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Soil-Plant-Microbial Relations in Hydrothermally Altered Soils of Northern California

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Soils developed on relict hydrothermally altered soils throughout the Western USA present unique opportunities to study the role of geology on above and belowground biotic activity and composition. Soil and vegetation samples were taken at three unaltered andesite and three hydrothermally altered (acid-sulfate) sites located in and around Lassen VolcanicNational Park in northeastern California. In addition, three different types of disturbed areas (clearcut, thinned, and pipeline) were sampled in acid-sulfate altered sites. Soils were sampled (0–15 cm) in mid-summer 2010 from both under-canopy and between-canopy areas within each of the sites. Soils were analyzed for numerous physical and chemical properties along with soil enzyme assays, C and N mineralization potential, microbial biomass-C and C-substrate utilization. Field vegetation measurements consisted of canopy cover by life form (tree, shrub, forb, and grass), tree and shrub density, and above-ground net primary productivity of the understory. Overall, parameters at the clearcut sites were more similar to the unaltered sites, while parameters at the thinned and pipeline sites were more similar to the altered sites. We employed principal components analysis (PCA) to develop two soil quality indices (SQI) to help quantify the differences among the sites: one based on the correlation between soil parameters and canopy cover, and the second based on six sub-indices. Soil quality indices developed in these systems could provide a means for monitoring and identifying key relations between the vegetation, soils, and microorganisms.

Abbreviations: ANPP, aboveground net primary productivity; AWCD, average well color development; EC, electrical conductivity; FAME, fatty-acid methyl ester; PC, principal component; PCA, principal component analysis; PLFA, phospholipid fatty acid; SQI, soil quality Indices; TOC, total organic C; VNP, Volcano National Park.

Soils developed on relict hydrothermally altered rock present unique conditions for biota given the often extreme differences in physical and chemical properties relative to soils developed in unaltered rock. Soil–plant–microbial relationships within humid ecosystems associated with hydrothermally altered rock in the Western USA have not been extensively studied; however, soil–plant relationships in similar, more arid Western USA ecosystems have shown that inherently low soil pH (due to high acid sulfate concentrations) and fertility (specifically low concentrations of N and P) help drive the occurrence of open pine forests in altered soils compared with sagebrush dominated communities on nearby unaltered soils (Billings, 1950; Salisbury, 1954; Schlesinger et al., 1989). Differences in N and water-use efficiencies between conifers and sagebrush have also been cited as reasons behind the starkly different plant communities in acid-sulfate altered and unaltered soils (Billings, 1950; DeLucia et al., 1988; DeLucia and Schlesinger, 1991). DeLucia et al. (1989) showed that low soil-P limited plant growth, in some

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cases by 90%, in hydrothermally altered Great Basin locations. Schlesinger et al. (1989) further suggested that coniferous vegetation is inherently adapted to such extreme conditions that they thrive under low pH and low soil-P conditions, whereas sagebrush is physiologically intolerant of such conditions. While the impacts of acid-sulfate soils on vegetation have been studied, the impact on soil microbial activity has not been explored in detail.

Recent work at semiarid sagebrush/conifer, hydrothermally altered andesite locations in NV and CA examined differences in microbial activity between altered and unaltered soils (Blecker et al., 2010). Activities of various enzymes and mineralizable-C and -N were found to be lower in the acid-sulfate soils, though microbial biomass-C was similar between the altered and unaltered soils. As with earlier studies, pH, P, and N were lower, while Al, S, and Fe were higher in acid-sulfate compared with unaltered soils. However nitrate N was similar between the two soils types and ammonium N was greater in the altered soils. In addition, total Ca and bioavailable Cu, K, Mg, Mn, and Ni were greater in the unaltered sagebrush soils compared with the altered conifer soils.

Monitoring the recovery of disturbed lands has been historically based on aboveground measures such as vegetative cover and composition. The addition of key chemical (e.g., pH, electrical conductivity (EC), metals and macronutrients) and physical (e.g., soil texture) parameters can provide further detail, with an even more complete picture of recovery gained through measures of soil microbial activity (Mummey et al., 2002; Ruiz-Jaen and Aide, 2005; Haney et al., 2008). One means of distilling such a wide array of information is by developing soil or ecosystem quality indices (SQIs), which can also provide a link between science and land management.

An example of an SQI is the multi-parametric index for agroecosystems developed by Karlen and Stott (1994). This index employed a framework of weighted and integrated soil parameters related to management goals such as productivity and maintenance of environmental quality. This concept was further developed utilizing a process of soil quality indicator selection, interpretation, and integration into an index of soil quality for agricultural soils (Andrews and Carroll, 2001), that has since been applied to other agroecosystems (Sharma et al., 2005; Masto et al., 2008), forests (Bastida et al., 2006), and rangelands (Rezaei et al., 2006). Such an index has the potential for monitoring the recovery of disturbed areas. We performed a study of acid-sulfate altered/unaltered soils in northeastern California to further examine soil–plant–microbial relationships in relict hydrothermal systems of a more humid region (i.e., higher elevation, increased precipitation) relative to earlier semiarid ecosystem studies. In addition, we examined the impact of disturbances associated with logging and pipeline installation in these altered soils. Finally, we used soil quality indices as a means of identifying key vegetation–soil–microbe relationships that could provide a tool to gauge ecosystem health and monitor recovery of disturbed areas.

METHODS

Site Description

Two study sites (Maidu and Lassen) were located in fossil acid-sulfate magmatic-hydrothermal systems within Lassen National Forest and Lassen Volcanic National Park (VNP) in northeastern California. The Maidu site (40.35° N, 121.56° W) was located in the Lassen National Forest at an average elevation of 1700 m. Late Pliocene hydrothermal alteration of the andesite in this area has resulted in replacement of original minerals (e.g., plagioclase and mafic minerals) with alunite, fine-grained Si, 1:1 clay minerals and Fe-oxides compared with the nearby unaltered andesite (John et al., 2005). Dominant soils in this area consist of Haploxeralfs and Vitrixerands. White fir (*Abies concolor*) dominates the unaltered soils, while white fir and *Pinus* sp. are fairly evenly distributed within the altered terrain. Manzanita (*Arctostaphylos* sp.) dominates the understory within areas of altered soils and is absent on the unaltered soils. Other shrubs such as *Ceanothus* sp. are found on the unaltered soils. Grasses and forbs are generally scarce within both the altered and unaltered sites.

The Lassen site (40.45° N, 121.55° W), approximately 10 km to the north of the Maidu site, was located in the southwestern portion of Lassen VNP near Brokeoff Mountain, at an average elevation of 2350 m. Pleistocene hydrothermal alteration of the andesites in this area was similar to that in the Maidu area, with primary minerals replaced by alunite, 1:1 clay minerals (kaolinite, pyrophyllite, dickite), topaz, pyrite, and a range of silica minerals in contrast to the surrounding unaltered andesite (John et al., 2006). Dominant soils within this area consist of Dystroxerepts. The mixed-conifer forest community at this site includes red fir (*Abies magnifica*) and white fir, while western white pine (*Pinus monticola*) and mountain hemlock (*Tsuga mertensiana*) are only found on the altered soils. As with the Maidu site, manzanita dominates the understory within areas of altered soils; it is not found on the unaltered soils. Coyote mint (*Mondarella* sp.) dominates the understory of the unaltered soils, with the unaltered soil also containing a greater variety and density of forbs and grasses. Climate data for both sites were taken from the nearby town of Mill Creek, CA (40.33° N, 121.52° W; elevation 1450 m), which has a mean annual precipitation (MAP) = 1430 mm and a mean annual air temperature (MAT) = 7.1°C (www.weather.com/weather/climatology/monthly/USCA0702; accessed 29 Jan. 2014).

Study Design

Soil samples were taken from three different disturbance/geologic regimes within the overall study site: (i) undisturbed/unaltered andesite (unaltered),(ii) undisturbed/hydrothermally altered (altered), and (iii) disturbed/altered (clearcut: an area that was clearcut and reforested approximately 20 to 30 yr before the current study; thinned: an area that was thinned an unknown amount of time before the current study, and pipeline: an area that was cleared and re-graded after pipeline installation 10 yr before the current study). The disturbed/altered areas were

all located within the Maidu study site, as no disturbances were observed within the Lassen study site. In addition, disturbed/unaltered sites were not available to sample.

At each site three random plots were selected on a similar aspect (150 to 210°). Within each plot, three 30-m transects (spaced 120° apart) were randomly established. An exception was at the pipeline site, which was sampled along the pipeline contour for the three transects to remain within the disturbed area. Soil samples were taken under a tree canopy and between tree canopies along each transect for a total of nine under-canopy and nine between-canopy samples per site. The soil surface was cleared of any litter then sampled from 0 to 15 cm. Samples were stored at 4°C in the field and passed through a 2-mm sieve on return to the lab. A separate soil core sample (0–15 cm), was taken using a slide-hammer for measurements of bulk density and soil moisture.

The same 30-m transects were used for vegetation measurements. A line-point intercept survey with 0.6-m intervals was conducted along each transect to determine the percentage of canopy cover and percentage of bare ground (n = 150 per plot). In addition, a 4-m belt transect was used to determine densities of trees (categorized by genus or species) and shrubs (categorized as *Arctostaphylos* sp. or other). Understory aboveground net primary productivity (ANPP) was estimated by harvesting all living plant material within a 0.5-m quadrat at three random locations along each transect (n = 9 per plot). All sampling was conducted in August 2010.

Soil Microbiological, Chemical, and Physical Analyses

Carbon and N mineralization potential was performed with a 10-d static incubation on 25 g of soil that was first brought to 60% water-filled pore space all contained within a 1 qt. mason jar. Five milliliters of 1 M NaOH were used to trap the CO_2 generated by the incubation, which was then determined by titration with 1 M HCl at the end of the incubation period (Robertson et al., 1999). Inorganic N (NO_3–N and NH_4–N) was determined by 2 M KCl extraction and flow injection analysis (Robertson et al., 1999). Enzyme assays relevant to the S-cycle (arylsulfatase) and P-cycles (acid and alkaline phosphatase) were performed on air-dried samples that had been stored for 4 to 6 wk following the method of Dick et al. (1996), which involved short-term incubation at controlled temperature and pH, followed by spectrophotometric analysis. A fluorescein diacetate (FDA) assay was performed on field moist samples (Green et al., 2006) utilizing a short-term incubation and subsequent spectrophotometric analysis, and provided a more broad based measure of enzyme activity. We qualitatively assessed functional diversity of microbial communities with community level physiological profiles using Biolog EcoPlates (Biolog Inc., Hayward, CA). Each 96-well EcoPlate contains 31 different C substrates and one water control, all replicated three times; each well also contains tetrazolium violet dye that, when reduced by microbial utilization of the C substrate, turned the well purple. Well color development measured at 24-h intervals for five consecutive days indicated the microbial community's ability to use a particular substrate, the assumption being that more functionally diverse communities will be able to use more substrates (Sinsabaugh et al., 1999). Average well color development (AWCD) data are presented from Day 4 (96-h) readings, which allowed for maximum color development response variance without exceeding the linear absorbance range (Garland, 1996).

Microbial biomass was measured using a hybird phospholipid lipid fatty acid (PLFA) and fatty-acid methyl ester (FAME) technique (Smithwick et al., 2005) based on a modified Bligh and Dyer (1959) method. Certain lipid "signatures" within the cell membranes of living microbes can be used to identify a portion of the microbial community: gram + and gram − bacteria, fungi, actinomycetes, and protozoa (Sinsabaugh et al., 1999). Total microbial biomass-C (on a C molecular weight basis) was estimated by summing abundances of all fatty acids.

Soil chemical analyses included pH using a 2:1 deionized water/soil ratio; (Thomas, 1996), EC on a saturated paste extract (Rhoades, 1996), inorganic C by pressure transducer (Sherrod et al., 2002), and total C and N using a Flash EA 1112 NC Elemental Analyzer (CE Elantech, Inc., Lakewood, NJ), where total organic carbon (TOC) was determined by the difference between total and inorganic C. Sodium bicarbonate–extractable P was determined colorimetrically via the Olsen method (Kuo, 1996), and represents an estimate of bioavailable-P. Though developed for more alkaline soils, it has been used effectively on more acidic soils (Muriaki and Barber, 1983; Sharpley et al., 1987; Schlesinger et al., 1989). Total metals concentrations were determined using a four-acid dissolution and subsequent ICP–MS analysis (Briggs and Meier, 2002). Bioavailable metals were determined using the Mehlich-III extraction method (Mehlich, 1984). Soil physical analyses included particle-size distribution using the hydrometer method (Elliott et al., 1999), bulk density from soil cores (Elliott et al., 1999), and gravimetric moisture analysis by oven-drying soils for 72 h at 110°C.

Statistical Analyses

Given the lack of disturbed/unaltered sites one-way analysis of variance and Tukey's honestly significant difference comparisons were used to determine the minimum significant difference between the unaltered and altered sites, and also between the altered and disturbed sites at a significance level (α) of 0.05 for each parameter. Data were analyzed for normality and variance and transformed as necessary for statistical analyses; all presented data are untransformed. All statistical analyses were performed using JMP software v 8.0.1 (SAS Institute, Cary, NC).

Soil Quality Index—Approach #1: Vegetation Based-Principle Component Analysis

A SQI was developed using methods adapted from Harris et al. (1996), Andrews and Carroll (2001) and Rezaei et al. (2006). A vegetation measurement (specifically canopy cover) was used to identify a minimum data set (MDS) of soil variables that

were transformed via scoring functions to produce a SQI. In the initial step, soil microbial, physical, and chemical variables were selected based on a Pearson correlation coefficient > 0.50 relative to canopy cover. To further reduce this dataset, the variables were analyzed by PCA. Only those principal components (PCs) that explained at least 5% of the variance were used for further analysis (Andrews and Carroll, 2001). Within those PCs, the highest weighted variable was selected, along with variables having an absolute value within 10% of the highest weighted variable. Multiple variables within a given PC were examined for colinearity by examining their multiple correlation coefficients. As with Andrews and Carroll (2001) and Rezaei et al. (2006), variables with correlations > 0.70 were considered redundant and subject for removal; those with the lowest correlation sums were retained in the MDS.

Variables from the MDS were transformed using nonlinear scoring functions with a "more is better" upper asymptote sigmoid curve, a "less is better" lower asymptote sigmoid curve, or a midpoint optimum bell shaped curve (Karlen and Stott, 1994). All microbial variables and macronutrients were assigned 'more is better' functions; bulk density and metals such as Pb were assigned 'less is better' functions; micronutrients, pH, EC, and soil moisture were assigned midpoint optimum functions. The *y*-axis values represented a normalized scoring range of 0 to 1 for each variable. The *x*-axis range was based on the mean and two standard deviations, compared with the approach used by Andrews and Carroll (2001), who set the *x*-axis range to within 5% of the observed range across all treatments. Other researchers have relied on expert opinion and/or published values to determine the *x*-axis range (Harris et al., 1996; Glover et al., 2000; Masto et al., 2008). Once the variable was transformed with the scoring function, it was then weighted based on the percentage of variance explained from the PC in which it was located. Finally, weighted scores of all MDS variables were added together determine the SQI.

Soil Quality Index—Approach #2: Sub-Index Based

For this approach, any variable with a significant difference in mean value between the undisturbed/unaltered and undisturbed/altered soils was selected. The resulting 27 variables (listed below in *italics*) were assigned to one of six user-defined sub-indices (Soil organic matter: *TOC, TN, C/N*; Biotic: *arylsulfatase, acid-phosphatase, alkaline-phosphatase, mineralize-N, AWCD, canopy cover*; Physical/Chemical: *pH, EC, soil moisture, bulk density*; Macronutrient: *Total-P,-Na, Mehlich-Ca,-K,-Mg,-SO_4*; Micronutrient: *Total-Co,-Cu,-Fe,-Mn, Mehlich-Ni,-Zn*; and Metal: *Total-As,-Sb, Mehlich-Pb*). Within each sub-index, PCA was used to determine the weighting for each variable. The variables were then scored using a 'more is better', 'midpoint optimum', or 'less is better' function as explained in the previous section. Each of the five sub-indices was weighted equally, with a maximum possible value = 1 and a maximum cumulative total SQI = 6.

RESULTS

Microbial Activity

Results for the microbial parameters are presented in Table 1. Microbial measurements in the unaltered soils exceeded the altered soils except for FDA, mineralized-C, microbial biomass-C and qCO_2. The clearcut soils had similar measures of soil microbial activity compared with the unaltered soils, except for lower mineralized-N. The lowest microbial activities were seen in the thinned, and pipeline soils, though values were statistically similar to the altered soils in most cases. Negative values for mineralized-N in the thinned and pipeline soils indicate that N immobilization exceeded N mineralization during the incubation. Respiration coefficients (qCO_2) were highly variable within a given soil, though values for disturbed soils tended to exceed undisturbed soils.

Soil Organic Matter and Macronutrients

Results for TOC, TN, and macronutrients are presented in Table 2. Total organic C and TN were similar between the clearcut and unaltered soils and greater than the thinned, pipeline and altered soils. Soil C/N ratios were lower for the unaltered soils compared with the altered, thinned and pipeline soils. Unaltered soils had greater NO_3–N concentrations compared with the other soils. Total-P concentration was similar among the unaltered, altered, and clearcut soils, and greater than the pipeline and thinned soils, while HCO_3–extractable P was similar across all study soils. In general, K, Ca, Mg

Table 1. Soil microbial parameters for unaltered (U), altered (A), and disturbed soils (clearcut, CC; thinned, TH; pipeline, PL). All data are means (± 1 standard error of measurement). Different letters indicate significant differences between means across rows for altered soils ($p < 0.05$). *Italicized* values indicate significant differences between the unaltered and altered soils.

	Undisturbed		Disturbed/altered		
Sample area	U	A	CC	TH	PL
Parameter	n = 18	n = 18	n = 6	n = 6	n = 6
FDA, mg kg^{-1}	52.3 (4.3)	36.3^{a} (5.4)	44.4^{a} (6.9)	32.0^{a} (5.7)	35.8^{a} (8.3)
Arylsulfatase, mg kg^{-1}	*71.5* (13.4)	26.5^{ab} (8.7)	37.7^{a} (3.5)	10.6^{ab} (1.8)	19.3^{b} (13.0)
Acid-phosphatase, mg kg^{-1}	*2832* (209)	1692^{ab} (237)	2102^{a} (154)	1057^{ab} (123)	993^{b} (322)
Alkaline-phosphatase, mg kg^{-1}	*930* (139)	390^{ab} (100)	718^{a} (84)	147^{bc} (70)	33.7^{d} (33.7)
Mineralized-C, mg C kg^{-1}	295 (43)	234^{a} (40)	358^{a} (39)	328^{a} (106)	310^{a} (47)
Mineralized-N, mg N kg^{-1}	*1.1* (0.36)	0.17^{a} (0.14)	0.07^{a} (0.26)	-0.46^{a} (0.33)	-0.64^{a} (0.34)
AWCD	*0.483* (0.09)	0.139^{a} (0.03)	0.279^{a} (0.06)	0.193^{a} (0.08)	0.198^{a} (0.07)
AWCD substrate richness, Rs	*14.8* (1.4)	5.7^{a} (1.2)	11.7^{a} (1.5)	7.7^{a} (2.2)	8.3^{a} (2.4)
Microbial biomass-C, nmol g^{-1}	26.9 (2.9)	23.0^{a} (5.1)	19.4^{a} (4.1)	19.2^{a} (4.3)	24.8^{a} (9.1)
qCO_2	1.1 (0.22)	1.6^{a} (0.62)	1.8^{a} (0.23)	2.3^{a} (0.87)	2.2^{a} (1.0)

concentrations were greater in the unaltered and clearcut soils compared with the altered, thinned, and pipeline soils. Unaltered soils had lower total-S but greater bioavailable-S relative to most of the other study soils.

Micronutrients and Metals

For the micronutrients, concentrations of total Co, Cu, Fe, Mn, Ni, and Zn were greater for the unaltered soils compared with the altered soils; the disturbed soils were typically intermediate in micronutrient concentrations (Table 3). This trend was similar for Mehlich Ni and Zn concentrations, while unaltered and altered soils had similar Mehlich Cu, Cr, and Mn concentrations. Unaltered and clearcut soils had roughly twice the total-Na of the altered soils, while the thinned and pipeline soils contained roughly half the total-Na concentration of the altered soils. Both total Al and Mehlich Al concentrations were greater in the unaltered compared with the altered soils. Aluminum values for the clearcut soils were similar to the unaltered soils, while the values for the thinned and pipeline areas were more comparable with the altered soils. The altered areas contained greater total As and total Sb compared with the unaltered areas, while disturbed soils have intermediate values.

Table 2. Soil organic matter and macronutrient concentrations for undisturbed/unaltered (U), undisturbed/altered (A) and disturbed/altered (clearcut, CC; thinned, TH; pipeline, PL) soils. All data are means (± 1 standard error of measurement). Different letters indicate significant differences between means across rows for altered soils ($p < 0.05$). *Italicized* values indicate significant differences between the unaltered and altered soils.

	Undisturbed		Disturbed/altered		
Sample area	U	A	CC	TH	PL
Parameter	$n = 18$	$n = 18$	$n = 6$	$n = 6$	$n = 6$
TOC, %	*5.0* (0.34)	2.8^{b} (0.28)	6.0^{a} (0.29)	3.5^{b} (0.42)	3.4^{b} (0.99)
TN, %	*0.21* (0.01)	0.09^{b} (0.01)	0.22^{a} (0.01)	0.08^{b} (0.01)	0.09^{b} (0.04)
Soil C/N	*24.5* (0.7)	32.6^{b} (1.7)	27.3^{bc} (1.0)	41.4^{a} (1.6)	42.1^{a} (5.5)
NO_3–N, mg kg^{-1}	*0.959* (0.35)	0.03^{a} (0.02)	0.007^{a} (0.006)	0.00^{a} (0.00)	0.018^{a} (0.018)
NH_4–N, mg kg^{-1}	1.4 (0.38)	0.90^{a} (0.18)	1.5^{a} (0.48)	1.1^{a} (0.37)	1.6^{a} (0.31)
Total-P, mg kg^{-1}	978 (68)	856^{ab} (70)	1118^{a} (27)	512^{c} (47)	570^{bc} (49)
HCO_3–P, mg kg^{-1}	0.21 (0.13)	0.18^{a} (0.07)	0.03^{a} (0.03)	0.10^{a} (0.06)	0.43^{a} (0.27)
Total-K, %	*1.1* (0.07)	0.78^{a} (0.05)	0.72^{a} (0.06)	0.82^{a} (0.07)	1.02^{a} (0.20)
Mehlich-K, mg kg^{-1}	*282* (33)	99^{b} (12)	390^{a} (25)	150^{b} (29)	119^{b} (26)
Total-Ca, %	*1.3* (0.09)	0.48^{ab} (0.05)	0.63^{a} (0.05)	0.27^{b} (0.04)	0.36^{ab} (0.10)
Mehlich-Ca, mg kg^{-1}	*1887* (248)	474^{b} (129)	1901^{a} (218)	389^{b} (51)	566^{ab} (80)
Total-Mg, %	*0.87* (0.04)	0.36^{a} (0.04)	0.44^{a} (0.02)	0.36^{a} (0.04)	0.43^{a} (0.06)
Mehlich-Mg, mg kg^{-1}	*246* (56)	34.3^{a} (21)	111^{a} (25)	47.2^{a} (20)	85.9^{a} (30)
Total-S, %	*0.32* (0.04)	1.1^{a} (0.12)	0.93^{ab} (0.10)	0.46^{b} (0.18)	0.44^{b} (0.13)
Mehlich-SO_4, mg kg^{-1}	*15.1* (1.9)	3.8^{b} (0.12)	15.0^{a} (0.10)	5.5^{b} (1.1)	5.7^{ab} (0.55)

Chemical/Physical Parameters

Soil physical and basic chemical data are presented in Table 4. The unaltered and clearcut soils had a slightly higher soil pH compared with the altered, thinned, and pipeline soils. Although differences existed, all EC values were quite low (0.015–0.026 dS m^{-1}). Soil moisture in the unaltered soils was almost twice that of the altered soils. The clearcut soils were similar to the undisturbed soils, while the thinned and pipeline soils were similar to the altered soil. Bulk densities of the altered, thinned and pipeline soils exceeded that of the unaltered and clearcut soils. The only difference in sand content was between the altered (57.3%) and clearcut (47.2%) soils, and no differences were found in clay content among the study soils.

Vegetation

Vegetation data are presented in Fig. 1. No difference existed among the different soils for total understory ANPP, though differences were present for the understory ANPP components. Manzanita was the dominant shrub on the altered, thinned, and pipeline soils and not present on the unaltered and clearcut soils, though other shrub species were present at the latter sites. Forbs dominated the unaltered soils, while forbs, shrubs, and grasses were more equally distributed on the clearcut soils; no grasses were present on any of the other altered soils. Total canopy cover and tree canopy cover were similar though highly variable

Table 3. Selected micronutrient and metal concentrations for undisturbed/unaltered (U), undisturbed/altered (A) and disturbed/altered (clearcut, CC; thinned, TH; pipeline, PL) soils. All data are means (± 1 standard error of measurments). Different letters indicate significant differences between means across rows for altered soils ($p < 0.05$). *Italicized* values indicate significant differences between the unaltered and altered soils.

	Undisturbed		Disturbed/altered		
Sample area	U	A	CC	TH	PL
Parameter	$n = 18$	$n = 18$	$n = 6$	$n = 6$	$n = 6$
Total-Al, %	*8.7* (0.11)	6.9^{bc} (0.31)	10.3^{a} (0.23)	8.3^{abc} (0.40)	6.3^{c} (0.85)
Mehlich-Al, mg kg^{-1}	*2217* (106)	1842^{c} (104)	2582^{a} (87)	2026^{abc} (87)	1897^{bc} (136)
Total-As, mg kg^{-1}	*17.8* (2.4)	34.3^{a} (3.9)	24.6^{a} (5.3)	19.4^{a} (1.8)	24.6^{a} (0.9)
Total-Co, mg kg^{-1}	*19.4* (3.6)	3.3^{b} (0.47)	9.5^{a} (0.74)	4.2^{ab} (0.49)	9.0^{a} (2.9)
Total-Cu, mg kg^{-1}	*45.1* (1.5)	26.6^{b} (2.9)	47.6^{a} (2.0)	53.7^{a} (6.3)	27.3^{b} (3.1)
Mehlich-Cu, mg kg^{-1}	0.77 (0.15)	0.51^{a} (0.11)	0.32^{a} (0.05)	1.1^{a} (0.26)	0.61^{a} (0.17)
Mehlich-Cr, mg kg^{-1}	0.11 (0.06)	0.10^{a} (0.05)	0.00^{a} (0.00)	0.29^{a} (0.08)	0.10^{a} (0.05)
Total-Fe, %	*4.3* (0.12)	3.1^{c} (0.35)	5.1^{a} (0.27)	3.1^{bc} (0.09)	2.8^{c} (0.43)
Mehlich-Fe, mg kg^{-1}	*200* (12)	251^{a} (13)	126^{b} (7.9)	238^{a} (10)	210^{ab} (42)
Total-Mn, mg kg^{-1}	*793* (120)	205^{c} (35)	889^{a} (155)	188^{bc} (37)	636^{ab} (283)
Mehlich-Mn, mg kg^{-1}	37.2 (9.6)	52.0^{b} (16)	100^{ab} (13)	55.8^{ab} (19)	146^{a} (51)
Total-Na, %	*1.0* (0.08)	0.51^{a} (0.05)	0.39^{ab} (0.03)	0.22^{b} (0.04)	0.27^{b} (0.08)
Total-Ni, mg kg^{-1}	*46.0* (11)	8.2^{b} (1.3)	22.3^{a} (4.2)	21.1^{a} (1.0)	16.3^{ab} (3.2)
Mehlich-Ni, mg kg^{-1}	*1.0* (0.38)	0.26^{b} (0.05)	0.08^{b} (0.05)	0.45^{ab} (0.13)	0.73^{ab} (0.11)
Total-Sb, mg kg^{-1}	*0.72* (0.06)	2.80^{a} (0.63)	2.1^{a} (0.11)	1.4^{a} (0.11)	2.2^{a} (0.30)
Total-Zn, mg kg^{-1}	*70.1* (4.4)	25.7^{b} (2.3)	64.8^{a} (3.0)	22.7^{b} (1.8)	39.2^{b} (5.7)
Mehlich-Zn, mg kg^{-1}	*2.3* (0.26)	0.95^{b} (0.13)	1.4^{ab} (0.14)	0.63^{b} (0.12)	1.4^{ab} (0.50)

Table 4. Soil chemical and physical properties for unaltered (U), altered (A), and disturbed (clearcut, CC; thinned, TH; pipeline, PL) soils. All data are means (± 1 standard error of measurement). Different letters indicate significant differences between means across rows ($p < 0.05$). *Italicized* values indicate significant differences between the unaltered and altered soils.

	Undisturbed		Disturbed/altered		
Sample area	U	A	CC	TH	PL
Parameter	$n = 18$	$n = 18$	$n = 6$	$n = 6$	$n = 6$
pH	*5.6* (0.15)	5.2^{b} (0.09)	5.7^{a} (0.05)	5.2^{b} (0.10)	5.2^{b} (0.07)
Electrical conductivity, dS m^{-1}	*0.024* (0.003)	0.015^{b} (0.002)	0.023^{ab} (0.003)	0.026^{ab} (0.01)	0.021^{ab} (0.002)
Soil moisture, %	*21.4* (2.0)	12.3^{b} (1.9)	16.5^{ab} (1.2)	7.8^{b} (0.6)	8.0^{b} (1.4)
Bulk density, g cm^{-3}	*1.05* (0.04)	1.27^{ab} (0.05)	0.99^{c} (0.05)	1.44^{a} (0.04)	1.29^{ab} (0.11)
Sand, %	52.5 (1.3)	57.3^{a} (2.2)	47.2^{b} (1.8)	55.0^{ab} (2.0)	53.8^{ab} (1.8)
Clay, %	16.8 (0.67)	17.5^{a} (2.1)	19.3^{a} (0.47)	12.7^{a} (2.2)	15.1^{a} (2.7)

among the soils. As with the understory ANPP, forbs and grasses contributed more toward canopy cover on the unaltered and clearcut soils, while shrub cover was more significant on the altered soils. For overall plant density, values were similar though highly variable among all soils. Shrub density was highest on the altered soils and lowest on the unaltered soils. The clearcut soils were dominated by a fairly even-aged stand of 2- to 8-m trees, while the other soils had a more uneven tree size distribution. Vegetation also differed between the Maidu and Lassen study sites. Except for the clearcut soils, the forests within the Maidu study site had greater canopy cover, where *Pinus* sp. (*ponderosa, jeffreyi and lambertina*) dominated the disturbed soils and *A. concolor* the unaltered soils. A more even mixture of tree species occurred on the altered soils. *Calcocedrus decurrens* and *Quercus* sp. were also noted within the unaltered soils of the Maidu study site and not found at all within the Lassen study site. At Lassen, both unaltered and altered soils were dominated by firs (*A. concolor* and *A. magnifica*), while *Pinus monticola* and *Tsuga mertensiana* were present on the altered soils.

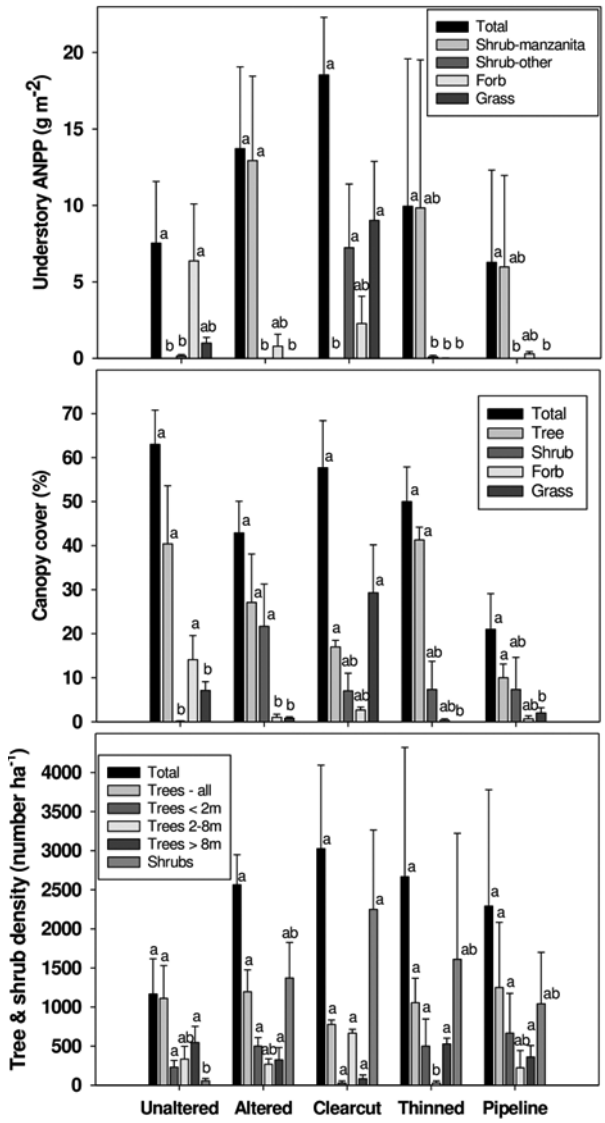

Fig. 1. Study area vegetation data. (a) Understory aboveground net primary productivity (ANPP; g m^{-2}), (b) canopy cover (%), (c) tree and shrub density (number of plants ha^{-1}). All data are means (± 1 standard error of measurement). Different letters indicate significant differences between means ($p < 0.05$) across soil types. For unaltered and altered sample areas $n = 9$; $n = 3$ for clearcut, thinned, and pipeline sample areas.

Principal Component Analysis–Soil Quality Index (Canopy Cover)

Table 5 lists all the soil variables with a significant Pearson correlation coefficient ($p < 0.05$) relative to canopy cover. The first four PCs explained approximately 89% of the variation in potential indicators. Potential variables within PCs 1 to 3 were correlated at $r^2 < 0.70$ and therefore were all selected for scoring in the SQI. Based on the relationship between the soil variables and canopy cover, AWCD, total Ca, and total K were scored with 'more is better' functions; pH, total Na, total Ni and Mehlich Cr were scored with 'midpoint optimum' functions, and total As was scored with a 'less is better' function. The SQI scores for the five different soils are presented in Fig. 2. Within a given soil, the PC1 variables (total-Ca, total-Ni, and total-As) contributed between 64 and 75% to the overall SQI score. The unaltered soils had the greatest average SQI scores (2.12), which were greater than other soils except the clearcut soil (SQI = 1.87). All of the individual soil variables scored lower for the altered soils compared with the unaltered soils.

Cumulative Sub-Index Soil Quality Index

The 27 variables selected using the sub-index SQI approach were assigned to one of six previously described user-defined sub-indices. Unaltered and clearcut soils had similar scores (5.12 and 5.20 respectively), with similar contributions from each sub-

index (Fig. 3). The other soils had statistically similar scores (altered = 3.04; thinned = 3.34; pipeline = 3.16) that were lower than the unaltered and clearcut soils. The pipeline soils had the lowest biotic sub-index score, while the altered soils had the lowest score for all other sub-indices.

Table 5. Potential minimum data set variables and results from the principal components analysis for the canopy cover based principle component analysis—soil quality index (PCA-SQI). Correlation direction indicates a positive (+) or negative (-) correlation with canopy cover at $p < 0.05$. *Italicized numbers* represent factors with the highest loading within a given principal component (PC) and those factors within 10% of the factor with the highest loading. *Italicized variables* represent those indicators selected for the SQI after redundancy analysis.

Statistic or variable		PC 1	PC 2	PC 3	PC 4
Eigenvalue		3.99	1.47	1.15	0.52
Percent variance explained		49.89	18.38	14.36	6.51
Cumulative percent		49.89	68.27	82.63	89.14
weighting		0.56	0.21	0.16	0.07
Correlation direction	Potential MDS variables	Eigenvectors			
+	*AWCD*	0.300	–0.104	*0.593*	–0.416
+	*pH*	0.329	–0.380	0.057	*0.775*
+	*Total-Ca*	*0.432*	0.249	0.285	0.119
+	*Total-K*	0.333	–0.041	*-0.551*	–0.035
+	*Total-Na*	0.345	*0.526*	0.225	0.150
+	*Total-Ni*	*0.400*	–0.410	–0.043	–0.134
–	*Total-As*	*-0.395*	0.238	0.244	0.413
+	*Mehlich-Cr*	0.262	*0.528*	–0.385	–0.023

DISCUSSION

Microbial Activity

All of the enzyme assays (except for FDA), along with mineralized-N and AWCD had lower values for the altered soils compared with the unaltered soils. Higher substrate richness (Rs) values for the unaltered soils (Table 1) also indicate potentially greater microbial functional diversity in these systems. However, microbial activity associated with the C-cycle (specifically mineralized-C and microbial biomass-C) did not differ between the unaltered and altered soils. These trends in microbial activity between unaltered and altered soils are generally consistent with results from previous research of acid-sulfate soils of more arid systems (Blecker et al., 2010). Thus the impact of acid-sulfate soils on microbial activity appears to exist across a wide range of climate conditions and ecosystems.

In most instances, microbial activity in the clearcut soils was similar to the unaltered areas, while the pipeline and thinned soils were similar to the altered soils. Pipeline soils showed the greatest degree of variability likely due to the variability of disturbance within this site. The higher qCO_2 values within the disturbed areas are consistent with studies from other disturbed systems (Insam and Domsch, 1988; Zhong and Makeschin, 2003), indicating a reduced efficiency in C utilization.

Soil Organic Matter and Macronutrients

Unaltered and clearcut soils contained roughly twice the soil TOC and TN relative to the altered, thinned, and pipeline soils. Total organic C and TN had strong correlations with almost all microbial parameters (Table 6), indicating the important link between soil organic matter and microbial activity. Schlesinger et al. (1989) reported a positive correlation between soil organic matter and net primary productivity in acid-sulfate soils, the latter being impacted by greater precipitation. Thus, increasing precipitation, along with changes in land use can modify impacts of acid-sulfate alteration. Lower C/N ratios (Table 1) for the unaltered and clearcut soils reflect the greater amounts of forbs and grasses in these areas (Fig. 1), as conifers (with greater C/N ratios) generally contribute to higher soil C/N ratios. The significance of the soil C/N ratio is also seen in Table 6, as higher C/N ratios correlate negatively with most of the microbial parameters.

As found in previous studies (DeLucia et al., 1989; Schlesinger et al., 1989) macronutrients such as Ca, Mg and K were depleted in the altered compared with unaltered soils. Bioavailable fractions of K, Ca, and SO_4 showed more frequent correlation with microbial activity than the total concentrations of these nutrients (Table 6), and could contribute to the differences in microbial activity between the unaltered and altered soils. Nitrate-N concentrations were greater in the unaltered soils while NH_4–N concentrations were similar between the soils. In more arid sagebrush/conifer systems NO_3–N was similar and NH_4–N was greater in the altered compared with unaltered soils (Blecker et al., 2010). The lack of positive correlations between inorganic N and microbial activity in the current and previous study suggests that inorganic-N is important in these systems, as the low concentrations could indicate more efficient utilization and thus less inorganic N available for measurement.

In previous studies, soil P was found in lower concentrations in altered soils, which was limiting to plant growth (Billings, 1950; DeLucia et al., 1989). Bioavailable-P was found in similar concentrations in both unaltered and altered studies of more

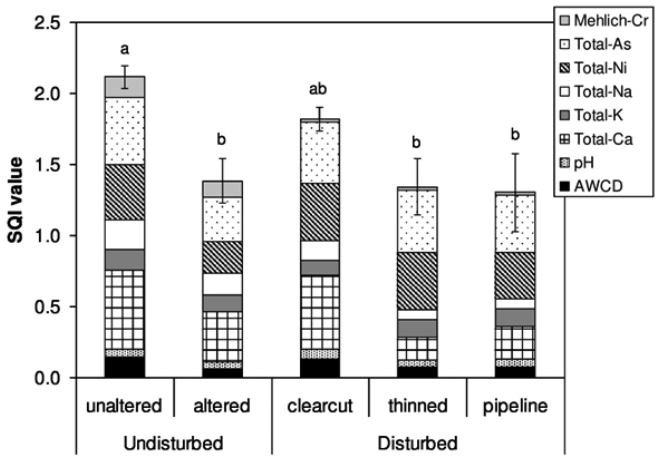

Fig. 2. Soil quality index (SQI) values for the canopy cover based PCA-SQI. Data presented are means ± 1 standard error of the mean. Different lowercase letters indicate a significant difference at $p < 0.05$.

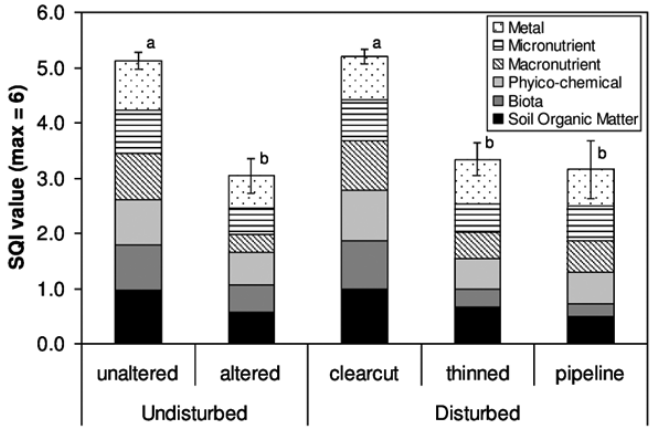

Fig. 3. Soil quality index (SQI) values for the sub-index based SQI. Data presented are means ± 1 standard error of the mean. Different lowercase letters indicate a significant difference at $p < 0.05$.

humid forested systems by Schlesinger et al. (1989) and in the current study (Table 3) and may help explain the lack of P correlations with microbial activity (Table 6). This similarity in P concentrations between the altered and unaltered soils may also be related to similarities in soil pH and bioavailable-Fe, which limits P availability at lower pH levels (Lindsay, 1979).

Soil-SO_4 concentrations showed contrasting trends between the current and previous studies. Much greater bioavailable-S (as SO_4) was found in altered soils of drier ecosystems (Blecker et al., 2010), while the unaltered soils contained greater bioavailable-S in the current study. Additionally, correlations between SO_4 and microbial activity differed as well (positive in the current study and negative in the previous work). The large differences in soil-SO_4 could relate to differences in geology and degree of hydrothermal alteration as well as the 10-fold increase in precipitation in the current study that could have leached out initially high levels of SO_4 found in the altered soils.

Micronutrients and Metals

The relatively high bioavailable-Al concentrations seen in previous studies of acid-sulfate soils (Blecker et al., 2010) were not found in the acid-sulfate soils of this study, as the unaltered soils had higher total and bioavailable-Al concentrations (Table 3). As with SO_4, differences in geology and climate between the two studies provide possible explanations. Bioavailable-Zn and -Ni and total-Na and-Co concentrations were greater in the unaltered soils, while bioavailable-Cu and -Mn were similar (Table 3). The numerous positive correlations between these elements and many of the microbial parameters (Table 6) show their potential impact on microbial activity in these systems. Correlations between these micronutrients, including Na, were also seen in acid-sulfate soils of more arid ecosystems (Blecker et al., 2010). Thus it appears that micronutrients could be important drivers of microbial activity across a wide climatic range of acid-sulfate impacted soils. Both As and Sb, which have adverse impacts on biota (Murata et al., 2005; Wang et al., 2011), were higher in the altered soils and tended to be negatively correlated with microbial activity.

Chemical/Physical Parameters

Though soil pH was lower in the altered soils (5.19 ± 0.09) compared with the unaltered soils (5.59 ± 0.15), the overall

Table 6. Correlation coefficients for selected microbial and abiotic soil parameters across the entire study area.

	AWCD	FDA	Aryl-sulfatase	Acid Phosphatase	Alkaline Phosphatase	Min-C	Min-N	Microbial biomass-C
TOC, %	0.57***	0.52***	0.77***	0.76***	0.670***	0.53***	0.17	0.44***
TN, %	0.56***	0.45***	0.82***	0.87***	0.79***	0.32*	0.29*	0.42***
Soil C/N	–0.22	–0.19	–0.44***	–0.59***	–0.54***	0.19	–0.30*	–0.22
NO_3–N, ppm	–0.01	0.10	0.07	0.27	0.08	–0.40**	0.31*	0.01
NH_4–N, ppm	0.14	0.15	0.31*	0.27	0.28*	0.20	0.02	0.19
Total-P, ppm	0.08	0.11	0.33*	0.48***	0.42**	–0.17	0.42***	–0.00
Olson's-P, ppm	0.10	0.38**	0.24	0.17	0.03	0.28*	–0.19	0.26
Total-K, %	0.12	0.08	–0.12	–0.10	–0.04	–0.27*	–0.00	–0.04
Mehlich-K, ppm	0.46***	0.15	0.38**	0.53***	0.58***	0.24	0.31*	0.29*
Total-S, %	–0.37**	–0.03	–0.20	–0.24	–0.28*	–0.16	–0.04	–0.36**
Mehlich-SO_4, ppm	0.63***	0.24	0.53***	0.58***	0.58***	0.46***	0.19	0.40**
Total-Ca, %	0.57***	0.41	0.59***	0.59***	0.52***	0.09	0.26	0.22
Mehlich-Ca, ppm	0.52***	0.16	0.42**	0.49***	0.54***	0.24	0.30*	0.30*
Total-As, ppm	–0.36	–0.39	–0.13	–0.02	–0.01	–0.22	0.189	0.14
Total-Na, %	0.41	0.30	0.54	0.57	0.47	–0.08	0.304	0.10
Total-Sb, ppm	–0.32	–0.36	–0.24	–0.23	–0.20	0.10	–0.25	0.23
Mehlich-Zn, ppm	0.52	0.35	0.66	0.72	0.68	0.36	0.23	0.42
pH	0.37**	0.09	0.13	0.09	0.16	0.15	0.02	0.18
EC, dS m^{-1}	0.44***	0.23	0.24	0.33*	0.24	0.55***	0.07	0.28*
Soil moisture, %	0.33*	0.09	0.56***	0.68***	0.66***	0.08	0.30*	0.30*
Bulk density, g cm^{-3}	–0.36**	–0.17	–0.56***	–0.59***	–0.66***	–0.25	–0.29*	–0.27

* Significant at $p < 0.05$.
** Significant at $p < 0.01$
*** Significant at $p < 0.001$.

difference was far less compared with previous studies in more arid climates, where the pH of acid-sulfate altered soils was typically <5.0 (Schlesinger et al., 1989; Blecker et al., 2010). One possible explanation is the 10-fold increase in precipitation in the current compared with previous studies, thus modifying the geologic impact on soil pH, an impact that was seen by Schlesinger et al. (1989). Though soil pH was significantly correlated with only one microbial parameter (AWCD; Table 6), its integration of numerous factors such as nutrient availability underlies a potential indirect role on microbial activity and diversity (Fierer and Jackson, 2006; Griffiths et al., 2011). In addition the similar pH values between the unaltered and clearcut soils may help to explain the similarities between these two soils for numerous other parameters. Electrical conductivity was twice as high in the unaltered compared with the altered soils, though overall quite low over the entire study area (Table 4). The impact of climate is again apparent as the EC values of the acid-sulfate soils in this study (0.015 ± 0.002 dS m^{-1}) were considerably lower than EC values of acid-sulfate soils of more arid systems (1.11 ± 0.31 dS m^{-1}; Blecker et al., 2010). The higher soil bulk density in the altered, thinned and pipeline soils could relate to lower soil organic matter and higher sand contents, with the added potential of compaction from disturbances related to the latter two soils. Negative impacts of higher bulk density on microbial activity are noted by the negative correlations (Table 6). Differences in soil moisture are likely due to a combination of vegetation, soil organic matter, particle size and bulk density, and are positively correlated with many of the measurements of microbial activity (Table 6). This is in contrast to previous work in a more arid climate in altered soils where correlations between soil moisture and microbial activity were largely absent (Blecker et al., 2010).

Vegetation

High variability likely masked statistical differences for many of the vegetation measurements (understory ANPP, canopy cover, shrub density), though differences in life form composition within these parameters were apparent (Fig. 1). The greatest difference in the understory vegetation was the abundance of manzanita in the lower pH, less fertile acid-sulfate soils at both Maidu and Lassen and its absence in the unaltered soils. This finding agrees with other research noting the tolerance of manzanita to lower soil moisture and pH conditions (Hubbert et al., 2001; Rose et al., 2003). *Pinus* sp. were more prevalent on the altered soils compared with the unaltered soils within Maidu, while both altered and unaltered soils within Lassen were dominated by *Abies* sp. Thus differences in tree community composition across the study area are impacted by both elevation/climate (Maidu vs. Lassen) and acid-sulfate alteration. Comparing acid-sulfate soil vegetation between the current and previous (more arid) study areas, coniferous trees dominate the altered soils in both areas, though climate likely drives differences in productivity for both the trees and understory vegetation (Schlesinger et al., 1989; Blecker et al., 2012).

Principal Component Analysis–Soil Quality Index (Canopy Cover)

This index approach suggests that a combination of lower concentrations of macro- and micronutrients along with elevated concentrations of certain metals in the altered soils could be impacting vegetation (as measured by canopy cover) in this ecosystem (Fig. 1). All of these nutrients, including Na, have demonstrated roles in controlling vegetative growth (Marschner, 2006), while As has been shown to inhibit growth (Smith et al., 1998; Eisler, 2004). Though pH had a minor contribution on the overall SQI score, its role in controlling element availability could be impacting the concentrations of the other elements in the SQI. The unaltered soils had the highest scores for each individual component and significantly differed from the altered soils except for pH and Cr (Fig. 2). Chromium was the only component that scored consistently lower for the disturbed soils (clearcut, thinned, pipeline) compared with the altered soils. Otherwise the clearcut soils scored higher, especially for the PC1 components (Table 5), which contribute the most to the overall SQI value. Though the thinned, pipeline, and altered soils had similar total SQI values, the individual components differed, especially concerning As, Ca, and Na.

In a previous acid-sulfate system study, unaltered soils also scored higher than their altered counterparts by an average of 52% (Blecker et al., 2012), compared with a 35% higher score for unaltered soils in this study. Climate likely plays an important role in narrowing the scores between unaltered and altered soils of the current study by modifying the impacts of acid-sulfate alteration. Common SQI indicator variables among the more arid sites (Blecker et al., 2012), and the current study were AWCD and Na, though all SQIs were comprised of one or two microbial variables and a combination of macro and micronutrients. Important variables in the more arid soils, sulfate and phosphate, did not differ among the soils in the current study (Table 1) nor correlate with canopy cover. Overall this approach not only differentiates among the different soil types, but also indicates which biotic and abiotic factors may be driving these differences.

CUMULATIVE SUB-INDEX SOIL QUALITY INDEX

The cumulative sub-index SQI approach produced a similar trend in SQI values (Fig. 3) among the soils as the PCA-SQI. The unaltered soils scored 41% higher on average compared with the altered soils, which was slightly higher than the previous SQI method (35%). Each sub-index scored higher for the unaltered soils, with the greatest differences in the micronutrient and metal sub-indices. As with the PCA-SQI approach, the clearcut soil scored similar to the unaltered soil, and significantly higher than the thinned and pipeline soils. Reasons for this difference could be greater recovery time since disturbance, and a more diverse and robust understory community, which would likely contribute to the higher SOM and biotic indices in particular. The physical-chemical sub-index scored higher for the clearcut soils, which had lower bulk density and greater soil moisture (Table 4). Again

these attributes would be more susceptible to disturbance than the nutrient and element concentrations, which are seen in the similarity of the macro-, micronutrient, and metal sub-indices among the clearcut, thinned and pipeline soils.

CONCLUSIONS

Increased precipitation in this system compared with more arid systems has narrowed the magnitude between vegetation and soil parameter differences at unaltered vs. acid-sulfate altered soils. Despite differences in soil chemical, physical, and biological parameters between geologically unaltered and relict hydrothermally altered areas, vegetative measurements of canopy cover, tree and shrub density and understory ANPP were largely similar. However, plant community composition differed as a function of geology/soils (unaltered v altered) and study site (Maidu vs. Lassen). The clearcut soils were more similar to the unaltered than the altered soils in terms of soil parameters, which were likely a function of the greater understory productivity compared with the other altered soils and similarities in integrating drivers, namely soil pH. Greater understory productivity and diversity, along with lower bulk density and higher soil moisture and organic matter content could also explain the greater microbial activity in the clearcut compared with the thinned and pipeline soils. Differences in macronutrients, micronutrients and metals also appear to drive microbial activity in the acid-sulfate altered systems. The SQI approaches identified similarities between the unaltered and clearcut soils, which scored higher than the altered, thinned and pipeline soils, and shows the potential utility of this approach as a monitoring tool and a means of identifying the key differences and drivers in this ecosystem.

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