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SOIL CHEMISTRY PATTERNS IN AN EDAPHIC ENDEMISM HOTSPOT: THE PEBBLE PLAINS OF THE SAN BERNARDINO MOUNTAINS, CALIFORNIA

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ABSTRACT

Pebble plains are a unique edaphic environment known only from the high valleys of the San Bernardino Mountains, California. The pebble plains have long been celebrated for the high vascular plant diversity they support, including at least six taxa endemic to the San Bernardino Mountains. Past research has shown that pebble plains soils differ most notably from nearby non-pebble plains soils in terms of their high clay content and loose, stony structure, especially in their upper-most horizon and on the soil surface. The stony upper horizon is probably the result of frost-heaving and erosion of soil particles by wind; the resulting accumulation of stone fragments at the soil surface is what inspired the name "pebble plains." The combined effects of a friable, rocky surface, heavy lower horizons, frost heaving, high solar insolation, and desiccating winds are thought to limit recruitment of shrubs and trees and foster the persistence of a unique pebble plains flora consisting of herbaceous annuals and low-growing perennials. Despite decades of research involving the pebble plains and their unique flora, the soil chemical properties of pebble plains versus surrounding (non-pebble plains) soils has not been thoroughly investigated. This study investigates the chemistry of pebble plains soils to determine if they are chemically divergent from adjacent non-pebble plains soils. To answer this question, we collected soils from nine pebble plains areas, sampling from both the pebble plains themselves and from surrounding, non-pebble plain forests or shrublands. These samples were subjected to analyses for 13 soil chemical properties. Multivariate analyses of these data indicate that habitat type (pebble plains versus non-pebble plains) is the single most important factor explaining the variation in soil chemical properties. Although only Zn concentration is significantly divergent between the habitat types, pebble plains soils are generally deficient in major- and micronutrients compared to adjacent non-pebble plains soils. Our results suggest that while physical factors such as frost heave may be the primary agents responsible for the original formation and persistence of the pebble plains flora, the soils of the pebble plains are chemically unique, which may reinforce physical constraints on floristic composition in these areas.

Key Words: edaphic endemism, ecology, rare plant, Transverse Ranges.

Plant-soil interactions play a key role in plant evolution and ecology, influencing local adaptation, speciation, and the formation of plant communities (Kruckeberg 1986, 2002; Rajakaruna 2004). Although it is easiest to think of soils as influencing plant ecology and evolution via completely abiotic effects, especially in the case of extremely chemically stringent soils like serpentine (Kruckeberg 1986), it is also well known that plant-soil interactions are a primary driver of soil formation and so the influence of soils on plants is often mediated by the plants themselves (reviewed in Ehrenfeld et al. 2005).

Recent research, especially on model soils like serpentine (Harrison and Rajakaruna 2011), has helped scientists to gain a nuanced perspective on how soils affect plant evolution, community assembly, and regional diversity (Anacker et al. 2011; Damschen et al. 2012; Anacker and Harrison 2012; Cacho and Strauss 2014; Burge and Salk 2014; Baldwin 2014; Anacker 2014). Nevertheless, only a handful of unusual soil systems other than serpentine have been examined in detail with respect to their physical and chemical properties and the influence of these properties on plant life (Moore et al. 2014; Saslis-Lagoudakis et al. 2014), preventing inference of general patterns concerning the role of soils in plant evolution and ecology. Here, we focus on the pebble plains of the San Bernardino Mountains, California. A pebble plain is a distinctively open, alpine-like, dwarf shrub- and herb-dominated habitat restricted to moderate elevations (1800–2300 m) primarily on the northeast side of the San Bernardino Mountains (Derby and Wilson 1978, 1979; Krantz 1994). Pebble plains are extremely limited in area, with less than 221 ha extant (U.S. Department of the Interior 2006). Pebble plains are found on flats, gentle slopes, and mesas in Bear Valley and Holcomb Valley, with only a handful of outlying occurrences (Fig. 1; Derby and Wilson 1979; Ciano 1984; Neel and Barrows 1990; Krantz 1994; U.S. Department of the Interior 2006).

Pebble plains have long been of interest to botanists due to the diverse and seemingly specialized flora that they support; at least 53 native vascular plant minimum rank taxa (MRT; species, subspecies, and varieties) are found in the pebble plains habitat, 27 of which (51%) have a high level of affinity for this habitat type in the San Bernardino Mountains

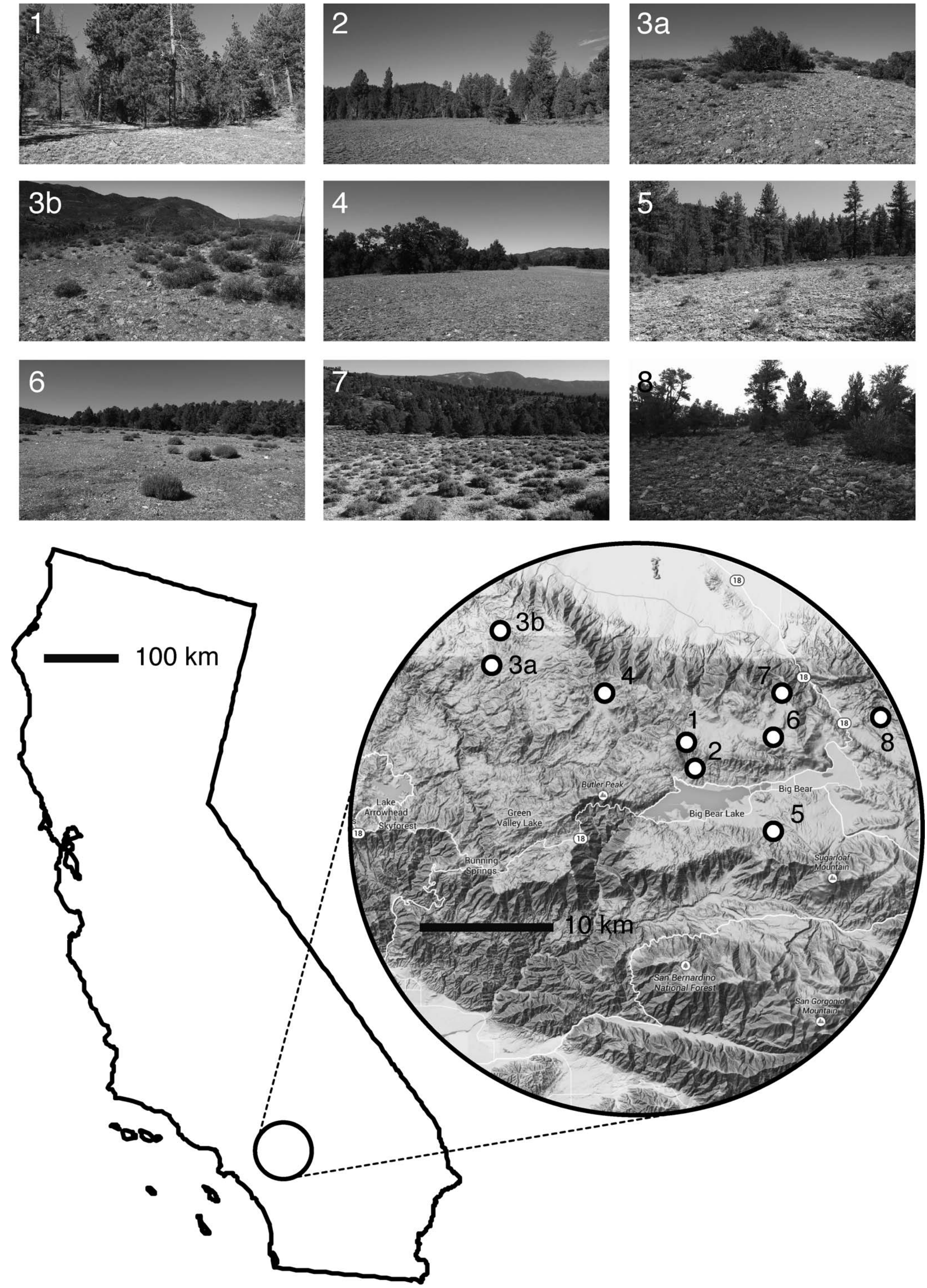

FIG. 1. Sampling map and site photos. Field sites (Table 1) indicated by circles on map of the San Bernardino Mountains. Map data for San Bernardino Mountains: Google.

(Appendix 1). These taxa are strong indicators of pebble plains habitats (Derby and Wilson 1978, 1979) but are occasionally found on carbonates or in vernal wetlands where heavy clay soils exist (Krantz 1994; Stoughton unpublished). This suite of specialists includes six MRT that are endemic to the San Bernardino Mountains and are predominantly found in pebble plains: *Boechera parishii* (S. Watson) Al-Shehbaz, *Castilleja cinerea* A. Gray, *Dudleya abramsii* Rose subsp. *affinis* K.M. Nakai, *Eremogone ursina* (B.L. Rob.) Ikonn., *Ivesia argyrocoma* (Rydb.) Rydb. var. *argyrocoma*, and *Linanthus killipii* H. Mason (Derby and Wilson 1978, 1979; Krantz 1983, 1994; Ciano 1984; U.S. Department of the Interior 2007). The suite of 27 specialists with high level of affinity for pebble plains (Appendix 1) also contains plants that may represent taxa new to science, including *Androsace elongata* L. aff. subsp. *acuta* (Greene) G.T. Robbins, *Echinocereus* sp. aff. *engelmannii* (Engelm.) Lem., *Gilia* sp. aff. *diegensis* (Munz) A.D. Grant & V.E. Grant, and *Primula* sp. aff. *hendersonii* (A. Gray) Mast & Reveal (T. Stoughton, unpublished data). Two of the pebble-plains associated MRT, *Eremogone ursina* and *Echinocereus* sp. aff. *engelmannii,* are apparently strict pebble plains endemics that occur nowhere else (Appendix 1).

Pebble plains soils overlay a variety of rock types, and are influenced to some degree by these host rocks. However, the unique soils of the pebble plains are probably not derived from geological parent materials found in the San Bernardino Mountains; instead, the soils of the pebble plains probably have a more ancient origin, in the Tertiary plains that predate uplift of the San Bernardino Mountains around 3 Ma (Krantz 1994; Sadler and Reeder 1983). Evidence of this origin is found in the pebbles that give the pebble plains their name, which are nearly invariably composed of quartzite, a geological parent material that is rare in the San Bernardino Mountains. Instead of originating in a montane environment, the pebble plains soils likely began as desert pavements, and were carried to their current elevations by uplift of the San Bernardino Mountains (Sadler and Reeder 1983). Today, these soils are widespread in the San Bernardino Mountains, underlying forests and shrublands as well as the floristically distinctive pebble plains (Krantz 1994). Despite a common origin, only some of these soils have given rise to pebble plains, and it is not yet clear what drove differentiation initially, or what maintains it, but it has been proposed by Krantz (1994) that their persistence in low slope-angle situations suggests a relationship with reduced erosion of the fine clays that (in part) make up pebble plains soils.

Pebble plains soils differ strongly from nearby non-pebble plains soils in having a higher clay content as well as a distinctive structure, with a loose, friable, pebble-rich (primarily quartzite) layer near the surface (Derby and Wilson 1978, 1979; Derby 1979 [tabulating unpublished data of M. Lund]; Krantz 1994; U.S. Department of the Interior 2006). The distinctive structure of pebble plains soils is probably influenced by frost-heaving during freeze-thaw cycles of the winter and early spring, which cyclically disrupt the soil surface, allowing wind to carry away fine soil particles, leading to the accumulation of stone fragments (predominantly quartzite pebbles) at the surface (Derby and Wilson 1978; Derby 1979; Derby and Wilson 1979; Krantz 1994; U.S. Department of the Interior 2006). Overall, the combined effects of cyclical frost heaving, heavy clay soil in the lower horizons, high solar insolation, and desiccating winds are thought to limit recruitment of woody perennial plants, especially trees, and foster the persistence of a unique flora consisting of annuals and low-growing perennials. Pebble plains are recognized by their barren aspect, forming variably sized glades within an otherwise forested region (Derby and Wilson 1978, 1979; Ciano 1984; Krantz 1994). Small pebble plains areas may include occasional shrubs or small trees, but more characteristic pebble plains are free of woody perennials with the exception of low-growing sub-shrubs with thick, woody caudices (Krantz 1994).

The plant community of the pebble plains is reminiscent of the isolated alpine flora of San Gorgonio Mountain, which reaches 3506 m, the highest point in the San Bernardino Mountains as well as the Transverse Ranges as a whole (Derby and Wilson 1979; Krantz 1994). However, the flora of the pebble plains occurs up to 1300 m lower than the alpine flora of San Gorgonio Mountain, in the midst of dense montane and sub-alpine forests, including pinyon-juniper woodlands. Derby and Wilson (1979) and Krantz (1994) suggested that the flora of the pebble plains originated during the most recent glacial period, when year-round snow and even small glaciers occurred in the highest elevations of the San Bernardino Mountains (Sharp et al. 1959, reviewed by Krantz [1994]). At this time the alpine flora of San Gorgonio Mountain may have extended down into Bear and Holcomb Valleys, where pebble plains now occur (Krantz 1994). This idea is based on the work of Axelrod (1966) on the Pleistocene (1 Ma) Soboba flora of the San Jacinto area, which showed a more than 1000 m depression of life zones during an apparent glacial period. Krantz (1994, p. 97) provided an eloquent summary of the idea: “During interglacials, the conifer forests climbed to their present levels, except on the clay soils which prevented their establishment and it is on these clay pebble plains that the Pleistocene alpine flora of Big Bear Valley persists to this day, now 1300 m below the alpine summit of Mt. San Gorgonio.” Although the alpine flora of San Gorgonio Mountain shares many similarities with the pebble plains (Derby and Wilson 1979; Krantz 1994; Stoughton unpublished), the authors of the present work are not aware of research that has directly addressed the hypothesis of an alpine origin for the pebble plains flora.

Although the pebble plains flora is unique, not least because of its distinctive physiognomy and unusual distribution at a much lower elevation than similar plant communities, the pebble plains may simply be a well-studied example of a more general phenomenon that occurs in high mountain and high latitude regions, where annual cycles of frost disruption and snow accumulation lead to the formation of distinctive plant communities, some of them at lower elevations than would be expected (Billings and Mooney 1968). Comparative research pursuing this idea would be a worthwhile effort, but is beyond the scope of the present work.

Despite their apparent long-term persistence in the San Bernardino Mountains, there is evidence for gradual degradation of small pebble plains areas, as well as the edges of larger pebble plains, by natural encroachment of forest or woodland vegetation (Derby and Wilson 1979). It is thought that the shade and litter-fall associated with established trees at the edges of pebble plains leads to the recruitment of new tree seedlings and the expansion of the forest habitat into former pebble plains habitat (Derby 1979, from unpublished work of M. Lund). However, the dynamics of this succession-like phenomenon have not been studied in detail as far as the authors know.

The strongly endemic flora of the pebble plains, combined with their very small area, makes them of conservation concern (Neel and Barrows 1990; U.S. Department of the Interior 2006). Though the pebble plains probably never occupied a large area, creation of Big Bear Lake, urbanization of Big Bear Valley, and off-road vehicle activity in San Bernardino National Forest lands have probably reduced the extent of the pebble plains by more than 20% since the arrival of Europeans in the upper elevations of the San Bernardino Mountains in 1845 (Neal and Barrow 1990; Krantz 1994). In addition to threats from urbanization and off-highway vehicle use, the pebble plains now also face the specter of increasing temperatures due to human-caused global climate change as well as increased competition with non-native species, highlighting the urgent need for research to understand the ecology of this unique habitat type and its associated biota before climate change alters it forever.

Even with decades of scientific interest (Ciano 1984; Derby and Wilson 1978, 1979; Krantz 1994) and conservation work (Neel and Barrows 1990; U.S. Department of the Interior 2006, 2007; Parker 2012) involving the pebble plains flora, little is known about how the pebble plains themselves formed and how their unique flora originated, with the exception of a few hypotheses brought forward by Krantz (1994), as described above. To our knowledge, no ecological studies have attempted to experimentally address the question of why certain species are associated with the pebble plains, or how the pebble plains endemic taxa evolved. For research and conservation purposes, it is important to learn how the pebble plains soils differ from adjacent non-pebble plains soils, and what properties allow them to support a unique collective flora. In addition to providing a better understanding of how edaphic endemism evolved in the pebble plains and how the pebble plains persist as an edaphic phenomenon, such work would lead directly to positive conservation outcomes by suggesting criteria for assessing the conservation value of pebble plains sites, and appropriate ex-situ conservation conditions for rare plants.

The present work originated during a series of discussions between the two lead authors on the problem of what edaphic endemism is and how it evolves. Because of their insular or outcrop-like geographic distribution (Ciano 1984; Krantz 1994), the pebble plains present an interesting parallel to better studied systems in which edaphic endemic plants are restricted to soils with a particular geological origin (e.g., serpentine soils derived from the erosion of serpentinite). We agreed to take a closer look at the pebble plains to examine more closely what makes them unique. The aim of our work was to find out whether pebble plains soils are consistently chemically divergent from adjacent non-pebble plains soils, similar to the way that serpentine soils differ from adjacent non-serpentines in terms of their fertility, Ca to Mg ratio, and heavy metals content (Kruckeberg 1986). To test this, we collected soils from nine pebble plains sites in the San Bernardino Mountains, sampling from the pebble plains themselves and from surrounding, non-pebble plain forests or shrublands. These samples were subjected to chemical analysis, with data obtained for 13 soil chemical properties including pH, conductivity, nitrate, and a suite of ten major- and micronutrients. Multivariate analyses of these data were carried out to summarize relationships among soils, determine soil properties associated with pebble plains versus non-pebble plains, and determine whether pebble plains soils are consistently chemically divergent from non-pebble plains soils.

MATERIALS AND METHODS

Assessing Parent Material

Surface-born pebbles were obtained from each of the nine sites, sampling haphazardly from the areas where soil samples were obtained; 1/2 kg of pebbles were obtained from each site. Pebbles were examined by T. S. to determine their geological origin using standard physical property tests (hardness, color, streak, luster, cleavage, and chemical reaction).

Soil Sampling Methods

On 2 and 3 August 2015 nine pebble plains sites were visited with the aim of representing all major areas of pebble plain distribution (Fig. 1; Table 1). At each site, two soil samples were collected, one from pebble plain habitat and one from adjacent scrubland or forest without the characteristic soil structure

TABLE 1. Soil sampling localities. Latitude and longitude reported in WGS 84 datum, accurate to 5 m or less; elevation from GPS at three-dimensional accuracy of 5 m or less.

Site	Latitude	Longitude	Elevation (m)
1	34.2876	−116.9196	2270
2	34.3068	−116.9279	2200
3a	34.3396	−117.0648	1784
3b	34.337	−117.0654	1767
4	34.2437	−116.8507	2178
5	34.305	−116.8501	2273
6	34.2994	−116.821	2088
7	34.2915	−116.8034	2097
8	34.2183	−116.7148	2399

and plant community of the pebble plains. At each site, the pebble plains and non-pebble plains samples were prepared by bulking five sub-samples. Sites for soil sub-sample collection were selected with the aim of representing the slope and aspect diversity of the site as well as varying distances from the interface between pebble plains and non-pebble plains habitats. Sub-samples were located not more than 100 m from one another. Sub-samples were collected using a garden trowel with a steel blade, excavating to a depth of 15 cm. After consolidation, the sub-samples were mixed thoroughly in a 19 L plastic pail, and a 0.5 L composite sample removed for chemical analysis.

Soil Chemistry Analyses

Soil chemistry analyses were carried out by the Texas A & M University Soil, Water, and Forage Testing Laboratory, and are identical to those used by Burge and Manos (2011). Samples were passed through a 2 mm sieve prior to analysis to remove stony fragments. Major nutrients (P, K, Ca, Mg, S) and sodium were extracted using the Mehlich III extractant (Mehlich 1978, 1984) and determined by inductively coupled plasma mass-spectroscopy (ICP). Micronutrients (Cu, Fe, Mn, and Zn) were extracted using a modified DTPA solution (Lindsay and Norvell 1978), and determined by ICP. Soil pH was determined in a 1:2 soil:deionized water extract (Schofield and Taylor 1955). Electrical conductivity (a proxy for soluble salts) was determined in a 1:2 soil : deionized water extract using a soil conductivity probe (Rhoades 1982). Finally, nitrate (NO_3^-) was extracted in 1 M KCL solution, reduced to nitrite (NO_2^-) using a cadmium column, and determined by spectrophotometer (Keeney and Nelson 1982). In total, 13 soil chemical properties were assayed (Table 2).

Statistical Analysis of Soil Chemistry Data

We treated the soil chemistry data in a multivariate statistical framework, visualizing the data and testing for differences between pebble plains and non-pebble plains soils using principal components analysis (PCA), analysis of similarity (ANOSIM), and t-tests. Analyses were done in R, version 3.1.2 (R Development Core Team 2015). Analyses were conducted using scaled data.

PCA was run using default parameters in R. The first two principal components were visualized in bivariate space to examine relationships among sites. The contribution of the soil chemical features to the principal components was determined based on the vector loadings. T-tests were then implemented in R to determine whether the individual soil chemical properties differed between pebble plains and non-pebble plains soils. More complex tests (e.g., via ANOVA) were deemed inappropriate due to the observational nature of the data. A Bonferroni correction for multiple comparisons ($P < 0.00038$) was applied to the results to determine significance.

Analysis of similarity (Clarke 1993) was used to test for overall chemical divergence between pebble plains and non-pebble plains soils. The analysis was carried out using the R package *vegan*, v. 3.2-4 (Oksanen et al. 2016). We used 1000 permutations

TABLE 2. Soil chemistry summary statistics. All statistics reported as average ± standard deviation. Conductivity (Con.) reported as μmol/cm; nitrate (NO_3) and elemental levels reported as parts per million. The t test results are from two-tailed tests that assume unequal variance; Loading PC1 and Loading PC2 are the loadings on the first two principal components from the PCA analysis. "—" indicates that a variable did not contribute to a particular PC axis.

Variable	Pebble plains	Non-pebble plains	T test	Loading PC1	Loading PC2
pH	6.21 ± 0.64	6.43 ± 0.58	0.4436	−0.307	−0.242
Con.	126 ± 30	150 ± 37	0.1266	−0.441	—
NO_3	0.62 ± 0.52	2.11 ± 2.66	0.1685	−0.136	0.147
P	35.34 ± 16.16	50.43 ± 22.13	0.07	−0.283	—
K	142.68 ± 51.65	183.78 ± 59.34	0.1249	−0.428	—
Ca	1908.85 ± 1357.94	2365.25 ± 796.62	0.1442	−0.413	—
Mg	284.33 ± 106.63	280.79 ± 155.72	0.8038	−0.308	−0.315
S	5.34 ± 1.68	6.79 ± 2.59	0.2229	−0.187	0.322
Na	4.70 ± 2.39	3.13 ± 1.90	0.2568	−0.125	−0.334
Fe	10.90 ± 4.25	18.08 ± 8.81	0.0615	−0.113	0.427
Zn	0.66 ± 0.26	1.42 ± 0.44	0.0004	−0.245	0.399
Mn	6.49 ± 3.98	11.21 ± 8.14	0.0963	—	0.449
Cu	0.43 ± 0.18	0.37 ± 0.21	0.4067	−0.181	−0.244

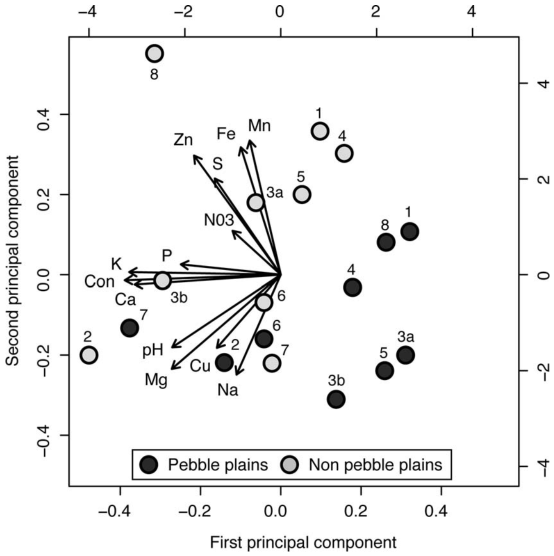

FIG. 2. Plot from principal components analysis (PCA) on soil chemistry. Biplot for first two principal components of PCA for 18 soil samples. Arrows represent direction and magnitude of loading on principal component axes. Symbols: Con = electrical conductivity; NO3 = nitrate.

for the ANOSIM test, with all other parameters at their default settings.

Assessing Plant Community Composition and Relation to Soil

We used multivariate analysis to test for a relationship between soil chemistry and plant community composition of pebble plains sites. All analyses were done in R, version 3.1.2 (R Development Core Team 2015) using the *vegan* package, v. 2.3-4 (Oksanen et al. 2016). To obtain data for these analyses, plant community surveys were carried out for the nine pebble plains sites (Appendix 1). Surveys were carried out by T. S. and D. J., noting all identifiable dead and living taxa present at each site over the same area in which soil samples were obtained; surveys lasted approximately 40 minutes per site.

Lists of taxa for each site (Appendix 1) were translated into a presence/absence matrix, which was used to generate a dissimilarity matrix (Jaccard distances). Only plant taxa found at more than one site were used to generate the dissimilarity matrix. A corresponding dissimilarity matrix was generated for the 13 soil chemical properties (Euclidean distances from scaled data). Community and soil dissimilarity matrices were visualized using hierarchical agglomerative clustering (Faith et al. 1987). The relationship between soil chemistry and plant community composition was then tested using a Mantel test (Legendre and Legendre 1998), comparing the soil matrix to the plant community matrix. For this test we used the Spearman correlation method, and 999 permutations to assess the significance of the test.

RESULTS

Soil Chemistry and Geological Parent Material

Principal components analysis (Fig. 2) provides the opportunity to visually examine the difference between pebble plains and non-pebble plains soils, as well as the differences between the nine sites. In our PCA, 80% of variance was accounted for by the first three principal components, with 36% of variance in the first principal component (PC), 26% in the second, and 17% in the third. The first PC is most strongly (negatively) correlated with conductivity (vector loading = –0.441; Table 2); other elements with strong vector loadings include K (vector loading = –0.428) and Ca (vector loading = –0.413). The second PC is most strongly correlated with Mn (vector loading = 0.449), though many soil chemical features have similarly high loading scores (Table 2), including Fe (vector loading = 0.427) and Zn (vector loading = 0.399). The biplot of the first two principal components (Fig. 2) indicates that pebble plains and non-pebble plains soils are chemically divergent, the divergence being generally associated with lower Zn, Fe, S, Mn, and NO_3 in pebble plains soils (Table 2). After correction for multiple comparisons, t-tests on all 13 variables indicate that only Zn differs significantly between pebble plains and non-pebble plains soils, with lower amounts in pebble plains soils. Analysis of similarity revealed a significant difference in dissimilarity ranks between pebble plains and non-pebble plains soils (ANOSIM R statistic: 0.1636; $P = 0.037$; Fig. 4).

Examination of rock samples revealed that pebbles from all nine sites were quartzitic in origin, with few if any differences among sites in terms of qualitative rock composition. Mainly, rock samples collected at each site had a fairly glassy texture and were hard, dense, and non-foliated, being comprised of interlocking grains of quartz.

Plant Community Composition and Correlation with Chemical Data

The composition of the pebble plains plant community varied strongly among sites (Appendix 1). A total of 32 taxa were identified at the nine target sites. Diversity varied between five and 20 taxa, with the highest number at site 8 (20 taxa) and the lowest at site 3b (5 taxa; Appendix 1). Hierarchical clustering demonstrates the plant community relationships among sites (Fig. 4A). In most cases, geographically proximal sites tend to have the most similar community (Fig. 4A). A Mantel test based on dissimilarity matrices for soil chemistry and plant community shows that there is not a significant relationship between soil chemistry and plant community composition ($r = –0.02485$; $P = 0.512$; Fig. 4).

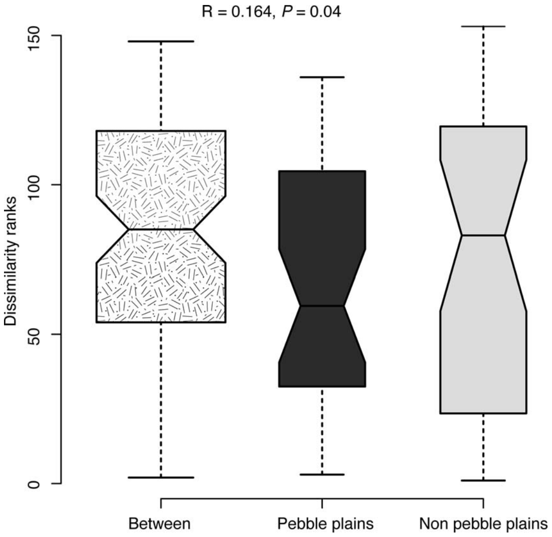

FIG. 3. Results of analysis of similarities (ANOSIM). Results presented as a histogram, with dissimilarity ranks between and within pebble plains and non-pebble plains soils.

DISCUSSION

Pebble Plains Soil Chemistry

Our work suggests that pebble plains sites vary strongly in terms of soil chemistry. However, they are also consistently different from adjacent non-pebble plains soils, with lower levels of major nutrients and micronutrients, particularly Zn. Although our results must be followed up by expanded studies on soil chemistry, as well as studies on physical phenomena that may be linked to pebble plains soil formation (frost heave, waterlogging, leaching), the results that we obtained corroborate our hypothesis that pebble plains soils are consistently chemically divergent from adjacent non-pebble plains soils, similar to the way that serpentine soils are consistently chemically distinct from non-serpentines (Kruckeberg 1986). This result seems to challenge the past assumption that physical conditions are the main factors that differentiate pebble plains soils from non-pebble plains soils (U.S. Department of the Interior 2006). Nevertheless, our results may be consistent with the physical explanation, in that chemical differentiation of pebble plains soils from non-pebble plains soils would be a natural expectation in a physically driven system; exclusion of trees by root-disrupting frost heave, for example, would reduce the amount of nutrients brought to upper soil horizons by decomposition of roots and leaf litter. In addition, exposed conditions in the pebble plains should accelerate leaching and wind-driven loss of soil particles, leading to depletion of vital plant nutrients.

The physical explanation for the persistence of the unique pebble plains plant community is also partly supported by past speculation on the existence of a succession-like phenomenon in pebble plains (Derby 1979; Derby and Wilson 1979), wherein small, isolated pebble plains and the margins of larger pebble plains are converted into forest or woodland by the gradual "creep" of trees and large shrubs into the pebble plain area. As alluded to in the introduction, this process could be driven by the shade and leaf litter cover provided by "nurse" trees at the edges of pebble plains (Derby 1979, citing unpublished data of M. Lund), which are thought to ameliorate the frost heave and extreme insolation experienced in exposed pebble plains, allowing germination and persistence of trees and shrubs (Derby 1979; Derby and Wilson 1979). Though there has been no detailed ecological study of

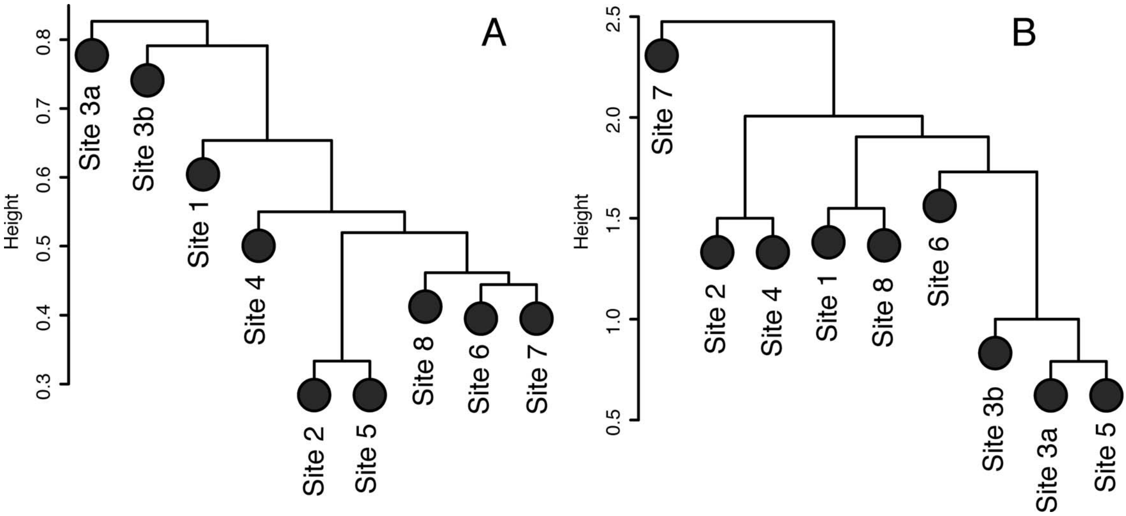

FIG. 4. Results of hierarchical agglomerative clustering based on dissimilarity matrices. A, clustering dendrogram for plant community data. B, clustering dendrogram for soil data.

this succession-like phenomenon other than preliminary studies by Derby (1979, citing unpublished data of M. Lund) on litter accumulation, the idea is consistent with physical rather than chemical factors at work in maintaining the pebble plains, as chemical factors would be expected to repel invasion by trees and shrubs despite the availability of shaded and stabilized sites for seedling germination. However, nutrient redistribution by litter accumulation might provide a chemical explanation. As indicated above, our results should be followed up by experimental work to test whether and how succession occurs in pebble plains.

Overall, our results suggest that while physical processes such as frost heave may be the primary agent responsible for the formation of pebble plains, the resulting soils of the pebble plains are chemically unique, with nutrient status that may be influenced by the feedback of biotic with abiotic processes.

Edaphic Endemism on the Pebble Plains

The pebble plains of the San Bernardino Mountains support a large amount of floristic diversity. This diversity is in the form of a unique suite of dwarfed annual and perennial herbs and subshrubs (~50 MRT; Appendix 1), many of which are strongly associated with pebble plains soils, or completely endemic to them (Derby and Wilson 1978, 1979), and several others which are widespread alpine plants that otherwise grow in the San Bernardino Mountains only around the summit of San Gorgonio Mountain (Krantz 1994). The flora of the pebble plains is reminiscent of floras from other unusual soils—for example serpentines (Kruckeberg 1986), limestone-derived soils (Kruckeberg and Rabinowitz 1985), and gabbro-derived soils (Alexander 2011)—in that they support a locally unusual and strongly endemic flora, and in some cases ameliorate the distributional extension of higher elevation plants into lower elevation habitats (Burge and Salk 2014). However, the pebble plains differ in that they do not appear to be derived from a single geological parent material, and may owe their unusual properties to physical processes instead of the chemical and biological weathering of a chemically unusual parent rock that leads to the formation of most other soils known to support highly edaphic-endemic floras. While our results suggest that pebble plains soils are chemically divergent from non-pebble plains soils, it is likely that this difference is linked to the unusual physical conditions that prevail in the pebble plains, especially frost-heave during freeze-thaw cycles. However, as noted above, the chemical differences that we found could be caused indirectly by frost heave, which would tend to exclude litter-depositing shrubs and trees that would otherwise improve soil fertility by translocating elements from lower horizons to upper ones. In addition, soils that are exposed and disrupted by frost heave would tend to lose nutrients more readily due to leaching and wind erosion.

Pebble plains represent a singular example of an edaphic system, similar to serpentine soil in terms of effect on plant community composition, structure, and endemism. However, much additional research will be needed to determine exactly how pebble plains soils differ from non-pebble plains soils, and how physical, chemical, and biological processes work together to support this unique environment. In particular, it would be desirable to see research that addresses the physical phenomena through observational studies, by looking closely at water content and temperature of pebble plains versus nearby non-pebble plains soils over the course of a year, to determine how freeze cycles, waterlogging, and frost heave might play a role in maintaining the unique structure of pebble plains soils. Experimental studies would also be helpful; for example, transplant or common garden experiments could help determine why woody perennials are not able to establish and thrive on pebble plains, and why certain species are associated with or endemic to pebble plains. The natural complement of such studies would involve experimental removal of tree, shrub, and leaf litter from non-pebble plains to determine whether pebble plains can be "created" by disrupting the climax vegetation type. Additional research is also needed to establish variation in physical properties across a larger number of pebble plains sites. Although such work is beyond the scope of the present study, it is nonetheless critical. As with the chemical study that we carried out, by linking physical information to species lists for each site, it might be possible to determine if there are physical soil properties that support larger amounts of diversity or particular endemics. It would also be possible to correlate the physical information with the chemical information, and thus learn more about how these two factors are interacting in the formation and maintenance of pebble plains. Such research would have clear conservation implications as it would allow for 1) more nuanced design of reserve boundaries to preserve rare plants and the habitats that support them, 2) assessment of habitat quality in the absence of growing plants (many of the pebble plain endemics are ephemeral annuals that might not grow every year), and 3) habitat quality assessments to determine how well "rescue" plants might fare after translocation from one location to another.

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APPENDIX 1. Minimum-rank native vascular plant taxa found on pebble plains. *Notes*. This appendix reports all minimum-rank taxa known to be associated with pebble plains. [1] The San Bernardino Mountains District, as defined by the Jepson Manual (Baldwin et al. 2012, p. 46). [2] Endemic to pebble plain habitat. [3] With some level of known affinity to pebble plain habitat (i.e., endemic or generally found on pebble plain habitat, at least within the San Bernardino Mountains portion of the species' distribution). [4] Putative taxon new to science (Stoughton unpublished data). [5] Federally listed Threatened or Endangered taxon.

Family	Taxon	SnBr[1] endemic	PP endemic[2]	PP affinity[3]	New taxon[4]	Endangered[5]	1	2	3a	3b	4	5	6	7	8
Alliaceae	*Allium parryi* S. Watson			x			x				x				
Apiaceae	*Lomatium nevadense* (S. Watson) J.M. Coult. & Rose			x							x	x	x		
Asteraceae	*Antennaria dimorpha* (Nutt.) Torr. & A. Gray			x							x				
	Artemisia nova A. Nelson			x				x				x	x	x	x
	Chaenactis glabriuscula DC. var. *glabriuscula*														
	Erigeron aphanactis (A. Gray) Greene var. *congestus* (Greene) Cronquist			x							x	x	x	x	x
	Gutierrezia sarothrae (Pursh) Britton & Rusby											x	x	x	
	Hymenopappus filifolius Hook. var. *lugens* (Greene) Jeps.			x											x
Boraginaceae	*Cryptantha simulans* Greene														
	Plagiobothrys tenellus (Hook.) A. Gray														
	Plagiobothrys torreyi (A. Gray) A. Gray														
Brassicaceae	*Boechera parishii* (S. Watson) Al-Shehbaz	x		x			x	x	x		x	x	x	x	x
	Boechera retrofracta (Graham) Á. Löve & D. Löve						x								x
	Cusickiella douglasii (A. Gray) Rollins			x							x		x		
Cactaceae	*Echinocereus engelmannii* (Engelm.) Lem.		x		x				x				x	x	
	Echinocereus mojavensis (Engelm. & J.M. Bigelow) Rümpler													x	
	Opuntia basilaris Engelm. & J.M. Bigelow								x				x		x
	Opuntia engelmannii Engelm.														
	Opuntia phaeacantha Engelm.								x	x			x	x	x
Caryophyllaceae	*Eremogone ursina* (B.L. Rob.) Ikonn.		x			x	x	x			x	x	x	x	x
	Minuartia pusilla (S. Watson) Mattf.														
Crassulaceae	*Dudleya abramsii* Rose subsp. *affinis* K.M. Nakai	x		x					x				x	x	x
Ephedraceae	*Ephedra viridis* Coville								x	x				x	
Fabaceae	*Astragalus purshii* Douglas var. *lectulus* (S. Watson) M.E. Jones			x							x	x	x	x	x
Lamiaceae	*Trichostema micranthum* A. Gray			x			x								
Montiaceae	*Lewisia rediviva* Pursh var. *minor* (Rydb.) Munz			x											
Onagraceae	*Epilobium brachycarpum* C. Presl														
Orobanchaceae	*Castilleja cinerea* A. Gray	x		x		x	x	x			x	x	x		x
Phrymaceae	*Erythranthe androsacea* (Curran ex Greene) N.S. Fraga														
	Erythranthe exigua (A. Gray) G.L. Nesom & N.S. Fraga			x											
	Erythranthe purpurea (A.L. Grant) N.S. Fraga			x											
	Erythranthe suksdorfii (A. Gray) N.S. Fraga			x											
Plantaginaceae	*Collinsia parviflora* Lindl.														
	Plantago patagonica Jacq.														

APPENDIX 1. CONTINUED

Family	Taxon	SnBr[1] endemic	PP endemic[2]	PP affinity[3]	New taxon[4]	Endangered[5]	1	2	3a	3b	4	5	6	7	8
Poaceae	*Bouteloua gracilis* (Kunth) Griffiths			x				x			x				x
	Elymus elymoides (Raf.) Swezey						x	x		x		x	x	x	x
	Poa secunda J. Presl subsp. *secunda*						x	x		x	x	x	x	x	
	Stipa hymenoides Roem. & Schult.								x						
	Stipa occidentalis S. Watson var. *pubescens* (Vasey) J.R. Maze et al.						x				x			x	x
	Stipa speciosa Trin. & Rupr.								x						x
Polemoniaceae	*Gilia diegensis* (Munz) A.D. Grant & V.E. Grant	x		x	x									x	x
	Leptosiphon breviculus (A. Gray) J.M. Porter & L.A. Johnson						x								
	Linanthus killipii H. Mason	x		x											
	Microsteris gracilis (Hook.) Greene														
	Navarretia breweri (A. Gray) Greene			x											
Polygonaceae	*Eriogonum kennedyi* S. Watson var. *austromontanum* Munz & I.M. Johnst.			x		x		x	x	x	x	x	x	x	x
	Eriogonum kennedyi S. Watson var. *kennedyi*			x											
	Eriogonum wrightii Benth. var. *subscaposum* S. Watson						x		x						x
Primulaceae	*Androsace elongata* L. subsp. *acuta* (Greene) G.T. Robbins			x	x										
	Primula hendersonii (A. Gray) Mast & Reveal	x		x	x										
Rosaceae	*Ivesia argyrocoma* (Rydb.) Rydb. var. *argyrocoma*	x		x			x	x			x	x			x
Selaginellaceae	*Selaginella watsonii* Underw.														
Violaceae	*Viola douglasii* Steud.			x							x		x		x

Appendix 2. Raw soil chemistry data. *Notes*. Conductivity reported as µmol/cm; nitrate and elemental levels reported as parts per million

Site	Habitat	pH	Conductivity	NO_3	P	K	Ca	Mg	S	Na	Fe	Zn	Mn	Cu
1	Pebble plains	5.26	97	1.57	31.4	111	966.8	145.6	4.93	1.06	14.02	0.59	10.7	0.42
	Non-pebble plains	5.52	120	0.12	44.3	126.4	1975.7	138.9	6.77	2.22	26.56	1.76	16.02	0.31
2	Pebble plains	6.52	147	0.07	41	219.2	2671.3	384	6.1	6.17	11.91	0.93	7.09	0.82
	Non-pebble plains	6.75	224	0.39	49.4	278	4150	641.9	3.89	4.73	20.26	1.43	10.19	0.85
3a	Pebble plains	6.57	96	0.54	26.4	70.3	1119.1	234.9	3.51	3.64	4.35	0.54	2.63	0.23
	Non-pebble plains	6.58	136	6.47	77.5	149.7	2165.3	155.2	7.78	0.82	8.73	1.45	6.08	0.25
3b	Pebble plains	6.44	138	0.29	37.3	115.4	1402.8	427.5	3.31	5.69	5.58	0.41	1.31	0.21
	Non-pebble plains	6.97	185	6.78	96.5	225.4	2690.7	330	6.5	3.6	10.2	1.09	4.74	0.23
4	Pebble plains	5.35	114	0.18	31	104.9	1115.9	253.7	7.36	8.13	16.6	0.67	11.18	0.55
	Non-pebble plains	5.48	125	0.56	40.6	107.6	1356.2	185.7	3.21	1.99	29.04	1.75	14.68	0.24
5	Pebble plains	6.04	111	0.6	18.1	122	1221.9	243.5	3.23	5.2	7.88	0.29	3.29	0.44
	Non-pebble plains	6.37	128	1.05	38.8	143.8	2459.1	164.6	9.09	1.12	19.83	0.95	7.7	0.23
6	Pebble plains	6.67	140	1.39	37.7	183.8	2195.6	383.4	6.34	4.9	10.4	0.91	3.87	0.42
	Non-pebble plains	6.9	132	0.38	44.9	184.5	1943.3	296.5	6.11	3.15	10.8	1.26	5.08	0.42
7	Pebble plains	7.2	189	0.58	73.5	213.1	5200.2	350.4	7.47	6.44	15.32	1.05	6.53	0.46
	Non-pebble plains	6.95	121	0.61	30.5	179.6	1842.3	330.8	5.99	6.9	8.18	0.87	6.38	0.57
8	Pebble plains	5.8	103	0.33	21.9	144.5	1286.1	135.9	5.83	1.1	12.02	0.54	11.78	0.36
	Non-pebble plains	6.36	177	2.62	31.4	259.1	2704.8	283.4	11.79	3.67	29.08	2.22	29.99	0.28