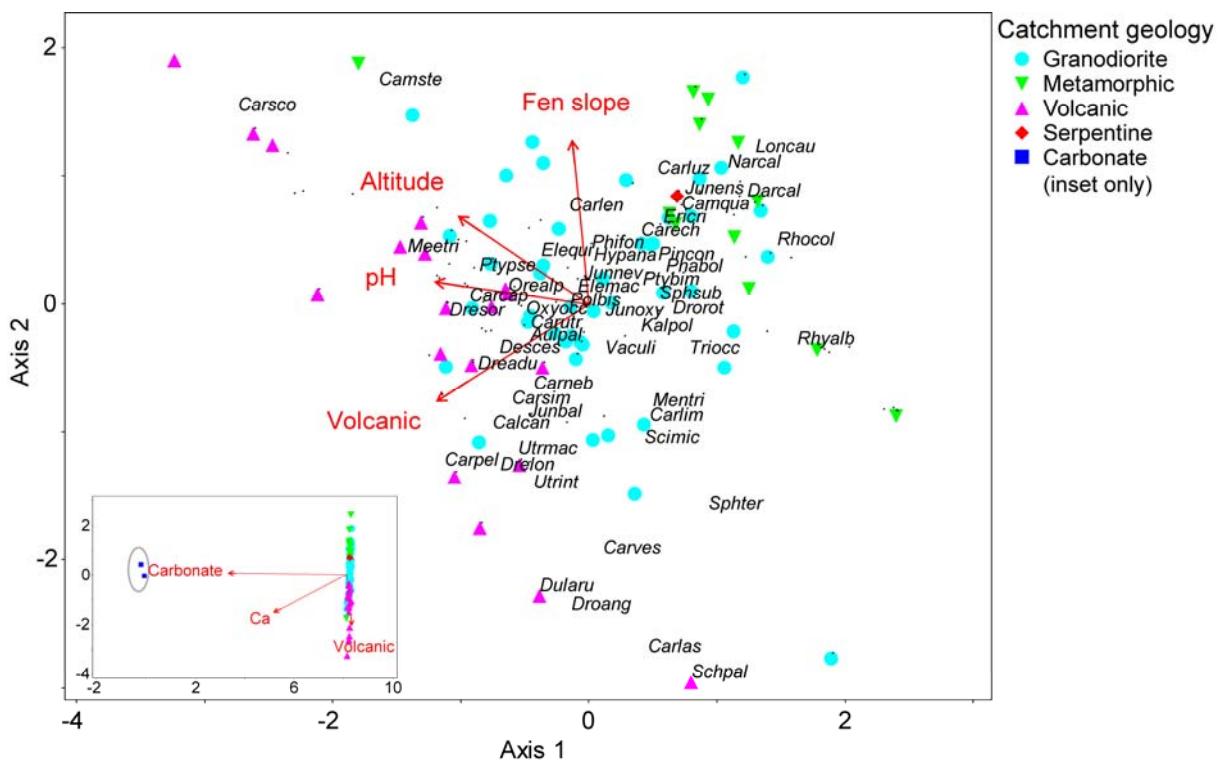


Figure 9. Canonical correspondence analysis (CCA) of the vegetation and environmental variables at 77 study fens, excluding the two carbonate fens. The CCA of all 79 fens is shown inset, indicating that the carbonate fens (blue squares, circled on left) are extreme outliers. Catchment geology is denoted by point shape and colour. Significant environmental factors ($R^2 > 0.24$) are shown as red vectors, the value of the factor increasing in the direction indicated by the arrow. Unlabelled species appear as small black dots in the ordination, and selected species abbreviations are: Aulpal = *Aulacomnium palustre*; Calcan = *Calamagrostis canadensis*; Camqua = *Camassia quamash*; Camste = *Campylium stellatum*; Carcap = *Carex capitata*; Carech = *Carex echinata*; Carlas = *Carex lasiocarpa*; Carlen = *Carex lenticularis*; Carlim = *Carex limosa*; Carluz = *Carex luzulina*; Carneb = *Carex nebrascensis*; Carpel = *Carex pellita*; Carsco = *Carex scopulorum*; Carsim = *Carex simulata*; Carutr = *Carex utriculata*; Carves = *Carex vesicaria*; Darcal = *Darlingtonia californica*; Desces = *Deschampsia cespitosa*; Dreadu = *Drepanocladus aduncus*; Drelon = *Drepanocladus longifolius*; Dresor = *Drepanocladus sordidus*; Droang = *Drosera anglica*; Drorot = *Drosera rotundifolia*; Dularu = *Dulichium arundinaceum*; Elemac = *Eleocharis macrostachya*; Elequi = *Eleocharis quinqueflora*; Ericri = *Eriophorum criniger*; Hypana = *Hypericum anagalloides*; Junbal = *Juncus balticus*; Junens = *Juncus ensifolius*; Junnev = *Juncus nevadensis*; Junoxy = *Juncus oxymeris*; Kalpol = *Kalmia polifolia*; Kobmyo = *Kobresia myosuroides*; Loncau = *Lonicera cauriana*; Meetri = *Meesia triquetra*; Mentre = *Menyanthes trifoliata*; Mimpri = *Mimulus primuloides*; Narcal = *Narthecium californicum*; Orealp = *Oreostemma alpigenum*; Oxyocc = *Oxypolis occidentalis*; Phabol = *Phalacroseris bolanderi*; Phifon = *Philonotis fontana*; Pincon = *Pinus contorta*; Polbis = *Polygonum bistortoides*; Ptybim = *Ptychosotomum bimum*; Ptypse = *Ptychosotomum pseudotriquetra*; Rhocol = *Rhododendron columbianum*; Rhyalb = *Rhynchospora alba*; Schpal = *Scheuchzeria palustris*; Scimic = *Scirpus microcarpus*; Sphsub = *Sphagnum subsecundum*; Sphter = *Sphagnum teres*; Triocc = *Triantha occidentalis* subsp. *occidentalis*; Utrint = *Utricularia intermedia*; Utrmac = *Utricularia macrorhiza*; Vaculi = *Vaccinium uliginosum*.

altitude sites in the lower right. The total inertia (variance) in the CCA is 10.25, and the Axis 1 eigenvalue (the amount of variance explained) is 0.542, or 5.3 % of the total variance. The Axis 2 eigenvalue is 0.454, explaining a further 3.8 % of the variance, making a combined two-axis total of 9.7 %. The Monte Carlo test showed that the correlation between the environmental matrix and the vegetation data is significant ($P = 0.03$).

DISCUSSION

The broad patterns of physical and biological processes that control fen distribution and diversity in the Sierra Nevada are relevant to the study of mountain peatlands throughout the world. The higher annual precipitation in the northern portion of the study area allows the development of groundwater flow systems that are sufficient to support fens at lower altitudes. By contrast, in the drier southern part of the Sierra Nevada, fens can form only under the cooler conditions at high altitudes. Because the northern Sierra Nevada contains little high-altitude landscape, there are few opportunities for fens to occupy this zone. In the southern Sierra Nevada the most likely reason for the lack of low-altitude fens is a combination of low precipitation and warm temperatures creating high evapotranspiration demand. However, fens occur in the semi-arid mountains of northern Chile, where annual precipitation rarely exceeds 25 cm (Squeo *et al.* 2006), further illustrating the overwhelming importance of groundwater flow paths for the maintenance of saturated soil conditions and peat formation.

In addition to providing insights about the locations and landscapes where mountains fens form, the relationships between peat thickness and catchment area, fen slope and organic matter content have implications for the vulnerability of mountain fens to future climate changes, including severe droughts. Most fens in small catchments have thin peat, perhaps due to a lower volume of local groundwater aquifers that may become depleted during periodic droughts, limiting peat accumulation. The variable that is most strongly correlated with peat thickness is organic matter content. While it is not suggested that the relationship is causative in either direction, it stands to reason that both thickness and organic content of peat would be similarly influenced by other processes such as mineral sediment input, decomposition rates and primary production rates. Wildfires, road construction and maintenance, and logging all occur frequently in National Forest

mountain landscapes and have the potential to increase sedimentation to fens and impact peatland ecological processes.

Because peatlands are formed and maintained through primary production of organic matter by wetland plants, understanding the environmental drivers of plant diversity and distribution is critical to the study of peatland function. Altitude exerts strong control over fen-level species richness and distribution. The most species-rich fens occur at lower altitudes. This altitude effect is probably due to a longer snow-free growing season and warmer temperatures at the lower sites. However, the lower-altitude sites also tend to occur in the northern Sierras where more precipitation falls, so it is also possible that the trend in species richness could be related to a hydrological gradient that we did not measure directly within the fens, or a regional species pool effect.

The reduction of species richness with increasing altitude is a well-known ecological relationship that applies to many taxa and mountain ranges throughout the world (Rahbek 1995, Grytnes 2003, Bruun *et al.* 2006). Mountain peatlands provide an interesting venue for exploring this relationship because many of the key ecosystem processes (e.g. hydrology, peat formation and water chemistry) that are thought to limit plant growth and survival in fens are not necessarily affected by changes in altitude. This study was not designed to address this question explicitly, but the pattern of decreasing richness with increasing altitude is significant nonetheless. Furthermore, the pattern of richness is not a function of larger fens having more species due to a species-area effect. Targeted investigations into the specific drivers of the richness-altitude pattern within mountain peatlands would help tease apart the various contributing environmental factors.

Water chemistry, particularly calcium concentration and pH, created the largest distinctions in fen species composition. The two carbonate fens, which had many unique species, high calcium concentrations and high pH, were the main drivers of this primary structure in our dataset. After removing the outlier fens on carbonate bedrock, water pH was one of the strongest drivers of plant distribution in our CCA analyses. This is well known from previous studies that have shown pH and the poor-rich gradient to be primary factors in determining fen vegetation (Sjörs 1950, Vitt *et al.* 1995, Chapin *et al.* 2004).

The fens of the marble regions of the Inyo National Forest are unique on the west coast of the USA from a floristic, ecological and biogeographical perspective (Major & Bamberg 1963). The dominance of calciphiles including *Kobresia*

myosuroides, *Trichophorum pumilum* and *Carex scirpoidea* is striking, and other extremely rich fens in the region should be more carefully investigated, as they have been in the Rocky Mountains and Canada (Vitt & Chee 1990, Cooper 1996). An example of this fen type is shown in Figure 3 (bottom right). In addition, the presence of communities similar to those in maritime coastal areas and dominated by *Narthecium californicum* should also be more thoroughly investigated. There are relatively few reports of fens in North America dominated by species other than mosses or Cyperaceae, and peat formed by a species belonging to the Liliaceae is unusual. A community dominated by *Narthecium ossifragum* and *Sphagnum tenellum* occurs in Britain, in what are characterised as oligotrophic flushes, or springs, in highly acidic rocks (McVean & Ratcliffe 1962). However, the lily-dominated California fens are not highly acidic.

The highly distinct vegetation and acidic conditions approaching poor-fen status at the Willow and Domingo Lake sites is unique in the study region and deserves further investigation. In addition, more fens on serpentine bedrock should be examined. It is well known that the high levels of magnesium and other toxic elements in serpentine soils and bedrock have profound effects on associated ecosystems (Harrison & Rajakaruna 2011). It is interesting that the environmental variables measured in this study highlighted the distinct vegetation of the carbonate sites, while the unique flora of the highly acidic sites was not strongly differentiated in the CCA analysis. This is almost certainly due to the fact that the two carbonate sites were the only examples of sites associated with that bedrock type that we studied, whereas we sampled at a number of other volcanic-bedrock sites in addition to the uniquely-vegetated Willow and Domingo Lake sites.

The past and present influence of pack stock (horses) and livestock (primarily cattle and sheep) on fens is a critical scientific and resource management question. Many fens that are not presently used for pasture were heavily grazed in the 19th century and may not have recovered (Dull 1999), due to threshold-crossing impacts such as erosion gully formation and loss of soil organic matter. While there is considerable interest in current pack stock and livestock use, the effects of current use may be additive to historical grazing impacts. Continued research on past and present impacts to fens is clearly needed to inform restoration efforts, which should be a top priority for land managers and include the removal of hydrological modifications, road and stock impacts, and the re-introduction of local genotypes of fen-dominant species to sites from which they have now disappeared.

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Appendix

Table A1. Some key characteristics of the 79 study fens. Forest or Park: NP=National Park, all others are National Forests. Bedrock: c=carbonate, g=granodiorite, m=metamorphic, s=serpentine, v=volcanic. Landform: c=bedrock contact, m=spring mound, b=basin, s=slope. OM(%)=percent soil organic matter. EC=Electrical Conductivity. Sites are ordered by decreasing latitude to highlight the regional pattern of increasing altitude and decreasing precipitation from north to south.

Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (°C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
South Fork Mt. Fen	Shasta-Trinity	40.6044	-123.5490	2095	140	m	s	4.90	0.63	14	75	---	---	---	5.4	19	1.7	0.3	1.4	18
Cooper Swamp	Lassen	40.4925	-121.1533	1948	140	v	b	90.15	20.00	0	180	19.0	170	42	6.3	65	7.4	2.0	2.0	22
Drakesbad Mdw.	Lassen NP	40.4441	-121.4062	1740	198	v	c	248.81	1.40	3	135	---	50	60	7.6	87	4.5	2.4	4.7	24
Juniper	Lassen	40.4195	-121.2711	1921	165	v	s	116.78	0.04	11	200	14.0	45	28	7.2	50	4.3	1.9	2.2	14
Lee Camp Fen	Lassen NP	40.4152	-121.3243	1576	140	v	s	119.51	2.97	5	157	---	---	---	6.6	66	2.9	1.3	2.1	22
Willow Lake	Lassen	40.4022	-121.3568	1652	165	v	b	597.00	1.00	0	305	---	---	---	4.3	63	1.4	0.9	5.3	18
Domingo Lake	Lassen	40.3972	-121.3634	1778	163	v	b	16.65	0.28	0	113	20.0	135	62	6.3	19	1.7	0.4	1.1	18
Saddle Gulch Fen	Shasta-Trinity	40.3871	-123.0839	1207	114	s	s	20.74	0.06	19	110	---	---	---	6.9	302	8.9	28.9	3.0	15
Humbug	Lassen	40.1336	-121.2641	1310	152	v	m	17.07	2.00	2	90	---	167	90	7.1	182	20.8	8.2	5.3	29
Grizzly Creek 1	Lassen	40.1312	-121.3332	1776	165	v	s	94.18	0.36	12	150	---	40	61	7.2	73	7.8	3.3	2.2	24
Willow Creek 1	Lassen	40.1257	-121.4668	1566	191	v	s	37.73	0.12	11	260	---	60	92	7.4	108	10.2	5.5	3.2	31
Willow Creek 2	Lassen	40.1237	-121.4707	1560	191	v	s	14.42	0.60	7	164	17.0	120	86	7.4	151	17.7	5.0	3.7	42
Oxypolis	Lassen	---	---	---	---	v	s	---	---	---	---	---	---	---	---	---	---	---	---	22
Butterfly Valley	Plumas	40.0123	-120.9919	1478	104	m	s	62.33	0.16	11	150	---	74	---	5.7	22	1.0	1.8	0.7	31
Smith Lake	Plumas	39.9915	-121.0252	1269	114	m	s	107.03	0.12	7	200	---	45	39	6.0	97	13.6	3.5	1.9	20
Silver Lake	Plumas	39.9579	-121.1311	1765	185	g	b	293.75	0.35	5	80	---	88	82	---	36	7.0	0.3	2.8	22
Waters Bog	Plumas	39.8690	-121.0371	1722	165	m	s	9.45	0.81	16	20	---	---	---	---	58	6.1	0.7	3.6	19
Arkansas	Plumas	39.8263	-121.1765	1775	218	m	s	2.72	0.10	6	260	15.0	40	62	6.4	35	3.3	2.0	0.4	21
First Fen	Plumas	39.8221	-121.1740	1748	221	m	s	2.68	0.08	9	185	13.0	120	54	6.4	43	3.3	2.4	0.7	20
Terraced Fen	Plumas	39.8149	-121.1677	1705	216	m	b	14.21	0.40	10	210	17.0	50	50	6.4	35	3.1	2.4	0.4	18
China Gulch	Plumas	39.8083	-121.1709	1657	216	m	s	4.43	0.14	8	332	16.0	40	79	6.4	47	3.7	2.8	1.1	20
Greens Flat	Plumas	39.8033	-121.1908	1718	216	m	s	10.93	0.50	7	110	14.0	170	89	6.4	32	2.1	2.1	0.6	32
Severed Limb	Tahoe	39.4375	-120.2804	2080	140	v	s	6.71	0.09	19	112	14.0	50	41	7.0	171	16.1	7.7	5.5	20
Bottomless Fen	Tahoe	39.4327	-120.2802	2067	147	v	s	498.19	0.12	8	20	10.0	253	86	7.0	20	1.5	0.2	2.0	32

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Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (°C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
Kiln Fen	Tahoe	39.4311	-120.2587	1991	114	v	c	8.09	7.50	11	20	12.0	115	83	7.0	381	35.4	16.7	9.9	34
Mason Fen	Tahoe	39.4291	-120.2427	1964	114	v	c	122.69	0.24	8	48	14.0	40	80	7.0	141	15.4	5.6	4.3	15
Murphy Flat	Tahoe	39.4264	-120.7054	1876	191	g	s	11.50	0.14	7	196	12.0	70	85	5.0	26	2.3	0.3	2.7	22
Bowman View Fen	Tahoe	39.4203	-120.6964	1808	191	g	s	0.43	0.04	21	100	12.0	40	34	6.5	18	1.8	0.1	1.7	24
Hidden Fen	Tahoe	39.4189	-120.7074	1860	191	g	s	0.50	0.02	21	285	10.5	68	57	5.0	158	14.4	7.2	4.7	20
Pat Yore Flat	Tahoe	39.4137	-120.7052	1870	191	g	s	2.59	0.09	14	180	13.5	100	60	5.2	12	1.1	0.1	1.2	37
McKinstry 3	Eldorado	39.0451	-120.3342	2118	165	g	c	27.51	0.03	5	170	16.0	60	29	5.9	28	3.6	0.3	1.4	15
McKinstry 4	Eldorado	39.0400	-120.3500	2089	165	m	c	66.13	0.18	1	170	8.0	50	70	5.9	8	1.2	0.1	0.3	15
McKinstry 2	Eldorado	39.0396	-120.3462	2118	165	m	c	66.13	0.18	2	188	8.0	60	78	5.9	8	1.2	0.1	0.3	25
McKinstry Mdw.	Eldorado	39.0341	-120.3407	2089	165	g	c	215.83	0.16	0	220	13.0	60	31	5.9	28	2.1	0.3	1.8	9
Sun Rock	Eldorado	38.9199	-120.3344	1886	165	g	s	24.70	0.25	3	204	16.0	40	34	5.6	22	1.7	0.4	2.0	16
Buckbean Bog	Eldorado	38.9036	-120.2613	2282	165	g	b	51.18	0.40	1	340	16.0	100	73	5.6	39	2.2	0.9	2.6	18
Lost	Eldorado	38.9013	-120.2558	2303	165	g	s	3.61	0.01	9	28	---	80	44	5.6	43	4.7	0.5	2.9	14
Morattini Mdw.	Eldorado	38.8983	-120.2831	2115	165	g	s	14.29	0.32	5	210	---	140	78	5.7	23	2.7	0.2	1.5	20
Wrights Lake 3	Eldorado	38.8357	-120.2268	2147	165	g	s	0.61	0.01	9	230	12.0	50	---	5.5	42	5.0	0.4	3.0	15
Wrights Lake 2	Eldorado	38.8330	-120.2193	2184	165	g	s	14.11	0.11	11	340	---	40	36	5.5	11	1.0	0.1	0.7	23
Wrights Lake 1	Eldorado	38.8323	-120.2204	2208	165	g	s	9.72	0.06	18	350	13.0	70	87	5.5	---	---	---	---	26
Wilson Ranch	Eldorado	38.8250	-120.2734	2087	165	g	s	11.66	0.14	3	323	15.0	55	32	5.5	23	1.6	0.3	2.1	18
Montgomery Mdw.	Stanislaus	38.3614	-119.9223	1901	140	g	s	122.33	0.45	3	220	14.0	40	44	7.0	151	9.5	1.4	20.2	9
St. Mary's Pass	Stanislaus	38.3436	-119.6452	2953	140	v	c	37.93	0.60	16	180	9.0	140	92	6.6	65	6.3	3.1	1.4	23
Smokey Fen	Stanislaus	38.3429	-119.6477	2932	140	v	c	17.20	0.38	20	216	7.5	40	33	6.8	65	5.9	2.3	2.4	11
Mound Fen	Stanislaus	38.3327	-119.6426	2901	140	v	m	27.17	1.02	11	28	9.5	110	69	6.9	195	19.9	7.3	7.6	6
Eagle Mdw.	Stanislaus	38.2790	-119.8357	2311	165	v	s	24.56	0.18	12	44	10.0	60	44	6.8	75	4.9	4.9	1.9	20
Happy Isles Fen	Yosemite NP	37.7307	-119.5603	1230	95	g	s	45.12	0.18	3	55	12.0	87	34	6.1	30	2.9	0.4	1.6	9
Mildred Lake	Inyo	37.5433	-118.8717	2973	89	c	b	50.06	3.20	0	350	9.0	18	38	7.5	225	47.8	0.5	0.8	14
Hornfels Fen	Inyo	37.5344	-118.8701	3020	89	m	c	1.67	0.07	3	56	12.0	117	63	6.2	95	15.4	0.4	2.0	8
Hanging Fen	Inyo	37.5336	-118.8661	3049	89	c	c	14.70	0.14	13	270	10.0	55	19	8.0	257	48.6	0.6	0.8	13
Long Mdw.	Sierra	37.4897	-119.5764	1939	140	g	s	3.53	0.60	7	230	---	80	73	6.7	142	15.0	1.8	8.5	23
Mack Lake	Inyo	37.4269	-118.7506	3130	89	g	b	53.11	0.09	2	83	9.0	53	22	6.1	49	4.7	0.6	1.8	2
Crispy Fen	Inyo	37.4266	-118.7512	3173	89	g	s	48.62	0.05	3	83	10.0	59	53	6.5	96	8.6	5.0	3.1	9
2m Fen	Inyo	37.4104	-118.7564	3204	97	g	b	593.09	0.05	1	8	12.0	192	28	5.2	15	2.1	0.1	0.5	2
Steep Mdw.	Sierra	37.4040	-119.5156	2061	165	g	s	8.36	0.24	14	40	16.0	20	27	6.2	---	---	---	---	14
Trapezoid Mdw.	Sierra	37.4033	-119.5277	2052	165	g	s	24.07	0.63	6	260	17.0	163	64	6.2	20	2.2	0.1	1.5	26

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Site name	Forest or Park	Latitude	Longitude	Alt. (m)	Precip (cm)	Bed-rock	Land-form	Catch. (ha)	Fen (ha)	Slope (%)	Aspect (azm.)	Soil temp. (°C)	Peat (cm)	OM (%)	pH	EC (µS/cm)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Species richness
Roadside Mdw.	Sierra	37.4004	-119.5132	2093	165	g	m	13.18	0.21	3	130	---	135	---	6.3	---	---	---	21	
Abbot View Fen	Inyo	37.3989	-118.7595	3233	99	g	b	383.14	1.20	2	355	11.0	40	16	6.3	13	1.9	0.1	0.6	13
Poison Mdw.	Sierra	37.3975	-119.5197	2044	160	g	s	42.79	0.77	5	190	16.5	170	82	6.3	13	1.1	0.1	1.4	22
North Dinky Lake	Sierra	37.1660	-119.0662	2818	114	g	s	5.54	0.05	19	210	---	40	---	6.0	36	4.0	0.2	1.5	15
Pond Below Dinky	Sierra	37.1657	-119.0693	2816	114	g	b	499.89	0.00	2	180	14.0	65	---	5.6	---	---	---	7	
East Dinky Lake	Sierra	37.1646	-119.0650	2816	114	g	b	493.90	0.49	0	260	12.0	40	84	5.9	13	0.3	0.1	1.4	11
Swede Lake	Sierra	37.1579	-119.0745	2815	114	g	s	0.75	0.02	18	195	13.0	73	85	5.8	23	2.7	0.1	1.5	16
Upper Snow Corral	Sierra	37.0388	-119.0756	2246	140	g	s	11.85	0.20	3	210	---	50	58	6.2	60	6.2	0.5	4.1	16
Snow Corral	Sierra	37.0295	-119.0730	2145	140	g	s	86.84	4.50	3	180	---	100	---	6.2	---	---	---	14	
Lower Ahart	Sierra	37.0117	-119.0444	2181	114	g	s	13.82	0.08	3	270	---	80	41	6.2	76	6.1	0.8	4.1	15
House Creek Mdw.	Sierra	36.9996	-119.0410	2120	130	g	s	35.05	0.03	7	314	16.0	80	24	6.2	46	6.2	0.4	1.9	19
Rowell Mdw.	Sequoia	36.7175	-118.7382	2692	89	g	m	385.53	0.60	3	210	13.5	170	64	6.1	42	5.2	0.4	2.4	32
Moraine Fen	Sequoia	36.7150	-118.7498	2640	89	g	s	10.91	0.10	9	226	14.0	40	30	6.1	25	2.2	0.2	1.2	17
Sphagnum Fen	Sequoia	36.7111	-118.7281	2736	89	g	s	167.46	0.04	7	226	15.0	70	77	6.0	19	2.8	0.1	0.6	13
Fire Fen	Sequoia	36.7090	-118.7235	2740	89	g	m	139.93	4.00	2	338	14.0	165	43	6.1	23	2.9	0.2	1.2	11
Junction Mdw.	Sequoia	36.1759	-118.5641	2253	79	g	s	216.22	0.32	5	63	16.0	71	62	6.4	37	3.6	0.5	2.8	18
Piped Mdw.	Sequoia	35.9941	-118.3522	2596	89	g	s	75.93	0.14	12	70	11.0	89	54	6.5	---	---	---	14	
Jupiter Mushroom Mdw.	Sequoia	35.9865	-118.3389	2542	89	g	b	193.43	0.15	7	72	13.0	130	87	7.0	61	7.1	0.7	4.2	14
Middle Round	Sequoia	35.9667	-118.3551	2782	89	g	s	44.80	0.09	23	230	---	15	---	6.0	31	2.5	0.4	2.4	12
North Round	Sequoia	35.9656	-118.3586	2741	89	g	s	136.33	1.70	5	206	14.0	165	---	6.7	23	2.2	0.2	2.2	14
Split Mdw.	Sequoia	35.9607	-118.3515	2780	89	g	s	28.39	0.06	29	236	12.0	54	67	6.9	35	3.1	0.7	3.3	19
Mosquito Mdw.	Sequoia	35.9515	-118.3540	2680	89	g	s	60.54	0.30	14	338	14.0	50	18	6.0	34	3.5	0.6	3.1	15