RESEARCH ARTICLE

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Soil Patterns in Three Darlingtonia Fens of Southwestern Oregon

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ABSTRACT: The *Darlingtonia* fens, found on serpentine soils in southern Oregon, are distinct communities that demonstrate a balance among high water tables, shallow soils, the presence of heavy metals, and limited nutrients. While conservative efforts have been made to preserve them, soil patterning or the specific processes that appear to underlie soil variability are poorly understood. I investigated the relationship of fire-free period on soil gradients and succession in three *Darlingtonia* fens, each with a different amount of time since last fire. Changes in vegetation and belowground variables were distinguished across fen, savanna, and shrub communities and across the three sites. I suggest that belowground gradients may be more important than time since fire at preserving these uniquely adapted systems, since vegetation undergoes post fire succession from fen to shrub to savanna after approximately 100 years since fire. Although restoration of ecosystem structure and processes was not the primary focus of this study, my data suggest that time since fire may drive ecosystem processes in a trajectory away from the normal succession cycle and that soil moisture decreases and nitrogen levels increase with an increase in fire-free period.

Index terms: *Darlingtonia* fen, Jeffrey pine savanna, soil ammonium, soil gradients

INTRODUCTION

Soil gradients in terrestrial ecosystems are often conceptualized as having discrete but mutually dependent above and belowground components (Smith et al. 1986; Hook et al. 1991; Jackson and Caldwell 1993). While there is a rich history of soil ecological research and a general recognition of the importance of soil chemical and physical properties (Huston 1979; Robertson et al. 1988; Tilman 1988; Keddy 1989), the extent to which belowground processes can affect aboveground community structure and patterns has been largely understated. This is especially true for serpentine soil ecosystems.

Darlingtonia fens are part of a complex mosaic of fen and pine savanna communities found on serpentine soils in southwestern Oregon. The fens display distinct aboveground, savanna-fen ecotones, both floristically and physiognomically, and can create high variability in the spatial characteristics of local plant communities. Perennial springs presumably maintain the savanna-fen ecotone in the southwestern Oregon ecosystems (H. Glasheen, unpubl. data; V. Stansell, unpubl. data; Lang 1999), while the maintenance of similar boundaries for pine savannas in the southeastern United States is attributed to fire (Wells and Skunk 1931; Christensen 1977; Christensen 1985; Rome 1988). Plant carnivory is an important characteristic of these serpentine ecosystems and reflects the unique soil requirements of contrasting forms of plant growth that also include a grass understory and a pine overstory, but disfavors plants of an intermediate stature such as shrubs (Whittaker 1960). Although a number of rare plant species are common to these communities, the dominant understory species includes the carnivorous plants *Darlingtonia californica* and the sedge *Carex mendocinensis,* while scattered Jeffrey pine *(Pinus jeffreyi)* constitute the upper canopy (Whittaker 1954; Franklin and Dyrness 1988). Few other ecosystems demonstrate a comparable balance among high water tables, shallow soils, the presence of heavy metals, and limited nutrients where fire is presumably the primary factor restricting the formation of a closed canopy forest in the succession cycle.

In the fen ecosystems of southwestern Oregon, two important aboveground factors are believed to influence the vegetative patterns and composition (Proctor and Woodell 1975; Mellichamp 1983). The most important is vegetative position relative to soil moisture. Fens reside in perennial streams and typically are characterized by a rich floral community dominated by *Darlingtonia californica* and *Carex mendosinensis*. The second factor is position relative to fire intensity, which ultimately depends on hydrology. Unburned vegetation growing on saturated soils can create distinct patterns of vegetation growth between fen and savanna. If this is the case, then soil nutrients should reflect corresponding transitions or discontinuities in vegetative patterns.

While soil patterning is unclear on serpentine soils, the specific processes that appear to underlie soil variability are more

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poorly understood. Even less certain is the persistence of vegetative patterns: (1) are they controlled by soil gradients and (2) to what extent do gradients change with regard to time since last fire? Several above and belowground variables in these ecosystems are theoretically quantifiable, yet few studies have attempted to evaluate their relative importance to aboveground vegetative structure and composition.

This study addresses such questions as: (1) do soil gradients exist in these serpentine soils? (2) do they mimic aboveground patterns? and (3) what effects do fire-free period, serpentine soil, and soil moisture have on vegetation patterns across boundaries in these plant communities? To answer these and similar questions, this study examines the subterranean patterns in serpentine soils at three *Darlingtonia* fen sites with different fire-free periods to determine site variability in vegetation-soil relationships associated with *Darlingtonia* fens. My goals were to determine the presence of biogeochemical gradients in these sites and to determine if length of time since fire influences biogeochemical gradients. I hypothesized that soil moisture would decrease and that nutrient levels would increase with increase in fire-free period. Soil nutrient levels should be highest at the site with the longest fire-free period, especially following the establishment of a shrub community.

METHODS

Study Area

The research was conducted at three *Darlingtonia* fens, each approximately .5-1 ha in extent and located within the Siskiyou National Forest in southwestern Oregon (42° 07' 30" N, 123° 37' 30" W, elevation 700 m) (Figure 1). The study area is located within the Josephine ultramafic sheet, a geologic region of southwestern Oregon characterized by unweathered rock fragments underlain by Jurassic-aged marine sediments (White 1971; Orr et al. 1992). Surface sediments consist of weathered ultramafic rock (serpentinite and partly serpentinized peridotite), which contributes to the serpentine soil chemistry: (1) high levels of exchangeable magnesium relative to other cations; (2) lower calcium levels than those found on nonserpentine soils; (3) lower levels of nitrogen, phosphorus, and potassium than are required for normal plant growth; and (4) high concentrations of heavy metals (chromium and nickel) with molybdenum levels insufficient for normal plant growth (Walker 1954; Kruckeberg 1984).

The fen soils belong to a laterite clay series rich in olivine and pyroxene minerals and serpentinized to various extents, giving them a dark, blue-green color (Becking 1997). Immediately surrounding the fens are shallow red soils with stony profiles that vary in surface depth depending on age of the laterite, amount of erosion or surface movement to which it has been subjected, degree of fracturing and alteration of the parent rock, history of precipitation in the area, vegetative cover, and composition of the parent rock (Ramp and Peterson 1979). The upper surface (depth from 0-.3m) is typically dark, reddish-brown soil with minor organic residue and abundant to minor amounts of iron oxide pellets and chromite grains (variable amounts of relatively unweathered peridotitie boulders) (Ramp and Peterson 1979), slightly acidic in pH (6.6 to 6.8), and low in nutrients (Walker 1954; Kruckeberg 1984). Beneath this (.3-1m), a yellow-brown soil with variable amounts of partly weathered peridotite occurs. A shrub community soil, surrounding the fen at Eight Dollar Mountain, is intermediate in both hydroperiod and organic layer, slightly more than the savanna, and slightly less than the fen, but still saturated for most of the year.

The sites used in this study were selected for their distinct boundaries, unique vegetative requirements, and burn histories. Two of the study sites, Cedar Log Creek and Josephine Creek, include pine savanna and fen plant communities. The third site, Eight Dollar Mountain, is forested, adjacent to a mesic shrub community and most closely resembles the southeastern United States' carnivorous plant communities. This shrub community (unique to Eight Dollar Mountain) is characterized by *Rhamnus californica* and *Rhododendron occidentalis,* while scattered Jeffrey pine and incense-cedar *(Calocedrus decurrens)* constitute the upper canopy (Whittaker 1954; Franklin and Dyrness 1988). At the time the study was initiated, time since last fire was: five years at Cedar Log Creek, eight years at Josephine Creek, and approximately 100 years at Eight Dollar Mountain. Eight Dollar Mountain had the longest fire-free period, a significant expanse of shrub community, and a number of endemic species. The fens ranged from 3-12 m in width and 300-600 m in length, while the savannas surrounding the fens were expansive (1-300 km^2). The sites had moderate slopes (2-10 %).

During the comparatively dry months of August and September, maximal fuel loads and sources of ignition (primarily lightning) result in fires, the majority of which were, until the summer of 2002, small in spatial extent due to fuel breaks of bare serpentine rock and topographic discontinuities (Frost and Sweeney 2000). The 1986 burn in the Josephine Creek site was a prescribed ground fire that removed all flammable herbaceous biomass and most of the accumulated litter; the fire scorched only the lower needles of pines. The 1996 burn in the Cedar Log Creek site was also a prescribed fire that burned over both communities. Both burns occurred during the late summer, corresponding to the fire regime for the area (D. Borgias and J. Beigel, unpubl. data).

Soil and Vegetation Sampling

Replicate transects were established across each vegetation community within each site and 1m^2 quadrats were sampled for soil and vegetation variables both continuously and adjacently across each transect. Transects were oriented perpendicular to community boundaries and to the main environmental gradients (perennial stream and topography) (Knapp 1984; Palmer and Dixon 1990). Each transect contained a minimum of nine and a maximum of 12 soil and vegetation sample quadrats, with a total of six transects in each site. Transects at the Eight Dollar Mountain site extended an additional 5 m to ensure sampling of the shrub to savanna communities. Sample quadrat size was increased to 5 m x 5 m in

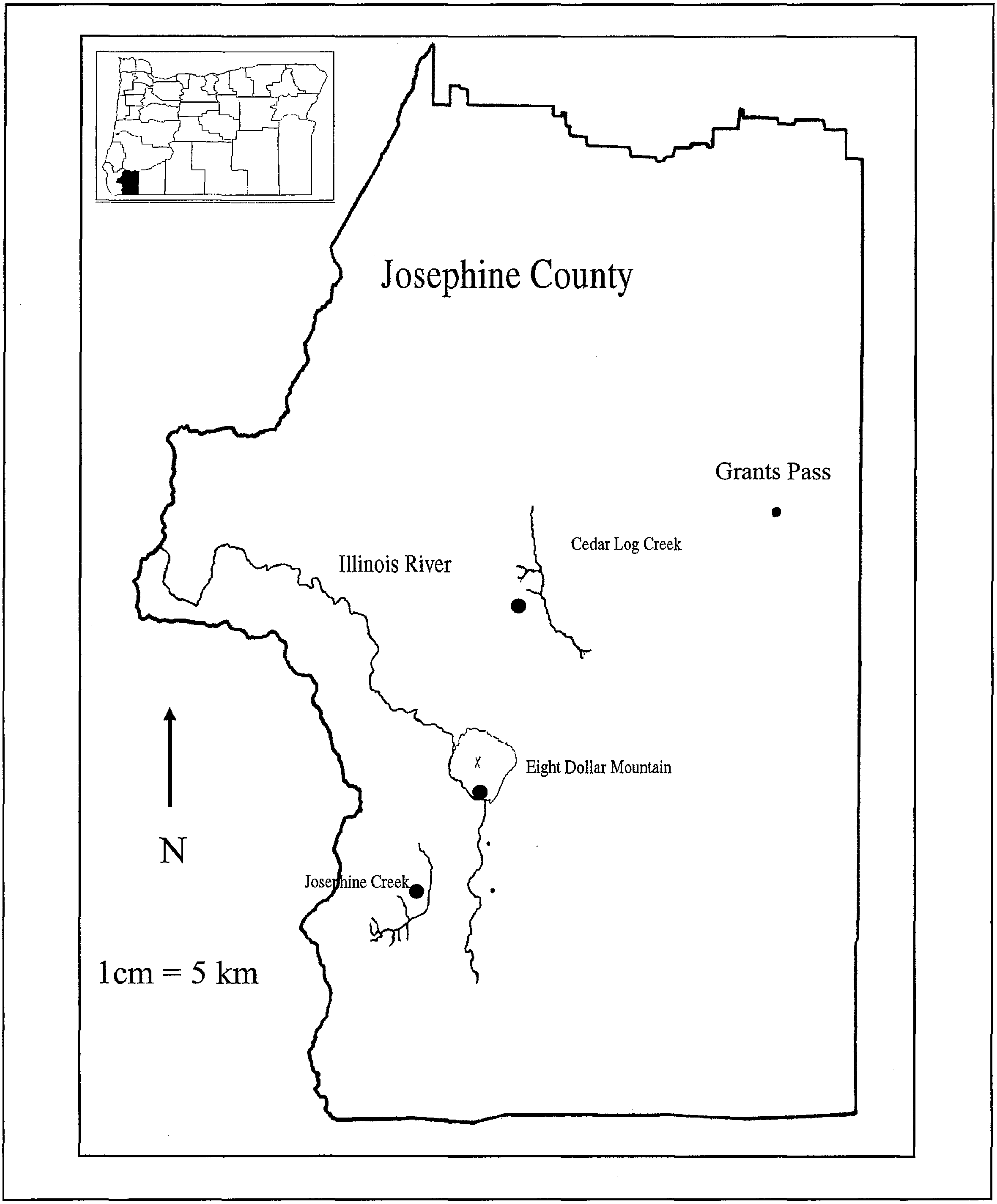

Figure 1. Study sites, Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain, located in Josephine County, Oregon.

both the shrub and savanna communities. Sampling at the Eight Dollar Mountain site included an additional 72 sample quadrats to include the shrub community. Two hundred and nineteen samples were collected from the three sites that collectively contained 2682 m^2 of sampling area. Soil samples were collected along transects at each site during June, July, August, and September over four consecutive years (1999-2002).

Vegetation Analyses

Vegetation data were recorded throughout the growing season from June to October. Plants were identified to species where possible, after Hickman (1993). Some plants remained in a vegetative state throughout the season and were identified only to genus, resulting in the grouping of several species. Percent cover for each species was estimated using one of six cover classes (<1%, 1-4%, 5-25%, 26-50%, 51-75%, and 76-100%) (Braun-Blanquet 1965).

Soils Analyses

Variation in soil chemistry across community boundaries was assessed using soil samples collected along transects during June through September at each site over four consecutive years (1999-2002). One core (12 cm deep and 3 cm in diameter; 340 cm^3) was taken from each 1m^2 quadrat for chemical and physical characteristics: NO_3, NH_4, soil moisture, bulk density, pH, cation exchange capacity (CEC), soil texture, and organic matter. In shrub areas (the Eight Dollar Mountain site) where sample area was larger, three cores were taken randomly within a quadrat and composited. All soil cores were taken between shrub root zones. Soil pits were dug within each community at each site and described using Soil Conservation Service soil survey guidelines (Borine 1983).

Soil samples collected for nutrient analysis were air dried at 70° C for 48 hours and passed through a 2 mm sieve to remove stones and coarse roots. All subsequent analyses were performed on this sieved material. Soil pH was determined in a 1:1 soil-water paste (McLean 1982). Soil ammonium and nitrate were extracted in a 1:10 soil 2 N KCl solution using the Bremmer method (Bremmer and Keeney 1965). Extracts were analyzed colorimetrically on a Technicon II auto analyzer. Organic matter content was determined by loss on ignition (Shulte and Hopkins 1996) and CEC by extraction with 1 N ammonium acetate solution (Rhoades 1986). Physical soil characteristics (sand, silt, and clay) were determined by pipette according to MacKeague (1978). Soils were also analyzed gravimetrically for soil moisture according to Western States Laboratory Proficiency Testing Standards (Gavlak et al. 1997).

Statistical Analyses

To ordinate vegetation of the study sites, I used canonical correspondence analysis (CCA) (ter Braak 1986) by means of the CANOCO program v.3.1 (ter Braak 1987). Vegetation data for the analysis were based on percent cover estimates for each quadrat along the transects and were recorded during the peak of the growing season (June). Since a primary objective was to gain information on biogeochemical gradients relative to community structure and composition, the species matrix included percent cover of observable species from each community. These species were: *Ceanothus pumila* (CEPU), *Festuca idahoensis* (FEID), *Arctostaphylos viscida* (ARVI), *Tofieldia glutinosa* (TOGL), *Hastingsia bracteosa* (HABR), *Darlingtonia californica* (DACA), *Sanguisorba microcephala* (SAMI), *Rudbeckia californica* (RUCA), *Carex mendocinensis* (CAME) and *Agrostis* spp. (AG) which characterized large communities of heliophytes (plants tolerating full sun). *Rhododendron* (RHOC) and *Rhamnus* (RHCA) characterized the shrubs while Jeffrey pine (PIJE) and incense-cedar (CADE) constituted the upper canopy community. Site scores from species scores were screened for outliers (> 2 standard deviations from site score) prior to analysis; three samples were found outside of distinctive clusters of vegetation by running a principal components analysis (PCA) and removing them from the total (n = 216).

The environmental matrix of the CCA included 10 soil variables: (1) soil moisture (gravimetric water determination), (2) bulk density, (3) pH, (4) NO_3, (5) NH_4, (6) organic matter, (7) sand, (8) silt, (9) clay, and (10) CEC. Bulk density and pH are continuous variables while soil moisture is a proportionate variable (wet: dry wt./vol.) ranging from 22 to 573%. I log transformed the variables CEC, soil pH, NO_3, NH_4, and bulk density. Soil moisture, organic matter, sand, silt, and clay and variables of vegetation abundance required square root and arcsine transformations prior to analysis to more closely approximate the assumptions of normality (Jongman et al. 1995). The final analysis incorporated both soil and species variables; 14 vegetation variables and 11 soil variables comprised the matrices.

Multivariate analyses used the program CANOCO v. 3.1 (ter Braak 1987). Species variables were ordinated with respect to soil variables using CCA (ter Braak 1986). Significance levels for the first and second axes were set at $p \leq 0.05$. A forward-selected CCA ordination was then used to determine which soil variables accounted for the greatest amount of variance in the distribution of the plants. This process chooses variables that explain significant ($p \leq 0.05$) and independent directions of total variation in the spatial distribution of plant vegetation. The significance of each variable added in this fashion was tested using a Monte Carlo permutation test with 999 unrestricted permutations. Following the CCA, a non-parametric median test between sites was used to confirm that the communities represented statistically different populations (Sokal and Rolf 1982).

Among multivariate methods, the eigenvector method (CCA) preserves the chi-square distance among points, and is appropriate when the responses of the dependent variables are expected to be unimodal along environmental gradients. Unimodality for this analysis was confirmed using an unconstrained analysis, detrended correspondence analysis (DCA), on the species data; all gradient lengths were greater than 3.5 and indicated high spatial variability among species.

To display and interpret relationships between plant communities and environmental variables biplots of species ordination, scores and the centroids of the environmental variables scores were used. Directional arrows from the environmental variable centroids represent the weighted averages of each of the species with respect to each of the environmental variables. Proximal distances from the centroids indicate relatively weaker relationships to the environmental gradients than the more distant locations.

RESULTS

Fourteen species were used in the analysis (Table 1). Two tree, four shrub, and eight herbaceous species were inventoried from all quadrats at the three sites. One tree species, Jeffrey pine (PIJE), along with nine herbaceous genera, *Darlingtonia* (DACA), *Hastingia* (HABR), *Festuca* (FEID), *Rudbeckia* (RUCA), *Sanguisorba* (SAMI), *Tofieldia* (TOGL), *Agrostis* (AG), *Arctostaphylos* (ARVI) and *Carex* (CAME) (stellulatae group), were recorded at each of the three sites. Incense-cedar (CADE) and two of the four shrub species, *Rhamnus* (RHCA) and *Rhododendron* (RHOC), were present at Eight Dollar Mountain. These two shrub species dominated a shrub community of the Eight Dollar Mountain site while the remaining two shrub species, (*Ceanothus* (CEPU) and *Arctostaphylos* (ARVI)), were represented in the savanna communities at all three sites (Table 1).

Table 1. Mean and standard error of the mean (±) of cover values (%) for the species matrix data for Eight Dollar Mountain, Josephine Creek, and Cedar Log Creek sites. Variable codes presented in the results appear in parentheses.

Genera (Variable names)	Eight Dollar Mountain	Josephine Creek	Cedar Log Creek
Darlingtonia (DACA)	13.0±1.8	31.2±4.2	11.4±2.5
Tofieldia (TOGL)	0(0)	0.9±0.1	4.3±1.2
Arctostaphylos (ARVI)	5.6±1.4	0.2±0.1	1.2±0.5
Agrostis (AG)	33.0±1.0	1.1±0.4	6.4±1.3
Carex (CAME)	23.5±2.7	22.0±3.1	5.4±2.0
Rudbeckia (RUCA)	23.0±2.5	0.2±0.01	9.9±1.5
Rhododendron (RHOC)	25±3.3	0(0)	2.6±1.0
Ceanothus (CEPU)	0.30±0.01	0.7±0.6	2.3±0.8
Hastingsia (HABR)	11.4±1.8	11.0±2.0	0.5±0.3
Sanguisorba (SAMI)	9.4±1.3	3.0±0.6	6.8±1.7
Pinus jeffereyi (PIJE)	12±2.1	1.5±0.8	5.9±2.0
Festuca (FEID)	18.2±3.0	2.9±0.9	8.6±2.1
Calocedrus (CADE)	0.9±0.5	0 (0)	0.6±0.4
Rhamnus (RHCA)	6.1±1.4	0 (0)	3.8±1.5

From the 10 soil variables used in the analysis, several biogeochemical gradients were evident (Table 2). The Cedar Log Creek site had the lowest concentrations of soil NO_3 compared to the other sites. Within the Cedar Log Creek site, soil NO_3 was lowest in the fen and highest in the savanna communities (Table 2). Soil ammonium levels at this site were also lowest but were considerably higher than NO_3 levels (14 to 33 times higher), with decreasing values from center of fen to savanna across all transects. A strong soil moisture gradient was present at Cedar Log Creek from the fen to the savanna with gravimetric moisture as low as 21% in the savanna community and supersaturated conditions in the fen community. There are no clear bulk density, soil texture, or CEC gradients at Cedar Log Creek; however, bulk density levels were similar to both the Josephine site and the savanna community at the Eight Dollar Mountain site. Organic matter levels were relatively consistent across communities with a median pH of 6.7.

Josephine Creek showed a slight soil NO_3 gradient across communities from the fen to the savanna (Table 2). However, there was a stronger soil NH_4 gradient from the fen to the savanna, with the levels of NH_4 dropping slightly from 40 ppm in the fen to 29 ppm in the savanna (a 70% decrease). As with the Cedar Log Creek site, levels of NH_4 were considerably higher than the NO_3 levels (30- to 40-fold greater). Organic matter levels decreased from fen to savanna but there were no apparent gradients for soil texture, bulk density, or CEC. The median pH was 6.8 at this site.

In general, two strong gradients occurred at the Eight Dollar Mountain site – a soil NO_3 gradient that increased from fen to savanna and an NH_4 gradient that decreased from fen to savanna with NH_4 levels superseding NO_3 levels in some cases by a factor of 200 (Table 2). This range of values coincides with changes in organic matter that were highest in the fen, lowest in the savanna, and intermediate in the shrub community. Additional gradients at this site were soil texture with a sand gradient decreasing from fen to savanna, a clay gradient that increased from fen to savanna, and a bulk density gradient that increased from fen to savanna and from source of fen to the outlet. The median pH of this site was 6.6.

Canonical Correspondence Analysis

The canonical coefficients represent the weight that each soil variable contributed to the ordination axes, and the inter-set correlations (site scores from species scores) reflect the correlation between the environmental variables and the ordination axes (Table 3). Both axes 1 and 2 of the CCA ordination were significant ($p \leq 0.05$), with high eigenvalues ($\lambda_1=0.46$, $\lambda_2=0.29$). Species-soil correlations (0.790 for axis 1, 0.795 for axis 2) accounted for 15% of the variance explained by the soil

Table 2. Mean and standard error of the mean for soil variables at all communities, fen, shrub (s), and savanna (sav) at each site. Shrub vegetation is restricted to the Eight Dollar Mountain site. Soil texture at all three sites is sandy clay loam. Significant median comparisons (Kruskal-Wallis) are indicated by an asterisk (*).

	Eight Dollar Mountain (100 years since fire)		Josephine Creek (8 years since fire)		Cedar Log Creek (5 years since fire)	
Soil NO3 (ppm)	Fen	1.0 ± 0.05	Fen	0.8 ± 0.08	Fen	0.6 ± 0.05
	S	1.0 ± 0.12				
	Sav	2.5 ± 0.2	Sav	1.2 ± 0.2	Sav	0.9 ± 0.1
Soil NH4 (ppm)	Fen	147.5 ± 14.3*	Fen	36.7 ± 3.2*	Fen	20.5 ± 1.8 *
	S	62.4 ± 7.9				
	Sav	8.2 ± 0.46*	Sav	32 ± 3.4*	Sav	15.4 ± 4.2*
Avg. pH		6.4		6.8		6.7
Bulk density (g/cc)	Fen	1.0 ± 0.01*	Fen	1.5 ± 0.03*	Fen	1.3 ± 0.03 *
	S	0.9 ± 0.03				
	Sav	1.4 ± 0.009*	Sav	1.6 ± 0.04*	Sav	1.4 ± 0.04 *
Soil moisture (%)	Fen	318.0 ± 23.3	Fen	98.0 ± 7.7	Fen	71.0 ± 5.7
	S	90.0 ± 10.3				
	Sav	10.7 ± 0.8	Sav	69.0 ± 6.3	Sav	20.5 ± 3.2
CEC (meq/100g)	Fen	31.5 ± 1.6	Fen	31.8 ± 1.16	Fen	40.7 ± 0.3
	S	36.0 ± 0.3				
	Sav	28.0 ± 0.9	Sav	28.1 ± 1.5	Sav	47.0 ± 0.8
Organic matter (%)	Fen	21.0 ± 1.4	Fen	7.9 ± 0.4	Fen	12.1 ± 0.7
	S	19.4 ± 0.6				
	Sav	9.1 ± 0.8	Sav	6.5 ± 0.59	Sav	13.2 ± 0.6
Slope (%)		2-5		2-5		10

variables. Six out of 10 soil variables (soil moisture, NO_3, NH_4, CEC, bulk density, and clay) were significant at $p \leq 0.001$. Inter-set correlations (Table 3) show soil chemical factors, such as NH_4, make significant contributions to axis 1, whereas axis 2 likely represents a gradient that is related to the physical properties of the soil affected by either time since fire or soil moisture. All results indicated that plant species separate widely.

The first CCA axis ordered sites along an NH_4 gradient (-.66) and soil moisture (-.58) ranging from recently burned sites (5 and 8 years) to long-time since fire (100 years) (Figure 2). Species occurred across a range of moisture conditions with *Darlingtonia* (DACA), *Sanguisorba* (SAMI), and *Hastingsia* (HABR) clumping tightly in a wetter habitat while *Ceanothus* (CEPU), *Arctostaphylos* (ARVI) and *Festuca* (FEID) clump more tightly in the drier habitats. In these sites, the savanna separated from the fen communities (Figure 2). Along the second axis, bulk density occurred as a slight gradient from Jeffrey pine savanna to *Darlingtonia* fen communities, increasing from low to high, respectively. Separation within sites across communities and between all three sites was clear with the exception of the savanna community in the Eight Dollar Mountain site (Figure 3). The non-parametric median comparison (Sokal and Rolf 1982) indicated significant differences in soil NH_4 ($p < 0.001$) and bulk density ($p < 0.001$) between sites. Other variables were suggested to be significantly different between sites (Table 3), and while knowing this provides insight, it does not provide the firm conclusion that could be provided by replication of sites and a broader statistical rigor (Hurlbert 1984).

In summary, the findings from the CCA on soil gradients yield information concerning the relative importance of spatial and environmental processes operating at stand and landscape scales in the *Darlingtonia* systems. Three main soil relationships exist with these serpentine sites: (1) soil NH_4 increases, (2) organic matter increases, and (3) bulk density decreases with increasing fire-free period.

Table 3. Summary of canonical coefficients and inter-set correlations of environmental variables. Significance ($\alpha \leq 0.05$) is indicated by * (between sites) and ** (within sites).

Environmental Variable (label)	Canonical coefficients		Inter-set correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Soil moisture (smoist)**	-0.24	0.43	-0.58	-0.14
pH (pH)*	-0.06	0.09	0.15	0.21
Soil N03-N (sNO3)**	0.44	-0.05	0.44	-0.20
Soil NH4-N (sNH4)**	-0.64	0.08	-0.66	-0.27
Organic matter (orgmat)*	-0.14	0.01	-0.35	-0.53
Cation exchange capacity (cec)**	0.05	-0.40	0.15	-0.27
Soil bulk density (bdens)**	-0.23	0.60	0.26	0.66
Soil texture (sand)*	0.49	-0.15	-0.45	-0.37
(silt)*	0.30	-0.19	0.45	0.05
(clay)**	0.35	0.63	0.39	0.46

DISCUSSION

The results of this ordination analysis show observable differences in the types of plants grouped between and within sites in three southern Oregon serpentine soil communities. Specifically, the analysis indicates that soil-related variables offer partial explanation about patterns and distributions of plant species in combination with fire-free period. Four main trends suggest that some pattern of plant distribution within a site can be attributed to soil ammonium and soil moisture; at a landscape scale, soil ammonium may be a larger factor determining the presence of communities within a site. In short, this study suggests that succession without fire on these serpentine sites proceeds toward increasing soil ammonium levels.

Use of Kruskal and Wallis (Sokal and Rolf 1982) median comparisons shows statistically significant differences in soil NH_4 and bulk density between sites. Soil ammonium accounts for a major portion of the variance in the gradient analysis: .79 of the species-soil correlation and 15% of the variation in spatial distribution of plants within each site. These results are consistent with Bedford et al.'s (1999) review of nutrient-poor fens and bogs in temperate North America and with Andreu et al. (1996) in their study of soil ammonium changes following burning. *Rhododendron*, *Rudbeckia*, and *Carex* (Figure 2) occupy sites having high NH_4 relative to *Ceanothus, Festuca,* and *Arctostaphylos,* whereas shrub community plants incense-cedar and *Rhamnus* occur somewhere between the wettest sites for *Darlingtonia* and the driest sites for *Ceanothus* and *Festuca.* Along with community separation by soil NH_4, the ordination separates the three sites based on fire-free period. However, understanding of the influence of ecosystems over time is not possible without replicated sites within each fire-free age class. These findings cannot suggest stand age effects between sites or conclude site comparisons but instead fire-free, time-related soil characteristics, particularly at Eight Dollar Mountain, where NH_4, NO_3, and organic matter levels are highest. These findings should be attributed to individual site differences due to the inherent limitations of pseudoreplication (Hurlbert 1984; Stewart-Oaten et al. 1986).

Examination of these sites (Figure 3) shows that Josephine and Cedar Log Creek are juxtaposed with regard to bulk density. The Josephine Creek site values do not correspond with fire-free period where they would hypothetically exist – intermediate between the Eight Dollar Mountain and Cedar Log Creek sites. This suggests that either eight years is insufficient time to build higher soil NH_4 levels than those found at Cedar Log Creek or that the slightly higher sand content at this site creates effectively drier (higher matric potential) soil conditions. In addition, a range of other site-specific variables may account for these relationships (Lu et al. 2006; Tolman 2006).

Both soil texture and bulk density are important in shaping post-fire communities. The ordination values show that bulk density (strongly correlated with sand content) accounts for some spatial distribution of communities. Specifically, savanna plants increase in dominance with increasing bulk density. Fine-textured soils, on the other hand, with high total pore space (such as silt loams, clays, and clay loams) generally have lower bulk densities than sandy soils, especially if organic matter is present (Brady and Weil 1996). This relationship is most evident at the Eight Dollar Mountain site, where organic matter content is highest in the fen community, lowest in the savanna, and intermediate in the shrub community (Table 2). Plant species, and thus communities, separated widely, thereby demonstrating that soil variables (such as soil moisture, pH, bulk density, CEC, and soil texture) may contribute to site differentiation as strongly as fire-free period.

Flammable litter and branch dieback, both produced by savanna species, encourage frequent fire. In the event of a fire, litter is reduced and invading vegetation is eliminated, thus temporarily inhibiting soil development. By contrast, this research suggests another possibility; the absence of fire at the Eight Dollar Mountain site may promote the development of the current vegetation over successionally relevant time periods (i.e., approximately 100 years), causing litter decay and the development of a relatively nutrient-rich humus. This is commensurate with findings from studies on serpentine soils in the northeastern United States (Knox 1984; Latham 1993; Arabas 1997) where fire suppression and adequate moisture conditions promote litter accumulation and decomposition that raise soil organic matter

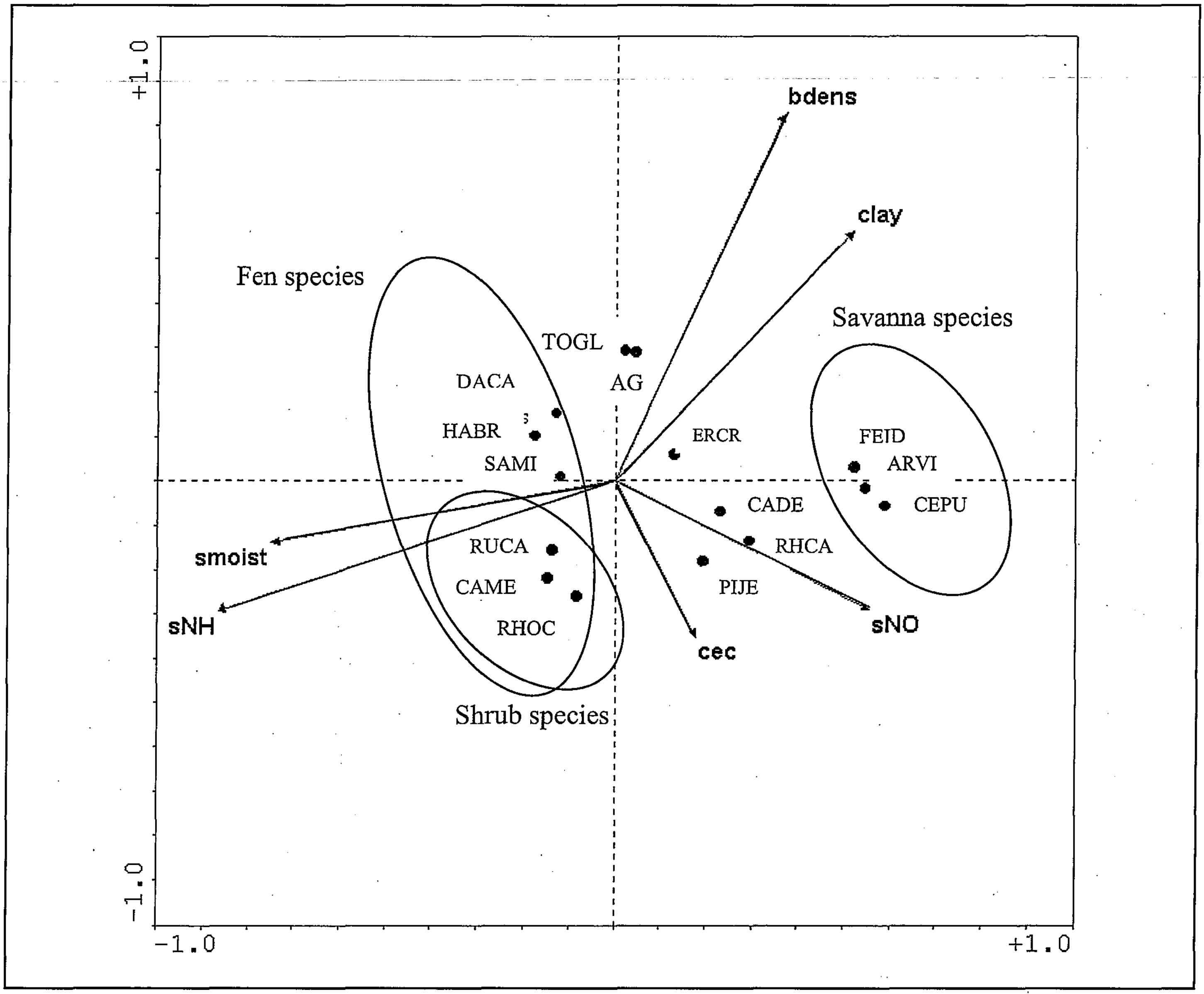

Figure 2. CCA ordination of species scores for environmental variables. Dots correspond to plant species (Table 1); large circles indicate plant communities. Species identifiers and abbreviations for environmental variables follow variable codes used in Tables 1 and 3, respectively.

and soil ammonium levels. Speculatively, shrub species at the Eight Dollar Mountain site may draw down moisture levels adjacent to the fen and facilitate faster decomposition, contributing to higher soil ammonium levels at this site. Earlier research has shown that surface plant distributions can influence belowground variables and nitrogen cycling through differences in litter quality and quantity (Hobbie 1992); and in nitrogen-poor systems, small changes in the soil organic matter fraction can have large effects on ecosystem N dynamics (Wedin and Tilman 1990; Wedin and Pastor 1993).

Soil gradients likely play a role in maintaining the carnivorous fens of these serpentine sites. At the point of decreasing water-saturated soils, along the gradients from savanna to fen, soil nutrients increase, notably NH_4. This is particularly evident in these systems, given increases in silicate clay content and subsequently higher levels of CEC. In a biogeochemical context, increases in clay contribute to the soil nutrient levels by subsequently elevating the NH_4 levels in the direction of the shrub community (Table 3). These soil-related variables and their subsequent levels are essential to the understanding of uniquely adapted systems – well worth considering for future research.

Management Implications and Further Research

The key to long-term understanding and management of fire-dependent ecosystems lies in answering important ecological questions concerning belowground variables. Management of the Siskiyou *Darlingtonia* fens has recently emerged as a conservation priority in the Pacific Northwest with little research to substanti-

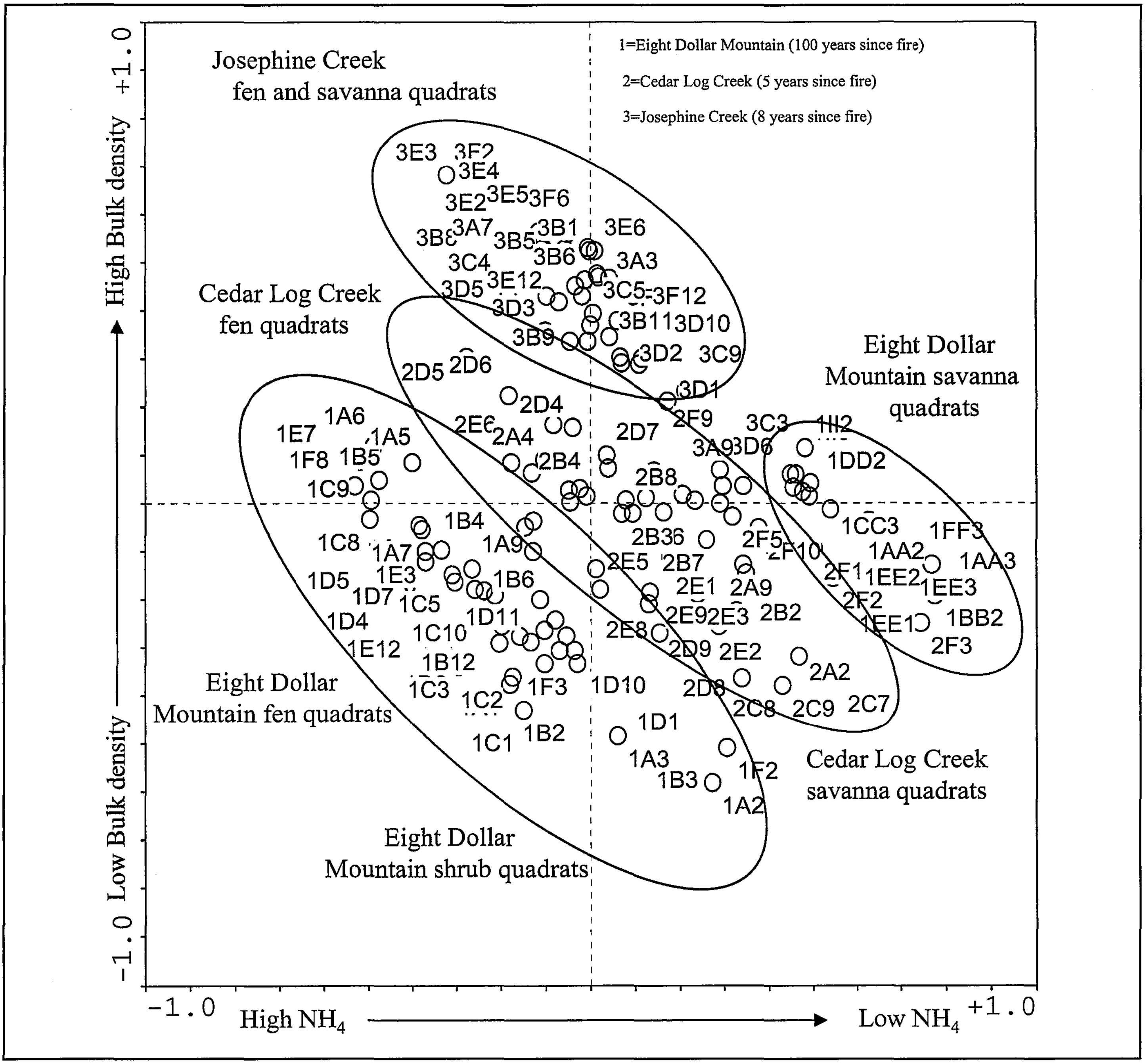

Figure 3. CCA ordination of a subset of sample scores and sites showing inter- and intra-site distinction. Prefixes of either 1, 2, or 3 indicate the separate sites.

ate management strategies. Thus, selection of appropriate management strategies in ecosystems adapted to high water tables, shallow soils, the presence of heavy metals, and limited nutrients in the context of fire and the succession cycle should recognize that fen vegetation patterns are strong reflections of soil gradients, soil moisture, time since last burning, and natural succession. Management decisions should more fully account for these subterranean details with increased appreciation of their consequent ecological processes in terms of the overall ecosystem. From this study, conservation efforts aimed at preserving the biologically diverse flora and fauna of the *Darlingtonia* fen ecosystems must consider a more regional landscape perspective. Prescribed burns, in particular, need to include belowground inventory and associated communities, particularly in the shrub community, which is likely maintained by fire suppression. Furthermore, water management efforts, such as maintaining water levels, should not be understated as anthropomorphically lowering these levels may alter microhabitat processes and artificially hasten the demise of the *Darlingtonia* fens (Tolman 2004).

Lacking appropriate definition of temporal scale or sufficient replication poses serious challenges for extrapolation and prediction of research results. Generalizations regarding ecosystem change require data collection over annual to decadal time scales. Thus, the greatest opportunities for further research in the *Darlingtonia* fens involve long-term monitoring or short-term controlled burns. Monitoring should include seedling and sapling surveys to establish long term regeneration patterns following either natural or prescribed burning. Prescribed burns must include expanded research on fire behavior in these ecosystems (e.g., individual species' responses to burns, ecotone responses to burns, community responses to burns) as well as N tracer research in nutrient cycling. Geomorphology, location of the fens relative to seeps and bare serpentine rock, topographic discontinuities, and genetic research regarding age of fens is also crucial to predict potential fire effects on succession. Since complex interactions between soil moisture, vegetation structure, litterfall and decomposition rates, and soil nutrient stocks are difficult to sort, more research on the litter component in these systems is required before its role in successional relationships can be fully understood. For example, do the community types differ in their N requirements? This in turn will influence litter chemistry and potentially the rate of decomposition. Second, information regarding post burn effects on gradients would be useful for a more comprehensive investigation.

As uniquely adapted plant ecosystems decline in the Northwest and more intensive management is required, detailed information of plant interactions with driving variables, such as hydrology or fire, can guide management actions and decisions. For example, an understanding of the extent of habitat specificity can contribute to the identification of the range of habitat variation necessary to maintain rare plants of restricted habitats. Understanding the extent to which subterranean variables contribute to plant distribution can influence decisions about habitat conservation. Ultimately, informed management decisions can help conserve the uniquely adapted and rare plant ecosystems of southwestern Oregon.

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