

POLLEN SURFACE SAMPLES FOR PALEOENVIRONMENTAL
RECONSTRUCTION FROM THE COAST AND TRANSVERSE RANGES OF
SOUTHERN CALIFORNIA

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ABSTRACT

Modern pollen assemblages from forty-one sites in the southern California cismontane region are described, which serve as a modern analog reference set for developing Holocene paleoenvironmental reconstructions from fossil pollen sites in the mountains east of Los Angeles and San Diego. The reference assemblages are derived from soil surface samples. The pollen characteristics of the samples are described in detail, organized according to the major vegetation types occurring in the southern California mountains and nearby cismontane foothill regions. The characteristics of the samples in terms of their patterns in multivariate taxon space (using the squared chord distance, SCD) are also described, which demonstrate that the major vegetation types can be successfully distinguished by their pollen using the SCD, with some overlap across types that share dominant plant taxa. Threshold values of pollen representation and ratios of the pollen proportions of important taxa are shown to be useful refinements to the SCD information to help distinguish between samples from overlapping vegetation types. The overall quality of the sample set is found to be well-suited for the purpose of paleo-reconstruction of past climate and vegetation at regional montane fossil sites.

Key Words: southern California, pollen, surface samples, palynology, paleoecology, paleoclimate, modern analog technique.

Pollen assemblages from the sediment surfaces of lakes and small forest hollows, from moss polsters, and from the soil surface in small clearings in vegetation are commonly used to develop reference sets of the modern pollen “rain” characteristic of particular kinds of vegetation (e.g., Maher 1963; McAndrews and Wright 1969; Overpeck et al. 1985; Anderson and Davis 1988; Anderson et al. 1989; Davis 1995; Calcote 1998; Minckley and Whitlock 2000; Anderson and Koehler 2003). These sets of “surface samples” are often compared with fossil pollen assemblages preserved in lakes, bogs, forest hollows, and mountain wet meadows with the goal of reconstructing the vegetation that produced the fossil assemblages (e.g., Maher 1972; Overpeck et al. 1985; Anderson et al. 1989; Anderson 1990; Anderson and Smith 1994; Davis et al. 1998; Davis 1999). When used this way, particular surface samples are called “analog” when they closely match a fossil pollen assemblage, and the vegetation that produced the fossil pollen is assumed to be similar to the modern vegetation at its analog sites (Overpeck et al. 1985; Calcote 1998; Davis et al. 1998). Conversely, a fossil pollen sample is said to be a “no analog” assemblage if it does not match any surface sample closely (Overpeck et al. 1985; Calcote 1998).

This analog method is often extended by the assumption that the climate associated with a particular surface sample site is a major factor determining the vegetation at the site. Thus, the assumed likeness of ancient and modern vegetation for an analog situation can be interpreted to imply a similar closeness of ancient and modern climates (e.g., Overpeck et al. 1985; Anderson et al. 1989; Guiot et al. 1989; Guiot 1990; Bartlein and Whitlock 1993; Anderson and Smith 1994; Peyron et al. 1998; Davis 1999; Davis et al. 2000). This technique of comparing modern and fossil pollen assemblages to reconstruct past climates and vegetation is termed the “modern analog technique” or MAT (Bartlein and Whitlock 1993; Davis 1995; Calcote 1998; Davis et al. 1998), as distinguished from other quantitative reconstruction strategies such as “transfer functions” and “response surfaces”, which associate modern and fossil pollen assemblages directly with climate parameters via regression equations and other mathematical fitting techniques (e.g., Webb and Bryson 1972; Bryson and Kutzbach 1974; Bernabo 1981; Howe and Webb 1983; Bartlein et al. 1984; Bartlein and Webb 1985; Bartlein et al. 1986; Prentice et al. 1991; Bartlein and Whitlock 1993; Webb et al. 1993; Bartlein et al. 1998).

The work presented in this paper describes a new surface sample set from the cismontane region of southern California (west of the eastern, desert crest of the coastal mountains; Fig. 1), whose purpose is to provide calibration data for climate and vegetation reconstructions from fossil pollen sites in the

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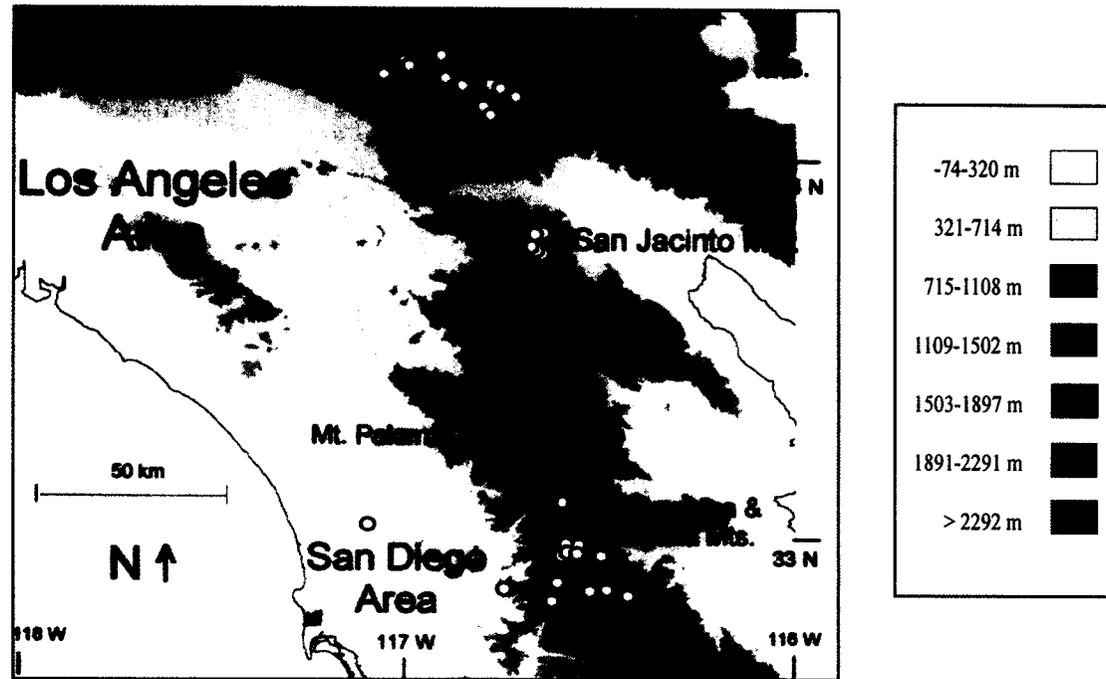


FIG. 1. Digital elevation map of southwestern California, U.S.A. Surface sample sites used in this study are shown as white dots. Contour lines are shown at sea level and 1500 m elevations. Dark gray-to-black shaded polygons approximately represent regional montane areas (>1500 m; max. elevation, 3474 m). Source data and elevation ranges for the DEM base map are from the United States Department of the Interior, Geological Survey.

region's Coast and Transverse Ranges (Wahl 2002; E. Wahl, Holocene paleoenvironmental reconstruction in the southern California Peninsular and Transverse Ranges, *in preparation*). The pollen representation of these samples is examined in two complementary ways: a) the pollen taxonomic characteristics of the samples are described and related to regional vegetation and climate characteristics; and b) the relationships among the samples are analyzed in terms of a multivariate distance metric commonly used for analog selection with pollen and other microbiological data (squared chord distance (SCD); Overpeck et al. 1985). The pollen/vegetation relationships of samples of special interest are examined in Appendix 1. The general issue of appropriate levels of SCD closeness for determining analogs is treated in Wahl (*in press*).

METHODS

Field Methods

Forty-one sites were sampled in the San Bernardino, San Jacinto, Cuyamaca, Laguna, and Palomar Mountains of southern California during 1996–1998 (Table 1, Fig. 1). Five to ten samples of sediment from the interface of the humus and underlying soil, or of the top few centimeters of the soil surface when humus was absent or not well developed, were collected within a radius of 20–40 m at

each site, following the methods of Adam and Mehringer (1975). Sampling was typically done in small to large openings (20–200 m across) in the vegetation canopy, or in a few cases in the understory of relatively open forests. This criterion was applied so that the sample sites would mimic as much as possible the pollen deposition characteristics of the wet meadows from which fossil pollen samples have been extracted (Wahl 2002). It is recognized that this mimicry is exclusive of pollen from vegetation restricted to the hydric meadow environments, which is taken into account in quantitative and qualitative comparison of the fossil and surface pollen assemblages. In the cases of the three mixed chaparral samples and the coastal sage scrub sample, the samples were taken in smaller openings (3–10 m across) and two to four adjacent openings were included in each case.

The samples cover the range of widely-occurring vegetation types in the mountain and adjacent locations of the study area, including: montane conifer forest and woodland; mixed conifer-oak forest and woodland; oak woodland; manzanita chaparral (dominated by *Arctostaphylos* spp); chamise chaparral (dominated by *Adenostoma fasciculatum*); mixed chaparral (including *A. fasciculatum*, *Rhus* spp., *Rhamnus* spp., *Quercus* spp., *Arctostaphylos* spp., *Ceanothus* spp., and other shrubs); sagebrush (*Artemisia tridentata*)-pine steppe; and coastal-area

TABLE 1. SURFACE SAMPLE SITES. Vegetation characterizations follow the usage of Munz (1974), Thorne (1988), and Hickman (1996). "Jeffrey", "Limber", and "Lodgepole" in the conifer-dominated forest group are common names of important regional pine species. The botanical names are *Pinus jeffreyi*, *P. lambertiana*, and *P. contorta* subsp. *murrayana*, respectively. Other botanical names are given in the text.

Sample	Main vegetation category	Latitude			Longitude			Elevation (m)	
		Deg	Min	Sec	Deg	Min	Sec	Sec	Min
1	Lodgepole/Jeffrey/Fir Forest	34	12	10	116	46	55	2774	
2	Western Juniper/Lodgepole Forest/Woodland	34	12	0	116	45	53	2746	
3	Fir/Lodgepole Forest	34	12	4	116	45	57	2707	
4	Fir/Limber/Juniper Woodland	34	12	30	116	51	19	2597	
5	Fir/Jeffrey/Lodgepole Forest	34	7	21	116	46	51	2499	
6	Jeffrey/Fir Forest	34	7	29	116	46	56	2481	
7	Pine/Fir/Oak Forest	34	14	6	117	3	7	2243	
8	Pine/Fir Forest	34	15	58	117	0	21	2228	
9	Pine/Fir Forest	34	16	5	117	0	22	2228	
10	Pine/Western Juniper/Fir Forest	34	10	20	116	43	4	2438	
11	Lodgepole/Limber Forest	33	48	2	116	40	21	2926	
12	Pine/Fir Forest	34	13	19	116	53	58	2402	
13	Pine/Fir Forest	34	16	53	116	54	51	2286	
14	Lodgepole/Fir Forest	33	48	24	116	39	12	2682	
15	Fir/Pine Forest—Aspen Grove (> dense with Aspen)	34	8	54	116	47	59	2170	
16	Fir/Pine Forest—Aspen Grove (< dense with Aspen)	34	8	54	116	47	49	2170	
17	Pine/Fir/Oak/Cedar Forest	32	56	56	116	36	16	1890	
18	Pine/Alder/Fir Forest	33	46	9	116	39	44	2405	
19	Pine/Fir Forest	33	46	9	116	39	44	2405	
20	Pine/Fir Forest	33	46	9	116	39	44	2402	
21	Manzanita Chaparral	32	56	38	116	29	28	1692	
22	Pine/Oak Forest	32	50	15	116	25	24	1829	
23	Oak/Conifer Forest	34	8	5	116	58	56	1682	
24	Cedar/Pine/Oak/Fir Forest	32	57	15	116	35	16	1573	
25	Pine/Oak Forest	32	51	9	116	28	56	1554	
26	Oak/Cedar/Pine Forest	32	58	2	116	35	8	1451	
27	Oak/Cedar Stand-in Pine/Oak/Cedar/Fir Forest	32	58	10	116	35	1	1448	
28	Pine/Oak Open Forest Clearing	32	58	15	116	34	26	1439	
29	Oak/Pine Forest	33	5	22	116	35	40	1228	
30	Cedar/Oak/Fir Forest—Burn Site	33	20	13	116	54	27	1573	
31	Meadow-in Pine/Oak/Cedar/Fir Forest	32	58	8	116	35	4	1439	
32	Meadow-in Pine/Oak/Cedar/Fir Forest	32	58	6	116	35	5	1434	
33	Mixed Chaparral—Mt. Mahogany dominated	32	56	58	116	33	35	1384	
34	Sagebrush Steppe (> open phase)	32	51	2	116	31	17	1132	
35	Sagebrush Steppe (> closed phase)	32	51	5	116	31	22	1125	
36	Oak Woodland (> closed phase)	33	17	28	116	50	2	1414	
37	Oak Woodland (> open phase)	32	49	9	116	37	7	1073	
38	Mixed Chaparral	32	52	9	116	36	29	1091	
39	Mixed Chaparral	32	49	21	116	37	17	1061	
40	Chamise Chaparral	32	51	21	116	44	30	817	
41	Coastal Sage Scrub	33	1	49	117	5	34	244	

sage (*Artemisia californica*) scrub. Two lower-montane meadow samples and a sample from a recently burned site in conifer-oak forest were also included for additional calibration. This coverage was designed to include vegetation types both within and beyond the probable range of vegetation that occurred during the Holocene surrounding the wet meadow fossil sites—based on both the modern vegetation/climate relationships in the region (Munz 1974; Thorne 1988; cf. companion paper, Wahl 2003) and the range of climate change from late-glacial to modern times in nearby portions of the Southwest, as determined by paleoecological records and comparisons of paleo-data with climate model simulations (cf. Thompson et al. 1993; Bartlein et al. 1998). The characterizations of the vegetation types follow Munz (1974), Beauchamp (1986), and Thorne (1988), and are based on the percentage cover of plant taxa at each site, documented in Wahl (2002). All scientific names for plants conform to those in Hickman (1996).

Laboratory Methods

The samples were prepared according to standard chemical methods for extracting pollen from sediments (Faegri and Iversen 1989; E. Cushing, *personal communication*), modified according to the characteristics of the specific samples in this study. These modifications were: a) each sample was initially dispersed in a 5% solution of sodium pyrophosphate and sieved through 120 μm and 8 μm mesh screens to remove coarse and fine debris; b) a hot KOH bath was used only on samples from the humus/soil interface; c) HCl acid wash was not used since these samples do not contain carbonates; and d) HF acid bath was not used on samples with little mineral content. A known concentration of exotic *Lycopodium* spores was added to each sample so that pollen concentrations could be calculated.

The samples were counted at 200 \times to 1000 \times magnification. 300–400 grains were counted for most samples; four samples had between 400 and 700 grains and in two samples 240–300 grains were counted. Reference pollen came from the collection of the University of Minnesota Herbarium (code designation MIN), and from the personal collections of M. B. Davis, K. L. Cole, and E. Wahl. Rules for summing *Pinus* (pine), *Abies* (fir), and Pinaceae-undifferentiated fragments are described in Wahl (2002). Unidentifiable pollen was characterized as degraded, crumpled, broken, corroded, or obscured, following the usage of E. Cushing (*personal communication*).

In Figure 2, the “Other Asteraceae” category includes all pollen of the *Ambrosia* tribe, along with Tubuliflorae-undifferentiated and Liguliflorae-undifferentiated pollen. The “*Rhus/Toxicodendron*” category also includes the pollen of *Malosma laurina* (laurel sumac), a characteristic species of the coastal sage scrub also known as *Rhus laurina*

(Munz 1974; Hickman 1996). With the exception of *Pinus*, where a genus name is given without a specific epithet, it means that pollen grains of species within the genus are not reliably distinguishable with standard identification techniques. Several individual species and groups of species of *Pinus* within the study region have pollen that is distinguishable, with allowance for intermediate and indeterminate characteristics (Wahl 2002). However, in Figure 2 and the analysis of SCD’s between the samples, *Pinus* is reported as a single type since most pine grains counted were either indeterminate or of the mixed *Pinus ponderosa/jeffreyi/coulteri* type and since few *Pinus* grains can be distinguished to sub-generic categories in the fossil pollen record for which these surface samples are used as an analog set.

The *Abies* pollen in these samples almost certainly comes from the species *Abies concolor* (white fir), which is the only native fir growing in the region (Munz 1974). No non-native firs were noted at or near any of the sample sites. The Cupressaceae-undifferentiated pollen in these samples most likely comes from *Calocedrus decurrens* (incense cedar) at most forest sites, from *Juniperus occidentalis*, var. *australis* (western juniper, *sensu* Munz 1974) at forest/woodland sites 2, 3 and 10, and from western juniper and *Juniperus osteosperma* (Utah juniper) at woodland site 4. Incense cedar, western juniper, and Utah juniper were the only native members of the Cupressaceae family at or near their respective sample sites (Munz 1974), and no non-native members of this family were noted at or near these locations.

Quantitative Methods

Temperature and precipitation values for each sample were assigned from instrumental data (NOAA) and precipitation map data (*California Annual Precipitation* 1999) by deriving six elevation/temperature relationships and eleven elevation/precipitation relationships for the individual mountain ranges and portions of individual ranges (Wahl 2003). The instrumental data coverage is as spatially fine as possible given available data sources. The normative period of record is 1961–1990, other periods as close to this period as possible were used when the full range 1961–1990 was not available for a specific station. The names and locations of the instrumental stations, the specific elevation/climate functions, and deviations from the normative period of record are detailed in Wahl (2003).

The squared chord distance (SCD) used to examine similarity and dissimilarity between the surface samples in multivariate pollen-taxon space is defined by the formula:

$$\text{SCD}_{jk} = \sum_i (p_{ij}^{0.5} - p_{ik}^{0.5})^2;$$

where p is the pollen proportion (expressed in the range 0–1) of a taxon included in the comparison, $i = 1 \dots n$ are the included pollen types, and j

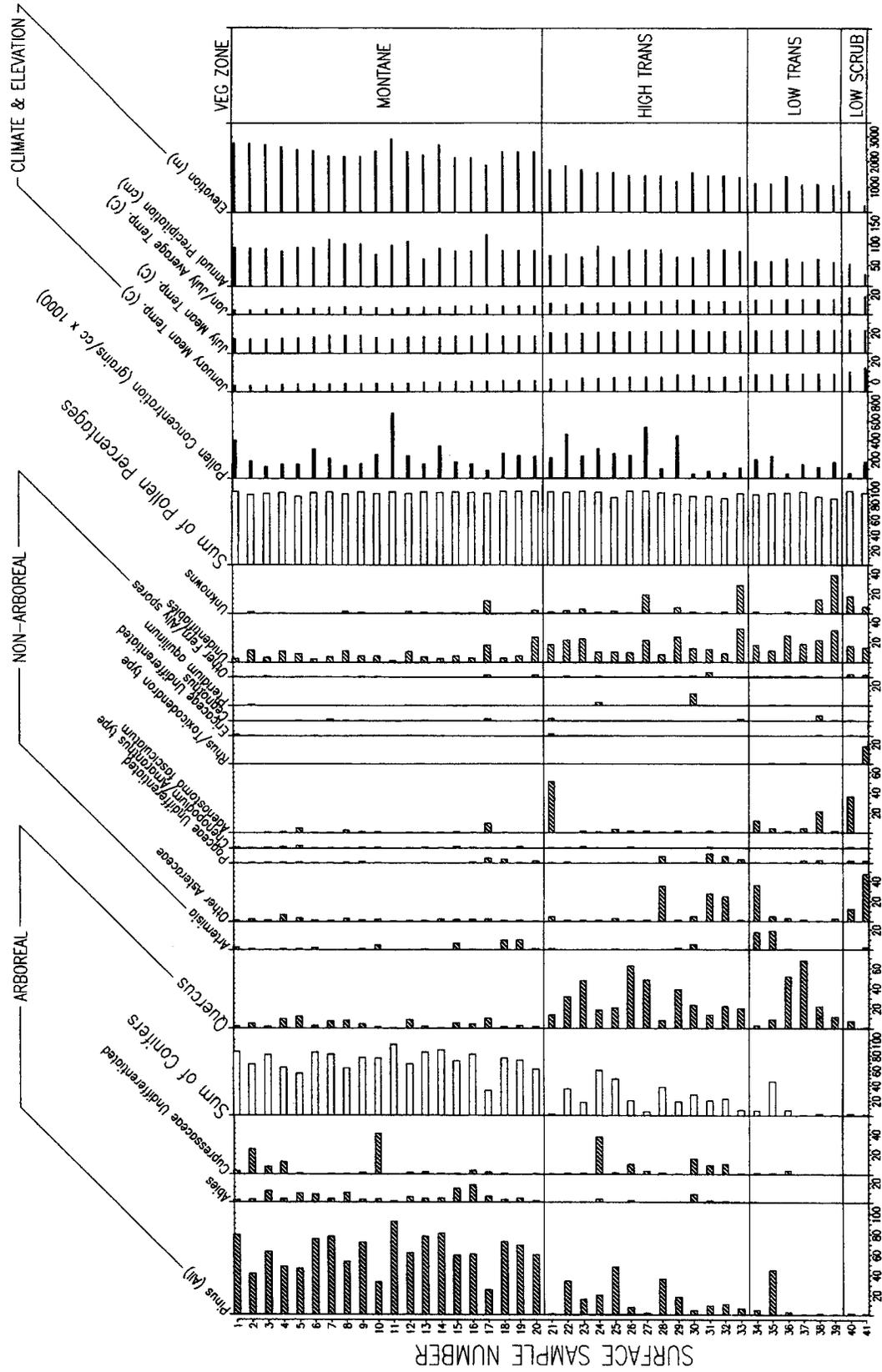


FIG. 2. Pollen diagram of surface samples. Sample numbering conforms to Table 1. Measurements on the horizontal axis are pollen percentages, except as defined otherwise. The term "High Trans" refers to the Lower-Montane Conifer-Oak Forests, Meadows, and Chaparral grouping in Table 1, sometimes called "high transition" vegetation in the region. The term "Low Trans" refers to the Steppe, Mixed Chaparral, and Oak Woodland grouping in Table 1, sometimes called "low transition" vegetation. The term "transition" (cf. Beauchamp 1986) refers to the lower montane and upper foothill areas of the region as a heterogeneous zone of vegetation between the montane conifer-dominated forests and the scrub chaparral and coastal sage vegetation that dominates the lower foothill and coastal plain areas.

and k represent the two samples being compared (Overpeck et al. 1985). The entire range of the SCD is zero to two. The range of best SCD values that jointly select like vegetation sample comparisons as analogs and exclude unlike vegetation sample comparisons as non-analogs is ~ 0.20 – 0.27 for this set of samples. This range of best SCD “cutoff” values was determined using a new analytical method that jointly minimizes the occurrence of false positive comparisons (misidentification of samples from different vegetation types as being from the same type) and false negative comparisons (misidentification of samples from the same vegetation type as being from different types), described in Wahl (in press).

The range 0.20–0.27 is generally larger than results from related studies examining SCD cutoff values for analog selection in North America. Specifically: a) Overpeck et al. (1985) determined cutoffs of 0.15 and 0.12 for vegetation formations and forest types in eastern North America, respectively; b) Bartlein and Whitlock (1993) used a cutoff of 0.205 for north-midwestern/northeastern North America vegetation formations; c) Calcote (1998) determined a cutoff of 0.05 for forest stand types (spatially and vegetatively finer-scaled than the definitions used by Overpeck et al. and Bartlein and Whitlock) in northern Wisconsin and the Upper Peninsula of Michigan; d) Anderson et al. (1989) identified 0.095 as the cutoff for “good analogs”/“strong analogs” for grasslands, parklands, boreal forests, and tundra in interior Alaska and far northwestern North America, and identified 0.185 as separating “analog” from “no analog” situations; e) Oswald et al. (2003) determined a cutoff of 0.075 for two different kinds of tundra vegetation in Alaska; and f) Davis (1995) determined a cutoff of 0.15 for a variety of vegetation types in large portions of the western and southwestern United States. With the exception of Oswald et al., these studies focus primarily on the reduction of false positive errors and do not rigorously consider the concomitant loss of information resulting from false negative errors, which reduces the strict comparability of their results and those from the data set reported here. The results of several new studies (Gavin et al. 2003; Oswald et al. 2003; Wahl in press) demonstrate that appropriate analog cutoff levels can be expected to vary among surface sample sets from different regions with associated differences in vegetation, and thus should be separately examined for regionally-specific data sets.

The taxa included in the SCD calculations are the same as those shown in the pollen diagram in Figure 2. The *Ceanothus* and *Chenopodium/Amaranthus* pollen types and the “Other Fern/Ally” spore category are summed together with the unknown and unidentifiable categories in the calculations. This grouping adds together the least represented non-arboreal pollen and spore types (with the exception of the Ericaceae-undifferentiated tax-

on, which in this region is largely associated with manzanita chaparral) with the unidentifiables and unknowns to form a generic category of largely non-arboreal pollen. Categorizing unknown and unidentifiable pollen as largely non-arboreal is justified based on experience in pollen counting, in which the pollen types of all the regional trees are known and the only kind of arboreal pollen that may have been included in the unidentifiable category due to poor preservation is *Quercus* (oak). (Poorly-preserved material with some resemblance to *Pinus*, *Abies*, *Alnus* (alder), *Populus* (cottonwood/aspen), or Cupressaceae-undifferentiated pollen either was positively identifiable as one of these types or could not be definitively considered to be pollen.) The possible *Quercus* grains that were included in the unidentifiable category are generally much less than 30% of the total unidentifiable pollen; the exceptions are in samples with otherwise high levels of *Quercus* pollen. At least, the combined, largely non-arboreal category represents pollen that is not from coniferous trees. Since the distinction between conifer-dominated forests and other kinds of vegetation in the region is the single most important characteristic of the pollen record in this study, including the unidentifiables and unknowns in this way preserves useful information. The proportions of the included categories were calculated on the basis of the sum of included pollen and spores, which is standard practice in calculating SCD (Calcote 1998). Due to idiosyncratic biases in the pollen representation characteristics of sample 17 (montane conifer forest on Mt. Cuyamaca), caused by site-specific orographic and vegetation factors (Wahl 2002), the *Adenostoma fasciculatum* and *Ceanothus* pollen types were excluded from the pollen sum of this sample in calculating the SCD's.

RESULTS

The location, elevation, and type of vegetation for each surface sample are listed in Table 1. Pollen percentages of the samples for 14 taxonomic categories, along with unidentifiable and unknown pollen, are shown in Figure 2; the pollen sum includes all pollen and fern/ally spores. The graphed categories account for over 90% of total pollen in 37 of the samples, and over 87% in the remaining four. The primary pollen count data are archived with the North American Pollen Data Base and are accessible on the World Wide Web at <http://www.ngdc.noaa.gov/paleo/pollen.html>. Figure 2 also gives January (monthly mean) temperature, July (monthly mean) temperature, average January and July temperature, and annual precipitation for each surface sample site. Average January and July temperature is included as an approximation of annual temperature, at the scale of resolution available in some paleoclimate model experiments that have been extensively compared to

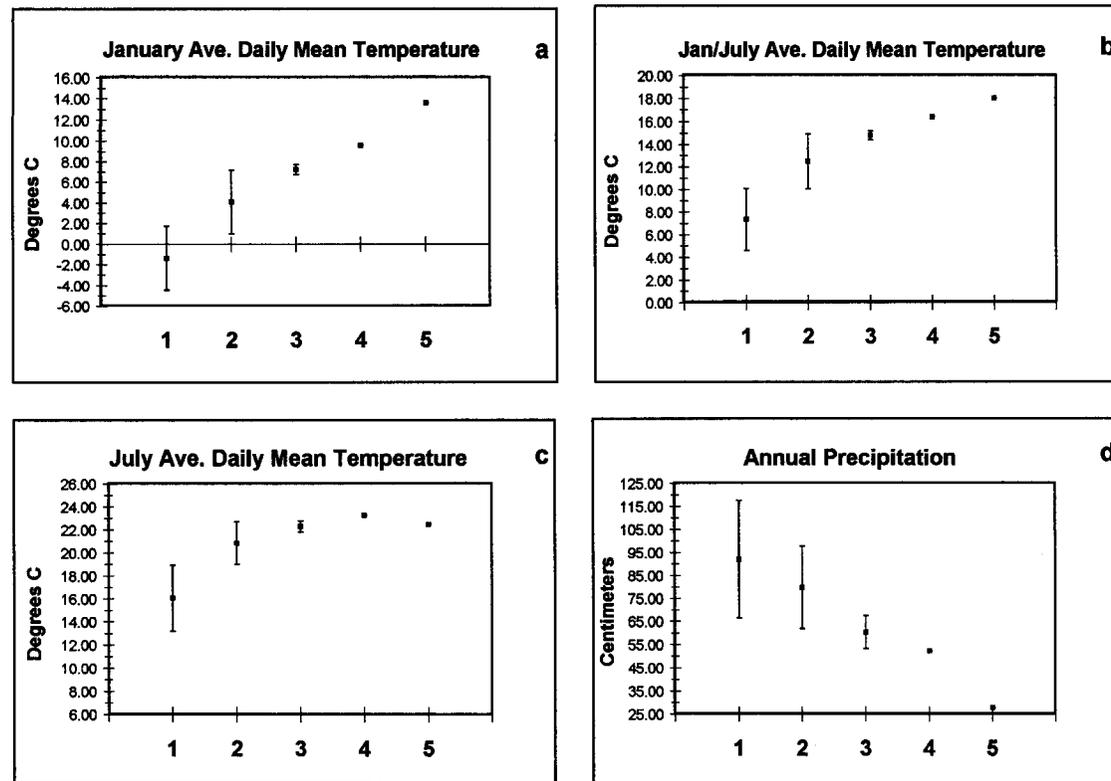


FIG. 3. Climate ranges of vegetation categories. Categories conform to Table 1 and Figure 2: 1) Upper- and Mid-Montane Conifer-dominated Forests; 2) Lower-Montane Vegetation; 3) Steppe, Mixed Chaparral, and Oak Woodland; 4) Chamise Chaparral; and 5) Coastal Sage Scrub. Data points and error bars for 1-3 show the mean and $2\times$ standard deviation for all samples in the category. Data points for 4-5 show the value for the one sample in the category.

North American paleoclimate data (COHMAP members 1988; Thompson et al. 1993). The average values and ranges of variation of the climate variables, organized by vegetation category, are shown in Figure 3.

Vegetation of the Samples in Association with Temperature and Precipitation

The vegetation at the sample sites corresponds closely with an elevation-related temperature gradient (higher elevation/lower temperature), and similarly, but somewhat less closely, with an elevation-related precipitation gradient (higher elevation/higher precipitation) (Figs. 2, 3). These correspondences are commonly noted in the botanical and ecological literature of the region (Munz 1974; Beauchamp 1986; Thorne 1988), and are validated independently here by determination of climate values specific to each sample site (Wahl 2003). The samples span an approximately continuous range of elevations between 800–2800 m, along with one near-coastal site at 244 m; they represent eleven vegetation types, which in turn can be aggregated into five broader vegetation categories (Table 1, Fig. 2). The categories and vegetation types in-

clude: 1) mid- and upper-montane conifer-dominated forests and woodlands; 2) lower-montane conifer-oak forests, meadows, and relatively cool-temperature manzanita and mixed chaparrals; 3) lower-montane and foothill sagebrush-pine steppe, oak woodlands, and relatively warm-temperature mixed chaparrals; 4) foothill chamise chaparral; and 5) low-elevation coastal sage scrub.

The vegetation categories, and types within each category, correspond most closely with the gradient of January temperature (Fig. 3) (Wahl 2003). Thus, in Table 1 and Figure 2 the samples are arranged in a nested order according to: a) average January temperature of the five categories, b) average January temperature of the vegetation types within each category, and c) January temperature of the individual samples within each vegetation type.

Pollen Characteristics of the Samples

Montane conifer forests and conifer-oak forests. The most salient characteristic of the pollen data is the distinction between the montane conifer-dominated forests/woodlands and the rest of the samples. This distinction is evident in the fourth and fifth columns of the percentages in Figure 2, which

show the sum of conifer pollen and *Quercus* pollen, respectively. The sharp switch from very little *Quercus* pollen in the montane coniferous forests to much greater percentages in many of the lower-montane and foothill samples closely parallels the presence/absence of oak trees and shrubs in the regional vegetation (cf. Munz 1974; Thorne 1988; Roberts 1995).

Specifically, samples from the relatively cooler, wetter conifer-dominated forests (1–20) can be readily distinguished from the relatively warmer, drier mixed conifer-oak forests (22–30) by the percentage of *Quercus* pollen in each forest type. In the samples reported here, *Quercus* pollen never exceeds 11.5% in the montane conifer-dominated forests and always exceeds 18% in mixed conifer-oak forests, with one exception. The exception is sample 28, from a relatively large opening (~60 m diameter) in mixed pine-oak forest; *Quercus* pollen representation would be 12.5% in this sample if the large percentages of Other Asteraceae and Poaceae-undifferentiated (grass) pollen that come from plants confined to the opening were eliminated. This distinction in pollen representation between forest types is strongly consistent with the pollen spectra reported from other California surface samples. *Quercus* pollen always exceeds 19% in mixed conifer-oak forests and never exceeds 9.5% in conifer-dominated forests (with one exception, discussed below) in the only other reported surface sample network from southern California (Anderson and Koehler 2003), and it averages 18% in “xeric forests” and 8% in “mesic forests” sampled between 34° and 38°N (Davis 1995). Moreover, the higher representations of *Quercus* pollen in Davis’ samples are associated with annual precipitation between 50–90 cm, a range similar to (but extending lower than) that of the conifer-oak forest samples reported here (Fig. 2; Table 3 in Wahl 2003). Adam and West (1983) demonstrate a similar relationship between elevation and *Pinus/Quercus* pollen representation for the area near Clear Lake in northern California, which they use to calibrate climate reconstructions over the last 128,000 years. Within the conifer-oak forests, the relative dominance of conifers and oaks in the vegetation is reliably reflected by the relative proportions of conifer and *Quercus* pollen in the surface samples: a conifer pollen/*Quercus* pollen ratio greater than one (>1) signifies a forest with more conifers than oaks, whereas a ratio less than one (<1) signifies a forest with more oaks than conifers.

Characteristics of conifer pollen representation for the surface samples in and near the fossil meadow sites are described in Appendix 1.

Chaparral, steppe, oak woodland, and sage scrub vegetation. The chaparral (21, 33, 38–40), steppe (34, 35), oak woodland (36, 37), and coastal scrub (41) samples are characterized generally by very low percentages (<6.5%) of *Pinus* and other

conifer pollen, and by significant percentages of pollen from plants specific to each site’s vegetation. The low *Pinus* pollen levels, even in vegetation relatively near forest with significant proportions of pine, are consistent with the results of Anderson and Koehler (2003), and with observations from nearby northwestern Mexico (Orvis 1998), the American Sonoran Desert (Hevly et al. 1965), and other parts of California (Davis 1995). For example, the highest pine pollen recorded in this group, 6.3%, is in sample 33, less than 2 km in the prevailing downwind direction (E and SE) from extensive pine-oak forest. Exceptions to these general characterizations are exhibited by: a) sample 21, which has a nearly mono-specific cover of manzanita shrubs, and yet has <2% Ericaceae-undifferentiated pollen (insect-pollinated) along with 51% *Adenostoma fasciculatum* pollen (wind-pollinated)—presumably from chamise plants at the fringe of the site; b) sample 33, which is a “cool” mixed chaparral dominated by *Cercocarpus betuloides* (mountain mahogany), and yet has <2% *Cercocarpus* pollen (presumably insect-pollinated); and c) sample 35, which was taken in a small pine stand within sagebrush-pine steppe and has 44% *Pinus* pollen—contrasting sharply with sample 34 (~200 m away in more open steppe with no pines), which has nearly the same proportion of *Artemisia* pollen as sample 35, but <5% *Pinus* pollen and a very high percentage of Other Asteraceae pollen (reflecting the plant cover between the sagebrush plants).

Unknown and unidentifiable pollen. The highest values of unknown pollen in this set occur in three chaparral samples (33, 39, and 40) and in an oak-cedar stand surrounded by conifer-oak forest (27). The highest values of unidentifiable pollen also occur in the non-forested samples (esp. 33 and 39), along with some high values in the conifer-oak forest samples (22, 23, 27, and 29) and a high value in one conifer forest sample (20). The high levels of unidentifiable pollen reflect the one significant disadvantage of using soil surface samples; biological activity within the soil and oxidative weathering in the aerobic conditions of the soil surface can lead to degradation in pollen preservation (Davis 1995; Orvis 1998). However, since the surfaces of the wet meadow fossil sites used in the paleo-reconstruction portion of this research are much more akin to soil surfaces than they are to the surfaces of moss polsters (the other potential source of analog samples widely available in the region, cf. Anderson and Koehler 2003), it was decided that soil samples would provide the best analogs for the fossil samples. Moss polsters are also subject to biases of representation from overhanging and adjacent plants that soil samples collected according to the methods of Adam and Mehringer (1975) avoid (Davis 1995). The high unknown pollen values in the three chaparral samples noted are attributable to: a) conservative identification criteria—a notable ex-

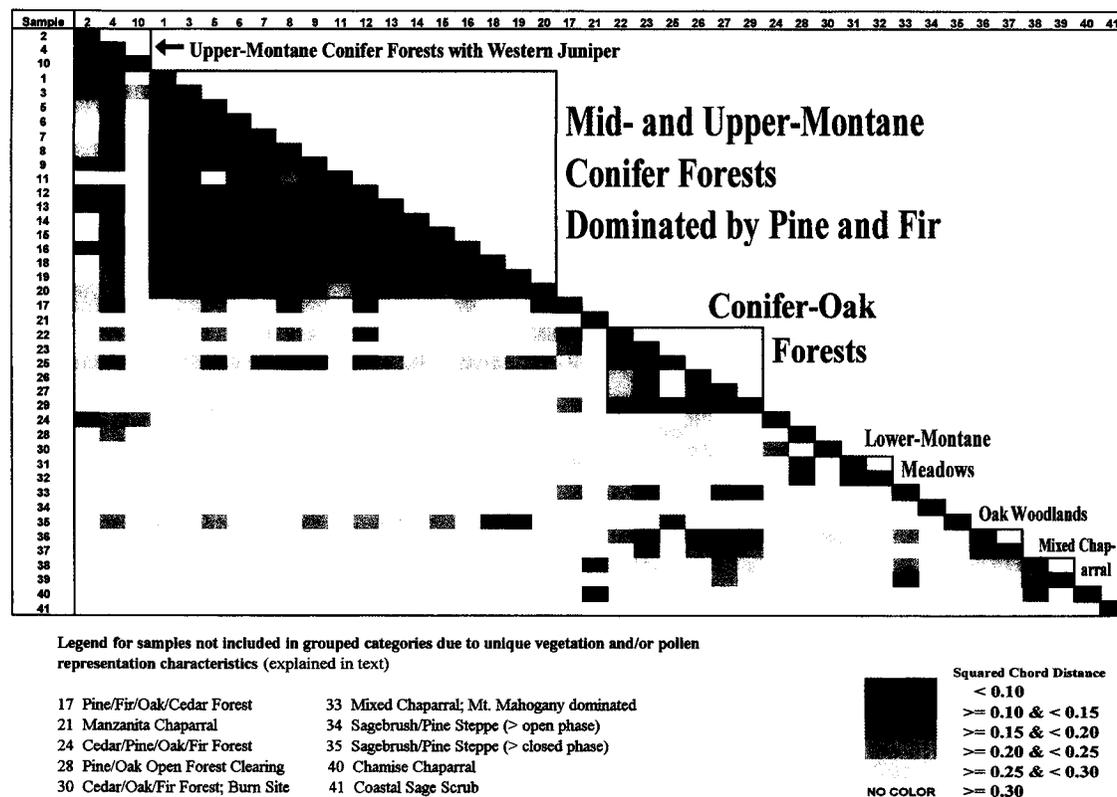


FIG. 4. Pair-wise comparison of southern California surface samples in terms of squared chord distance (SCD) dissimilarity metric. The numbers along the axes are the identification numbers of the samples from Table 1 and Figure 2, in the same order for each axis. Each cell along and below the diagonal indicates the SCD between two samples; for example, the values along the diagonal are all in the lowest (black) ranking, since these cells compare each surface sample to itself and thus have a dissimilarity value of zero. The sequence of the samples in Figure 4 varies slightly from the temperature ordering of Table 1 and Figure 2, in order to group together the three montane conifer forest/woodland samples with significant cover of western juniper (2, 4, and 10) and distinguish forest samples 17, 24, and 28, which have unique pollen-representation characteristics (Fig. 2). The heavy-outline boxes indicate comparisons between samples from similar vegetation. From upper left to lower right, these groups include: a) the three forest/woodland samples with significant cover of western juniper; b) all other samples from the montane conifer-dominated forests, with the exception of sample 17 (placed immediately after this group); c) the mixed conifer-oak forest samples, with the exception of samples 24 and 28 (placed immediately after this group); d) the two lower-montane meadow samples; e) the two oak woodland samples; and f) the two mixed chaparral samples. Samples not included in the outlined groups have relatively unique pollen characteristics, and are best considered separately for the purpose of examining the SCD's.

ample is a tricolporate type that might be immature *Adenostoma fasciculatum* pollen, but which could not be conclusively identified as such; b) the high heterogeneity of the vegetation at the mixed chaparral sites; and, to a lesser extent, c) the lack of a comprehensive manual for the pollen of the western United States (cf. Davis 1995). Combined values of unidentifiable and unknown pollen are greater than 33% in five samples (27, 33, 38, 39, and 40), and greater than 25% in ten samples (the five already listed plus 17, 20, 23, 29, and 36).

Similarities and Dissimilarities between Samples in Multivariate Space

Figure 4 shows the 861 possible comparisons among the 41 surface samples, in terms of the

SCD's between the pollen assemblages. Based on determination of SCD threshold values that maximally distinguish within-group comparisons from outside-of-group comparisons (described above), pairs of samples with SCD's ≤ 0.25 are characterized as "similar" in the results below.

"Within-group" comparisons. The most important feature of the SCD comparisons is that the closest similarities (represented by the darkest shadings) generally occur within the like-vegetation groupings. The only significant weakening of this general pattern occurs in the conifer-oak forest group, reflecting the heterogeneity within this vegetation type. In particular, samples 26 and 27 have SCD's > 0.25 with samples 22 and 25, reflecting the

significant differences in the relative dominance of pines (22 and 25) and oaks (26 and 27) at the sample sites.

“*Outside-of-group*” comparisons: *conifer-dominated forests*. Of the three conifer forest/woodland samples with significant cover of western juniper, two (2 and 4) are similar to a number of the samples in the main conifer forest group dominated by pine and fir, while the third (10) is not similar to any sample in this group at the 0.25 level. The number and closeness of analogs between these two groups is inversely related to the relative dominance of Cupressaceae-undifferentiated pollen in samples 2, 4, and 10. Because Cupressaceae-undifferentiated pollen in sample 4 is relatively low in relation to samples 2 and 10, this sample also shows similarity to lower-montane conifer-oak forests with relatively high *Pinus* pollen representation (samples 22, 25, and 28). The likeness between samples 4 and 28 in terms of *Quercus* and unidentifiable pollen representation also helps offset the difference between them in the Other Asteraceae category. Forest sample 24 with abundant incense cedar pollen also has low SCD's with samples 2, 4, and 10.

The most notable characteristic of the outside-of-group similarities for the block of conifer forests dominated by pine and fir is how sharply this group is distinguished from the other vegetation types. Along with the similarities with samples 2 and 4 noted above, the forests in this block have similarities with only four other samples: 17, 22, 25, and 35. The similarities between the main group of conifer forests and samples 22 and 25 reflect the high *Pinus* pollen values of the latter two samples in relation to the other conifer-oak forests. The SCD similarities between several of the conifer-dominated forests (including sample 4) and sample 35 (sagebrush-pine steppe) are driven by the anomalously high percentage of *Pinus* pollen in sample 35.

Along with the similarities it has with the other conifer-dominated forests, sample 17 is also similar to three samples in the conifer-oak forest group (22, 23, and 29), due to its relatively low percentage of *Pinus* pollen and relatively high percentage of *Quercus* pollen in relation to the other conifer-dominated forests. The similarity between sample 17 and mixed chaparral sample 33 also is related to the relatively low *Pinus*/high *Quercus* pollen representation of sample 17, and to its relatively high percentage of unknown pollen.

“*Outside-of-group*” comparisons: *conifer-oak forests*. Along with the similarities it has with the conifer-dominated forests, the block of conifer-oak forests has expectable similarities with the oak woodland samples (36 and 37). Forest sample 27 is similar to the three mixed chaparral samples (33, 38, and 39), due to significant *Quercus* pollen from scrub oaks in the chaparral, along with the low lev-

els of *Pinus* and high levels of unidentifiable and unknown pollen shared by these samples. Three of the other conifer-oak forest samples (22, 23, and 29) also are similar to sample 33 because of the high *Quercus* and unidentifiable pollen common to these forest samples.

The similarities between sample 28 and lower-montane meadow samples 31 and 32 are expectable, since sample 28 is from a relatively large forest opening (~60 m diameter) in the same kind of conifer-oak forest matrix as samples 31 and 32. In these comparisons, high levels of Other Asteraceae pollen compensate for the differences in *Pinus* pollen representation between sample 28 and the meadow samples.

“*Outside-of-group*” comparisons: *chaparral, steppe, oak woodland, and sage scrub vegetation*. Manzanita chaparral sample 21 has similarities with chamise chaparral sample 40 and mixed chaparral sample 38. These relationships result from the very low representation of Ericaceae-undifferentiated pollen and very high representation of *Adenostoma fasciculatum* pollen in sample 21.* The similarity between mixed chaparral sample 38 and chamise chaparral sample 40 is due to the high value of *Adenostoma fasciculatum* pollen in sample 38.

Along with the similarities it has with a number of conifer-oak forest samples, lower-montane mixed chaparral sample 33 has similar pollen proportions to the foothill mixed chaparral samples (38 and 39), resulting in low SCD's in these comparisons. These similarities are expectable since the mountain mahogany that dominates the vegetation of sample 33 is poorly represented in the pollen rain, and since these samples share high levels of unidentifiable and unknown pollen. The similarity between sample 33 and oak woodland sample 36 is driven by the damping effect of the “signal-to-noise” characteristic of the SDC metric (Overpeck et al. 1985), which diminishes the impact of the large differences in *Quercus* and unknown pollen percentages between these two samples.

DISCUSSION

Pollen Characteristics

The results presented demonstrate the ability of pollen surface samples to register vegetation differences in the southern California Peninsular and eastern Transverse Ranges. In particular, spurious representation of abundant producers (especially pines) that are not present in the vegetation (McAndrews and Wright 1969; Anderson and Da-

* In general, it is not possible to discern the presence of manzanita chaparral by the SCD method in this sample set. The presence of Ericaceae-undifferentiated pollen above trace levels in fossil pollen spectra can probably be interpreted to represent a significant coverage of plants from this family around the fossil sample site.

vis 1988; Lynch 1996) is generally of little significance. The clear distinction between non-forested and forest samples in terms of conifer pollen representation, even when the non-forested vegetation is nearby and downwind from forest (sample 33), allows this conclusion to be drawn with confidence. The general lack of problematic pollen over-representation allows subtleties of differential sizes of forest openings to be registered by the relative abundances of dominant arboreal pollen types, in particular *Pinus*, as shown by the transect from meadow edge into surrounding forest at Taquitz Meadow and by the transition from smaller to larger openings near and in Hual Cu Cuish Meadow (Appendix 1). The data from Hual Cu Cuish further demonstrate that a relatively low representation of *Pinus* pollen (10–15%) is indicative of the adjacent presence (<0.5 km) of forest or woodland with significant numbers of pines, in sharp contrast to the pollen representation threshold for pine noted in significant portions of North America east of the Rocky Mountains (McAndrews and Wright 1969; Lynch 1996) and some other portions of western North America (Davis 1995).

The lack of problematic pollen over-representation is apparently due to the character of the region's montane forests as islands of "Sierran" vegetation surrounded by various kinds of scrub and oak woodland (Thorne 1988). The forest cover in the southern California mountains is vastly less extensive in comparison to the forests of the Sierra Nevada, the Rocky Mountains, and eastern North America (Burns and Honkala 1990); it is also just downwind from one of the world's largest regions of effectively zero pollen production, the northeastern Pacific Ocean. The fetch over which pollen of abundant arboreal producers can be entrained is thus orders of magnitude smaller in the study region than it is in some of the larger western mountain chains and the East. The clear distinction between forest and non-forested samples in terms of conifer pollen representation is strongly mediated by this relative absence of background pollen. Sample 17 near the upwind edge of conifer-dominated forest on the western scarp of Mt. Cuyamaca also demonstrates this impact clearly; its percentage of *Pinus* pollen is the lowest of all the montane conifer-dominated forests and it has anomalously high levels of pollen from upwind chaparral plants (Fig. 2). A related lack of background *Pinus* pollen also occurs in the Interior Valley region of Oregon (Minckley and Whitlock 2000), which is also associated with a relatively small upwind fetch over which *Pinus* pollen can be entrained.

The only other set of surface samples reported from the montane portion of southern California (Anderson and Koehler 2003, based on moss pollsters rather than soil samples) shows pollen representation of specific plant taxa and discrimination between vegetation types that are generally consistent with the results reported in this paper. One sig-

nificant discrepancy between the results reported here and those reported by Anderson and Koehler occurs in the vicinity of Taquitz and Skunk Cabbage Meadows in the San Jacinto Mountains (samples 18–20 here; sample SJ-12 in Anderson and Koehler). These samples were all collected within ~2 km of each other, in a relatively homogenous mixed conifer forest (pine/fir) that does not contain oak trees or shrubs. In the results reported here, the pollen representation of samples 18–20 is typical of the monane conifer-dominated forests in both studies, with >55% *Pinus* pollen and <3% *Quercus* pollen. However, in Anderson and Koehler's study the sample from this forest has only 20% *Pinus* pollen and 26% *Quercus* pollen, a spectrum that would generally identify it with significant, even dominant, presence of oaks at the sample site. Since Anderson and Koehler report no representation of either arboreal or scrub oaks at the SJ-12 site, it is unclear what causes this discrepancy, especially because they also find generally low levels of background *Pinus* and *Quercus* pollen throughout the region. Overall, the primary differences between the results presented here and those of Anderson and Koehler are the inclusion in this study of a number of samples from the Cuyamaca, Laguna, and Palomar Mountains and nearby foothills in San Diego County and the elevated presence of unidentifiable pollen (Fig. 2), resulting from the use of soil surface samples. Since this kind of sampling most closely mimics the characteristics of the wet meadow fossil records for which this surface sample set provides analogs (cf. Davis et al. 1985; Wahl 2002), the fact that relatively high values of unidentifiable pollen do not degrade the quality of the samples' pollen/vegetation registration is a key validation of the use of these samples for paleo-environmental reconstruction.

Squared Chord Distance Patterns and Analog Relationships

The pattern of SCD relationships determined by the samples reflects the relative clarity of signal in the vegetation-pollen relationships in the region's mountains. The great majority of SCD relationships ≤ 0.25 are for comparisons of samples of like vegetation (Fig. 4). The overlaps between groups indicating inappropriate analogies fall into expectable patterns, largely determined by shared dominance of one of the region's two most important pollen types, *Pinus* or *Quercus*. The overlap between the mid- and higher-montane conifer-dominated forests and some conifer-oak forests reflects the high proportions of conifer pollen, especially *Pinus*, shared by these samples. The overlap between two of the three conifer-dominated forests with significant cover of western juniper and many of the other conifer-dominated forests also reflects the high proportions of *Pinus* pollen shared by these samples. The overlap between the conifer-oak forests and

oak woodlands reflects the high levels of *Quercus* pollen in both groups, as does the less strong overlap between the conifer-oak forests and the mixed chaparral samples. These overlaps indicate limits of resolution of the analog method when it is based on multivariate distance measures alone (cf. Calcote 1998).

Pollen representation and ratios as refinements of the analog method. In many cases of overlap, percentage representation of *Pinus* and *Quercus* pollen and ratios of these two pollen types can be used in addition to SCD relationships to determine a number of vegetation characteristics more precisely, and thereby greatly reduce the number of inappropriate analogies within the surface sample set. These capabilities include:

- 1) *Quercus* pollen $< \sim 11.5\%$ indicates the local absence of oak trees in samples selecting both conifer-dominated and conifer-oak forest analogs, and *Quercus* pollen $> \sim 18\%$ indicates the local presence of oaks in the same situation [sample 28 suggests that when relatively high levels of *Pinus* and Other Asteraceae pollen are combined in this situation, eliminating Other Asteraceae from the pollen sum might be useful to determine an oak percentage that is comparable to this criterion];
- 2) the ratio of conifer/*Quercus* pollen accurately reflects the relative coverage of conifers and oaks in samples selecting both conifer-dominated and conifer-oak forest analogs;
- 3) *Conifer* pollen $< \sim 6.5\%$ distinguishes scrub and oak woodland vegetation from conifer-dominated and conifer-oak forests when SCD relationships across these vegetation groups indicate analogy (with the exception of stands devoid of pine within a conifer-oak forest matrix [sample 27]); and
- 4) the percentage of *Quercus* pollen is more than two times larger in oak woodland samples than in mixed chaparral samples, allowing inappropriate analogies between these vegetation types to be resolved.

In addition, ratios of other pollen types can resolve inappropriate analogies that do not involve *Pinus-Quercus* relationships. A ratio of *Pinus/Cupressaceae*-undifferentiated pollen $< \sim 4.0$ successfully identifies the conifer-dominated forests with significant cover of western juniper from the rest of the conifer-dominated forests. This test cannot, however, distinguish forests with high representation of western juniper from conifer-oak forests with high representation of incense cedar (sample 24). In this case, the *Quercus* pollen representation test ($> \sim 18\%$) can separate sample 24 from the high-montane samples. The ratio of *Pinus/Artemisia* pollen successfully distinguishes the conifer-dominated forests from sagebrush-pine steppe vegetation; this ratio is 2.4 for sample 35 (steppe) and always exceeds 6.3 for the conifer-dominated for-

ests. This use of pollen ratios to resolve ambiguities that arise when using dissimilarity metrics for analog selection in this data set parallels the results of Calcote (1998).

Use of Surface Samples as an Analog Set for Paleocological Reconstruction

The SCD results reported here indicate that the analog method applied with this surface sample set is generally capable of distinguishing the important vegetation types in the montane and foothill regions of cismontane southern California—especially when extended by identification criteria based on specific pollen proportions and pollen ratios. Since the vegetation types in the region are associated with climate and elevation gradients, the ability of the extended analog method to distinguish the vegetation types suggests climate and apparent elevation reconstructions based on this method should be capable of good quality. Rigorous, quantitative tests of these conclusions are developed and examined in Wahl (2003).

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Fig. 1) form a transect from the meadow's edge (20) into the surrounding pine-dominated forest (19 and 18, respectively). (The pines in this forest are *Pinus jeffreyi* and *P. ponderosa*.) This transect is ~150 m long, going up a gentle SE-facing slope. The higher percentages of *Pinus* pollen (73% and 69%) in the samples further into the forest, in comparison to the meadow edge (59%), suggest that meadow sites may be expected to show diminished representation of conifer pollen in relation to smaller openings within surrounding forests. This suggestion is confirmed by the pollen spectra from samples in and near another fossil site, Hual Cu Cuish Meadow in the Cuyamaca Mountains (Table 1, Fig. 1). In this larger, lower meadow (~500 m × ~100 m, 1433 m elevation), a mid-meadow surface sample (31) has 20% conifer pollen (9% *Pinus*, 9% Cupressaceae-undifferentiated, and 2% *Abies*) and a second sample ~10 m from the forest edge (32) has 22% conifer pollen (11% *Pinus*, 10% Cupressaceae-undifferentiated, and 1% *Abies*).[†] Two nearby samples from smaller openings in the mixed conifer-oak forest surrounding the meadow have: a) 60% conifer pollen (37% Cupressaceae-undifferentiated, 20% *Pinus*, and 3% *Abies*) in part of the forest with tree-layer coverage of 30% incense cedar, 25% pines (*P. ponderosa*, *P. lambertiana*, and *P. jeffreyi*), 25% *Quercus kelloggii* (black oak), and 20% white fir (sample 24); and b) 38% conifer pollen (nearly all *Pinus*) in a forest opening with 70% pines (*P. jeffreyi*, *P. ponderosa*, or possible hybrids of these two taxa) and 30% black oak in the tree layer (sample 28) (coverage data from Wahl 2002).

The data from Hual Cu Cuish Meadow indicate that relatively low levels of conifer pollen (~20% total and ~10% *Pinus*) can occur in larger meadows surrounded by forest in which pine and other conifers are important, even dominant canopy trees. This characteristic is consistent with the results of Anderson and Koehler (2003), who also report 10% as the lower threshold for *Pinus* pollen where pine trees are present, and with surface samples from mountainous areas in nearby northwestern Mexico, in which a *Pinus* pollen threshold of 10–15% is reported as indicative of adjacent forest with a significant proportion of pines (Orvis 1998). This characteristic of pollen representation in the montane forests of southern California and nearby Mexico contrasts strongly with the pollen spectra of surface samples in many parts of North America east of the Rocky Mountains; in the latter part of the continent, *Pinus* percentages below 20–25% most likely indicate “background” levels, and few or no pines in the nearby vegetation (cf. McAndrews and Wright 1969; Calcote 1998).

[†] These two samples were taken from the typical surface of this meadow (away from the coring site in a small cattail (*Typha*) marsh), which is currently less saturated than those of the other meadow fossil sites (Wahl 2002). Few wet-indicating plants were growing at these sample sites (Wahl 2002) and very little pollen from wet-indicating taxa occurred in their pollen assemblages (Fig. 2); thus these samples are not subject to biases caused by coverage of hydric, meadow-specific vegetation and are comparable to the other surface samples.

APPENDIX 1

Characteristics of Conifer Pollen Representation at Fossil Meadow Sites

Samples 18–20 near Taquitz Meadow in the San Jacinto Mountains (~60 m diameter, 2399 m elevation; Table 1,