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Source: Madroño, 72(3) : 126-156

Published By: California Botanical Society

URL: https://doi.org/10.3120/0024-9637-250016

Madroño, Vol. 72, No. 3, pp. 126–156, 2025
DOI:10.3120/0024-9637-250016

CLAY AFFINITY AND ENDEMISM IN CALIFORNIA'S FLORA

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Abstract

While the role of harsh soils in shaping the endemic flora of California has been extensively studied (e.g., serpentine endemism), plant endemism to many other soils within California is still poorly explored. Clay soils present substantial physical, chemical, and hydraulic challenges to plant life due to the extreme chemical and physical properties of clay particles. We conducted an extensive search of California herbarium records to generate a list of minimum-rank taxa found within California with potential clay affinity which we supplemented with the Jepson eFlora and the California Native Plant Society's Rare Plant Inventory. We assessed over 53,000 herbarium voucher records to evaluate each taxon's affinity and endemism to clay soils and found evidence for endemism to clay soils in the California flora. We ranked affinity to clay soils for 217 taxa and found that a third of those taxa are endemic to clay soils. From the results, we provide a database of clay affinity with notes on life form, habitat associations, distribution, special status and rarity.

Key Words: argillic, California flora, clay, edaphic, endemism, geoecology, soils, Vertisols.

Due to its widely varied climate, topography, geology, and soils, California hosts a diverse flora with over 6500 minimum-rank vascular plant taxa (e.g., varieties, subspecies, species with no intraspecific taxa nested within them). Over 1600 of these minimum-rank taxa are endemic to California (Baldwin 2014). This flora contains a high proportion of edaphic (i.e., soil-associated) endemic species (over 13%), which also comprise 43% of special-status taxa in the state (Stebbins and Major 1965; Harrison 2013; Safford and Miller 2020). The state's floristic diversity and high number of endemic taxa is linked to California's diversity of soils (Kruckeberg 1969; Raven and Axelrod 1978): Over 2000 soil series have been described and classified in the state, with representatives from 11 of the 12 soil orders used by the USDA Soil Taxonomy system (Soil Survey Staff 2022).

Extreme Substrate Physical and Chemical Properties Drive Adaptation, Specialization, and Speciation in the California Flora

While present only within the uppermost few meters of the Earth's surface, soil serves as the great integrator between the biotic and abiotic worlds (Lavkulich 2022). Soil is the ecological interface between life and geology—in combination with climate, soil is a major abiotic driver of the distribution of plants (Jeffrey 1987). However, not all soils are equally hospitable to plant growth (Jeffrey 1987;

Rajakaruna et al. 2024). The selective pressure from harsh substrates can serve as a mechanism for speciation (Givnish 2010; Rajakaruna 2018), and harsh soils like serpentine soils derived from serpentinite and ultramafic rock have provided a valuable model system for speciation (Rajakaruna 2004; Anacker et al. 2011; Harrison and Rajakaruna 2011; Kay et al. 2011). There has been extensive work on edaphic endemism to soils with harsh soil chemistry defined by geologic parent materials like serpentinite (Safford and Miller 2020), gabbro (Medeiros et al. 2015), limestone (Lundholm and Larson 2003; Kiew et al. 2019), and gypsum (Guerrero-Campo et al. 1999; Palacio et al. 2007; Luzuriaga et al. 2012, 2020; Moore et al. 2014). Within California, the influence of extreme soil chemistry on plant ecology (particularly of soils derived from serpentinite and other ultramafic rocks) has been intensively studied (Raven and Axelrod 1978; Alexander et al. 2006; Harrison 2013; Lancaster and Kay 2013). However, there has been remarkably little study of the influence of extreme soil texture on plant endemism. In this study, we have attempted to evaluate plant affinity to soil texture: specifically, to clay.

Clay is an Extreme Soil Type

Clay in soil originates through one of two primary processes: 1) chemical weathering of parent material's primary minerals to secondary clay minerals, or 2) inherited directly from primary clay minerals within parent material (e.g., clay shale and other sedimentary rocks rich in clay minerals; Rhigi and Meunier 1995; Graham and O'Geen 2016; Alexander 2022). In chemical weathering, primary minerals including feldspar, mica, and pyroxene are altered to clay through hydrolysis, oxidation, and dissolution (Rhigi and Meunier 1995). Examples of clay soils in California include the San Joaquin Series, the Chicote series, and the Morenogulch series (Soil Survey Staff 1999, 2003a, b).

Soils with high clay content as a result of either process will tend to have different water dynamics than soils with less clay. The reduced infiltration of water through clay can lead to pooled water, and so vernal pool and alkali sink habitat are common where clay soils are found in California (Comer et al. 2024a, b). Higher salt accumulation is also common in clay soils of arid regions, where reduced precipitation leads to reduced leaching of solutes (e.g., in alkali sink habitat; Rhigi and Meunier 1995). For plant species restricted to vernal pools, alkali sinks, and highly sodic or saline soils of arid regions, it is difficult to separate hydrologic niche from the edaphic niche. However, this is not a new problem for the study of edaphic specialization. The serpentine "syndrome" similarly consists of a suite of combined edaphic characteristics that act as selective pressures that have resulted in a unique serpentine-associated flora (Jenny 1980; Kruckeberg 1984). Below, we discuss ways in which clay soils themselves present a similar "syndrome" in the combination of water stress, reduced aeration, altered plant mineral nutrient availability, and physical stress.

Soil texture. Soil texture is a physical property of soil and is determined by the relative proportion of different sized particles: sand (0.05–2 mm), silt (0.002–0.05 mm), and clay (<0.002 mm; Weil and Brady 2017; Soil Survey Staff 2022). Clay soil is defined as having >40% volume clay per volume soil. Soil texture has profound effects on soil properties, including water holding capacity, aeration and nutrient adsorption and supply (Weil and Brady 2017).

Clay minerology. The mineralogy of clays determines the physical and chemical properties of clay soils, which in turn affects the harshness of clay soil for plants. The extent of clay formation and the specific clay minerals formed are a result of the interacting effect of parent material, climate, time, and the movement of water (Jenny 1994). The clay in soil can originate from the chemical weathering of various types of bedrock or be inherited directly from a sedimentary bedrock type composed of clay particles (e.g., shale), which influence the types of clay found in the resulting soils. Clay minerals are phyllosilicates: minerals with structures consisting of repeating layers of mineral sheets. Each repeating layer is comprised of two types of sheets, including a tetrahedral sheet made of repeating silicate tetrahedra (SiO_4), and an octahedral sheet primarily composed of repeating aluminum-oxygen octahedra (AlO_6). The two types of clay are classified as "1:1" and "2:1" based on the composition of those sheets. A 1:1 clay is composed of a single tetrahedral sheet combined with a single octahedral sheet, and the two sheets are strongly bonded by hydrogen. A 2:1 clay is composed of an octahedral sheet sandwiched between two tetrahedral sheets, and the layers of 2:1 clay are weakly bonded by cations. The most common 1:1 clay found in soil is kaolinite and the most common 2:1 clay in soil is smectite (Velde 1995).

Clay soils can cause water stress. Clay has a high surface-area-to-volume ratio, and a high adsorptive capacity for water, and mineral ions. The small particle size of clay gives soils with a high fraction of clay an overall greater surface area than soils with higher fractions of silt or sand. Increased surface area allows for greater water retention and reduced drainage, which can hinder root respiration and create anaerobic soil environments harmful to plants (Salter and Williams 1965; Bhattarai et al. 2006). Despite this, high clay soils may at the same time induce drought stress for plants. Smaller particle size means that clay soils generally have a different distribution of soil pores—the areas between soil particles filled with air and water—than other soils, and in clay soils, this results in a much higher proportion of micropores compared to macropores (Diamond 1970), which causes decreased matric potential.

When the matric potential of soil becomes lower than the water potential of roots, the water becomes functionally unavailable to plants (Salter and Williams 1965; Kirkham 2011; Fensham et al. 2015). So, while clay soils generally have a larger range of "plant-available water" content (Kirkham 2005), that water is not equally accessible to plants across the range of soil water content (Letey 1985) and water held in clay soils requires greater energy for plants to access (Minasny and McBratney 2003). Both clay soils' higher bulk density (and with it, the mechanical impedance to roots; Atwell 1993) and potential for highly limited aeration (as with waterlogging) can reduce the non-limiting water range for plant growth (Letey 1985). This means that water content that might not otherwise limit growth in more coarsely textured soils can in fact limit plant growth in clay soils with the same amount of water—even when "plant-available" water appears high (Kirkham 2005). Thus, despite the potential of clay soils to adsorb large volumes of water, the proportion of water available to plants is relatively low: plants growing on clay soils can be subjected to extreme drought stress, especially in semi-arid to arid climates. (Hillel 1971; Velde and Barré 2010).

Clay soils tend to have low permeability to rainwater from precipitation (Dodd and Lauenroth 1997; Reynolds et al. 2004; Lauenroth and Bradford 2012). This can lead to seasonal water stress of a different kind: waterlogging and flooding, as seen in seasonally inundated habitats like vernal pools or alkali sinks where clay prevents the percolation of water downward through the soil (Comer et al. 2024a, b). The waterlogging of soil after seasonal precipitation when clay prevents percolation can induce stress due to an excess of water as well, by creating a hypoxic rhizosphere environment that limits root gas exchange and respiration, and reduces photosynthesis, thereby limiting growth in plants under hypoxic stress (Blackwell and Wells 1983; da Silva et al. 1994; Zhang et al. 2017; Daniel and Hartman 2023; Manghwar et al. 2024).

Clay soils can create chemical and mineral stress for plants. The high surface-area-to-volume ratio of clay that drives the high adsorptive capacity for water also drives higher cation exchange capacity (CEC): the ability of a soil to hold positively charged ions (Weil and Brady 2017). While CEC is a measure of the ability of soil to hold nutrients essential to plant growth, the plant-available nutrients in clay soils can be quite low depending on the age of the soil, its parent material, and mineralogy (Marschner and Rengel 2023). In some clay soils, certain cations can exceed the level tolerable to plants, giving rise to harsh soil environments as seen in sodic soils (exchangeable sodium percentage > 15) and serpentine soils (calcium:magnesium ratio < 1) (Parfitt et al. 1995; Soil Survey Staff 2022). The ease with which clay particles can be transported by water also means that a large proportion of clay soils are found in geologic basins (Hillier 1995). For clay soils in such basins, appreciable accumulation of sodium can occur when the collected water containing dissolved salts evaporates, and salts accumulate over time (Eghbal et al. 1989).

Clay soils can create physical stress for plants. The high density and soil strength of clay soils can create physical stress as finer-textured and clay soils have bulk soil density at which root growth is limited (Jones 1983): Plant roots in clay soils encounter higher mechanical resistance to root penetration (Atwell 1993) and plants in clay soils have reduced ability to modify the soil structure within the rhizosphere (Phalempin et al. 2021). The mineral properties of some types of clay can also introduce substantial physical stress for plants: When a 1:1 clay like kaolinite is wet, the water molecules remain outside the mineral layers of the clay and there is no major change in soil volume (Bates 1959). However, when a 2:1 clay such as smectite is wet, water molecules enter the particles between the weakly bonded mineral layers, resulting in substantial expansion of the soil's volume (Kovda and Mermut 2018). As smectite dries, the process reverses—as water molecules exit the mineral layers of the particle, the volume decreases, and the clay shrinks (Velde and Barré 2010; Soil Survey Staff 2022). This process repeating over time can lead to "self-churning" of the soil (pedoturbation; Stirk 1954; Velde 1995; Khitrov 2016).

The unique properties of smectite that result from its 2:1 structure mean that one type of clay soil can be particularly harsh and warrants additional consideration here: Vertic clay soils are defined by high clay content ($>50\%$), of which a high percentage ($\geq 20\%$) is smectite clay (Shirsath et al. 2000). These soils introduce physical stress for plants due to shrink-swell that occurs with wetting and drying due to pedoturbation and cracking upon drying (Ahmad 1975; Eswaran and Cook 1988; Velde and Barré 2010). Seasonal rainfall causes vertic clay soils to swell as water is absorbed between the mineral layers of smectite. During the dry season, the process is reversed. As water evaporates, the soil loses volume, forming deep cracks up to 3 cm wide and 1 m deep (Velde and Barré 2010; Soil Survey Staff 2022). This process creates physical stress for plants as cracking causes soil pore discontinuity and damaged roots (Whitmore and Whalley 2009).

Clay Soils in California

Clay is common throughout California, and every ecoregion in the state has examples of soils with high clay content (Fig. 1). However, clay soils are unequally distributed in the state and are the product of historic and current waterways, from weathering of heterogeneously distributed parent material, and in some areas, aeolian deposition (Graham and O'Geen, 2010). Areas with historic water deposition and high clay include basins and valleys like Tulare Lake in the

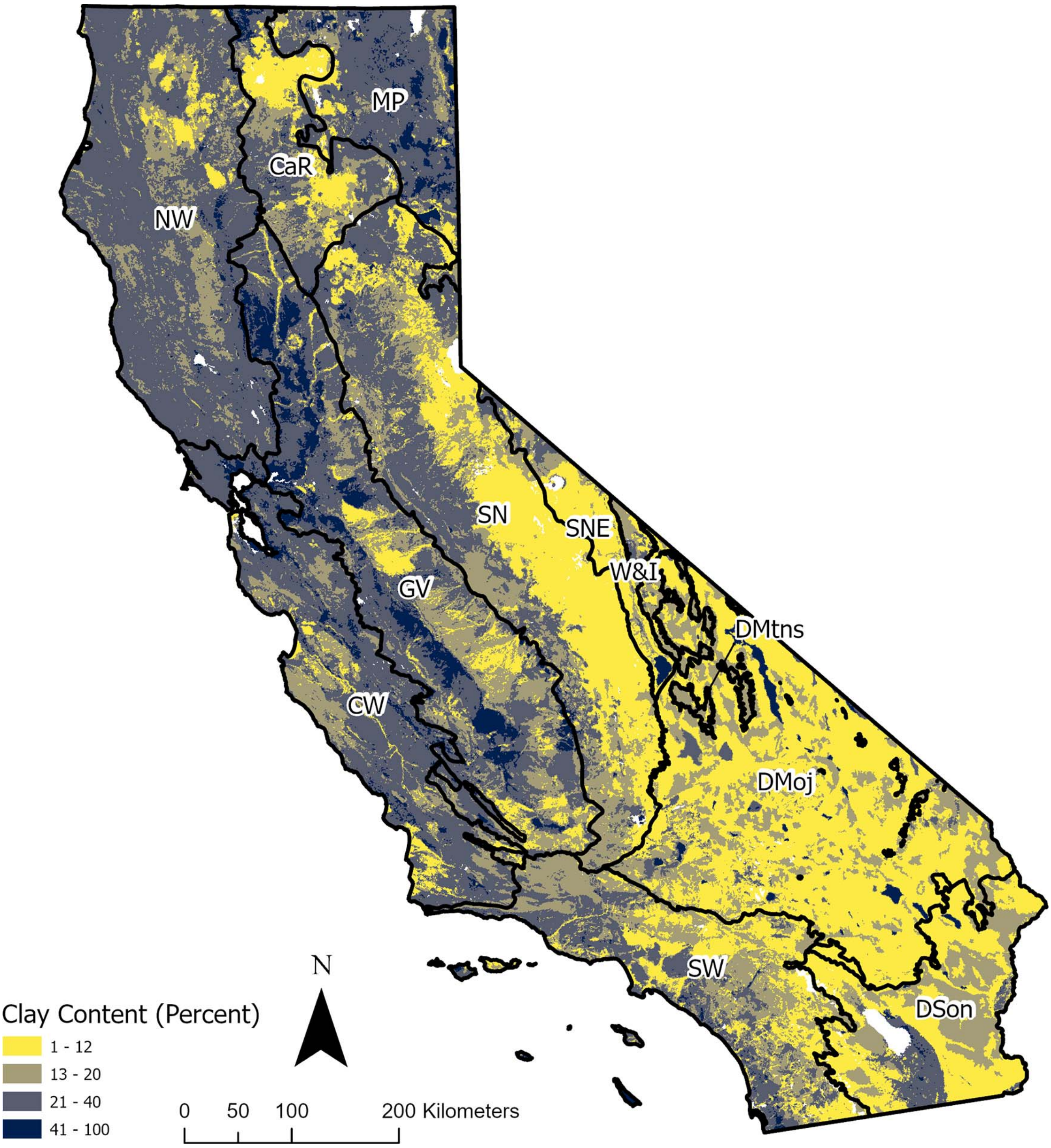

FIG. 1. Distribution of clay soils in California. Map shows data for clay particle percentages of soil at a depth of 0 to 25 cm, aggregated to 800 m grid cells from the Soil Survey Geographic Database (Soil Survey Staff 2025).

Central Valley, the Death Valley Basin, and the Temescal, San Jacinto, and San Bernadino Valleys (Graham and O'Geen 2016; Soil Survey Staff 2025). Within basins and valleys with clay from depositional origin, Tulare Lake, Mono Lake, Owens Lake, Soda Lake, the Salton Sea, and some ancient lakebeds in the Modoc Plateau have high sodicity and salinity due to the closed hydrologic nature of basin formations (Eghbal et al. 1989, O'Geen et al. 2007; Graham and O'Geen 2016). Regions with clay soils due to the weathering of parent material include the Panoche Hills and the Central Coast, where marine shale and ancient marine terraces weathered to clay, and many low areas host vertic clay soils (O'Geen et al. 2007; Graham and O'Geen 2016). Further, while Vertisols are not abundant worldwide, they are more common in California relative to many other states, and within California, occur primarily in the Central Valley, Central Coast, Modoc Plateau, Peninsular Ranges, and the Southern Coast Ranges (Ahmad 1996; Graham and O'Geen, 2010; U.S. Department of Agriculture Natural Resources Conservation Service 2024).

Study Rationale

Functional traits and adaptations that enable plants to tolerate edaphic stressors may reduce their competitive fitness on less stressful soils (Kruckeberg 1950, 1954; Whittaker 1954; Rice 1989; Huenneke et al. 1990; Freitas and Mooney 1996; Jurjavcic et al. 2002). Competitive exclusion from less challenging substrates and continued specialization to stressful soils can ultimately lead to higher edaphic affinity and subsequent endemism (Stebbins and Major 1965; Kruckeberg 1986; Macnair 1989; Brady et al. 2005, Rajakaruna 2018).

The few studies we are aware of that address any kinds of adaptation to clay soils relate largely to root traits: These include higher root tissue density, greater fine root production, and increased root exudate production to cope with both reduced nutrient availability and greater difficulty for roots to penetrate clay soils due to higher bulk density and reduced pore space (Jackson et al. 2000; Schenk and Jackson 2002a; Bengough et al. 2006; Borden et al. 2020; Ahmad and Li 2021; Freschet et al. 2021). These modifications to the root system can incur energy costs and therefore likely tradeoffs with competitive fitness: Higher root tissue density provides greater tensile strength for roots that is beneficial in expansive clay soils but requires greater energy and carbon investment (Ryser 1996; Craine et al. 2001). Greater fine root production comes with improved nutrient and water acquisition, but fine roots may be more prone to cavitation and have higher turnover (Gill and Jackson 2000; Lübbe et al. 2022). Higher root exudate production improves nutrient uptake and root penetration of clay soils but can be metabolically expensive (Wen et al. 2022). While shallow rooting with higher fine root investment by early-season or shorter-lived plants is frequently observed in clay soils due to the limited percolation of surface water (Schenk and Jackson 2002b; Jiang et al. 2021), this strategy also comes with increased reliance on surface precipitation. However, the alternative strategy of deeper rooting requires greater energy investment on clay soils: Because clay reduces water percolation severely beyond a depth of ~60 cm (Dodd and Lauenroth 1997; Reynolds et al. 2004; Lauenroth and Bradford 2012), the drier space between the soil layers with surface water from percolation and the soil layers with groundwater due to capillary action will be greater. This greater depth and the correspondingly deeper rooting needed therefore require higher investment from species utilizing that strategy on clay than would be needed on more coarsely textured substrates (Schenk and Jackson 2002b; Fan et al. 2017; Jiang et al. 2021). In expansive clay soils, a higher proportion of vertically oriented roots is a likely adaptation to the physical stress created when these soils dry down and shrink, forming vertical cracks which pull and eventually tear horizontally oriented roots (Ahmad 1975; Eswaran and Cook 1988; Whitmore and Whalley 2009; Velde and Barré 2010). While this adaptation reduces the number of roots lost to tearing as soils dry down and crack (White and Lewis 1969), in some species, lateral roots have been found to be more efficient for nutrient acquisition, so this adaptation may increase the cost of nutrient acquisition (Zhu and Lynch 2004).

Fitness trade-offs for adaptations to stressors found in clay soils have been observed in other types of soils. For instance, common drought adaptations—such as reduced leaf size, slower growth rates, osmotic adjustment, and deeper (phreatophytic) rooting—often come with trade-offs in photosynthetic efficiency or increased energy and carbon costs (Chandler and Bartels 2007; Sanders and Arndt 2012; Lopez-Iglesias et al. 2014; Fort et al. 2015; Jiang et al. 2021; Adeniji et al. 2024; Wang et al. 2024). Further, rooting adaptations and modifications in root-to-shoot biomass ratios for drought tolerance are typically linked to the timing of precipitation and the specific soil layer providing water. A species adapted to one soil water regime will experience fitness trade-offs if placed in soil with a different distribution of water or precipitation timing (Schwinning and Ehleringer 2001). For example, the phenological adaptation of avoiding drought (i.e., phenological escape) by timing growth to coincide with periods of higher precipitation can result in trade-offs if water availability is greater than expected (Pearse et al. 2020). Additionally, greater development of aerenchyma in roots is a common adaptation for surviving waterlogged and hypoxic soils. However, this adaptation also comes with a trade-off in the reduction of roots' mechanical strength (Striker et al. 2007).

Adaptation and competitive fitness trade-offs are key drivers of edaphic endemism on harsh substrates, as observed in other harsh soil environments (Kruckeberg 1950, 1954; Stebbins and Major 1965; Macnair 1989; Brady et al. 2005). Building on this concept, and the limited research available on clay soil adaptations, we hypothesized that some species may have evolved an affinity and specialization for clay soils due to their adaptation to these environments. There is some evidence that soil texture plays a role in driving the evolution of edaphic specialization (Hamer et al. 2016; Eckhart et al. 2017). Although several taxa have common names (Adobe Fritillary), specific epithets (*Calochortus argillosus* (Hoover) Zebell & P.L.Fiedl.), and published ecological references (e.g., ecology notes in the Jepson eFlora; Jepson Flora Project 2024) indicating an affinity for clay soils, we are unaware of any studies specifically examining or quantifying clay affinity in plants, nor any ecological studies that address this aspect (but see White and Lewis [1969], Welsh [1978], and Oberbauer [1993]). To investigate this further, we analyzed herbarium records to look for evidence of endemism to clay soils for minimum-rank taxa within the state of California (inclusive of the California, Great Basin, and Desert Floristic Provinces).

Methods

We compiled an initial list of minimum-rank plant taxa (both vascular and nonvascular) for which we sought to quantify clay affinity, based on apparent or likely affinity to clay soils indicated in ecology notes from the Jepson eFlora (Jepson Flora Project 2024) and the California Native Plant Society's Rare Plant Inventory (CNPS RPI; California Native Plant Society, Rare Plant Program 2024), and results from a query of the Consortium of California Herbaria's database (CCH2; Consortium of California Herbaria 2024) for terms that indicate clay soils. We used digitized herbarium records from the CCH2 database and limited our search to taxa found in the state of California and those portions of the California Floristic Province that extended beyond the geographic boundaries of the state. We included all CCH2 records for taxa addressed, including those from outside California. We reviewed each taxon's records from CCH2 to determine the percentage of voucher specimen records for which soil texture could be determined, and of those, what percentage indicated a soil high in clay. We binned taxa into ranked categories of clay affinity defined by what percentage of records with soil information indicated soils high in clay. While Safford et al. (2005) used similar affinity rankings, we used a more conservative approach to our interpretation of affinity by percentages based on the assumption that clay is recorded less often for substrate notes made for collections relative to other, more charismatic substrates like serpentine. For the same reason, we also examined every single record in CCH2 for each taxon rather than assessing only a subset of records by which to determine a percentage for records' soils by which to rank affinity.

Our initial list of taxa was compiled based on ecology notes from the Jepson eFlora and the CNPS RPI, and a search of the CCH2 database. We also included taxa for which we had extensive first-hand observations that suggested clay affinity. We searched the entire CCH2 database for terms indicating clay soils in collector notes on voucher specimen attributes, location, habitat, and substrate. Terms queried in CCH2 were "clay", "clayey", "adobe", "heavy soil(s)", "adobe soil(s)", "vertic clay", "Vertisol", "black soil(s)", "kaolinite", "smectite", "illite", and "montmorillonite". Of the CCH2 query results, we limited our analysis to taxa for which the query results suggested at least 30% of the given taxon's records included terms indicating clay soils.

In assembling our initial list of taxa, we retained species in addition to infraspecific taxa if the species and the infraspecific taxon (or taxa) came up in our search efforts independently, whether via the CCH2 queries, the CNPS RPI, or Jepson ecology addenda. Likewise, if a subspecies came up in our search, we did not add the species to our list unless the species also came up in our search. Where we have addressed both species and subspecies within said species, we have included subspecies records with the species records when addressing the species, i.e., *Acanthomintha obovata* Jeps. included records for *Acanthomintha obovata* subsp. *cordata* Jokerst and *Acanthomintha obovata* Jeps. subsp. *obovata*. In this case, *Acanthomintha obovata*, *A. obovata* subsp. *cordata* and *A. obovata* subsp. *obovata* all wound up on our initial list, and we therefore considered all three taxa, but our assessment of *A. obovata* was done including those records identified to the infraspecific level (so included records of *A. obovata* subsp. *cordata* and *A. obovata* subsp. *obovata*). This was the case with three species: *Acanthomintha obovata* (with two subspecies), *Cleomella hillmanii* A.Nelson (one subspecies), and *Lepidium jaredii* Brandegee (two subspecies). We have kept full species in these cases on the basis that we could not realistically identify all records to the infraspecific level where such identification was not done by collectors or herbarium workers, and to allow for infraspecific ecological considerations by readers.

From the initial list of taxa, we reviewed records only if a taxon had at least five voucher specimen records (though we did not rank clay affinity for all such taxa). Taxa we considered were limited to those with CCH2 records that are found within one or more of the following floristic provinces: the California Floristic Province, the Desert Province, and the Great Basin Province. Taxa in the database that are not found (either native or naturalized) within one of those floristic provinces at all were not addressed.

For each taxon from our initial list, we assessed all collection records for that taxon in CCH2. We eliminated duplicate records based on collector, collection date, and the collector's collection number. As our initial search of the CCH2 database conducted when compiling our initial species list could not account for context of the terms searched for, we next verified that records' use of our search terms were actual references to clay soils. Due to the dual use of the term, taxa for which "black soil" was referenced were retained only if records indicated that it referred to Vertisols or other clay soils, for which the term is sometimes applied; taxa were excluded if records indicated the term was used in the alternative sense, referring to soils high in organic material or humus. Care was taken to account for records caught by our CCH2 search terms that referred to places, roads, people, or locations with names including clay-related terms (e.g., "Clayton", "Adobe Canyon", "clay mines") that did not also include mention of clay explicitly regarding substrate.

Next, we read through every voucher specimen record for each species to determine whether each record had substrate information stated, and if so, if it included sufficient descriptions of soil texture to categorize each collection as on a clay soil or a soil predominantly of another texture. For all records read and assessed, we categorized the record as being either on clay soil, not on clay soil, or as lacking soil texture information. For records with soil texture information, we treated collections as "on clay soil" when records explicitly referred to clay or to clayey soils (clay loam, silty clay, etc.) or in equivalent terms (i.e., "heavy soils", "adobe soil", etc.). Collection records were treated as "not on clay soils" when collector notes indicated soils high in silt, sand, loam (clay loam was treated as a clay soil), described "light" soils, or otherwise described soils as "coarse", without reference to clay. Records describing soil texture as "fine" without additional information were treated as lacking sufficient description of soil texture because we could not determine from use of that term alone whether the soil texture referred to was predominately silt or clay. We then used the totals "on clay" and "not on clay" to calculate the percentage of records with soil texture information that were on clay for each taxon.

During this process, records with soil descriptions limited to particle sizes larger than sand were treated as lacking information on soil texture. We did not treat use of these terms ("stony", "rocky", "pebbly", "gravel", etc.) alone as sufficient to determine a lack of clay on the basis that the presence of gravel and other larger particle sizes does not preclude the possibility of clay in the soil matrix between large particles. This was supported by several records with substrate descriptions like "clay and gravel" that we came across in our searches. Additionally, particle size classes larger than sand, like gravel and cobble, exceed the size of particles which define soil texture (the term applies to particle sizes < 2 mm; Soil Survey Staff 2022), and we therefore treated their mention as independent of soil texture descriptions.

While records noting gravel could not be interpreted as precluding the presence of sand, silt, or clay particles, we did treat "talus" and "scree" as an absence of clay soils, on the basis that talus and scree are composed of loose, coarse fragments with inadequate particles of smaller size to infill and bind the coarse fragments together into any meaningful buildup of soil (Duchaufour 1977). Rock outcrops and plants growing in rock crevices were treated as lacking information on soil texture unless the presence and texture of any soil within the crevices was explicitly described.

Some parent materials such as gabbro, peridotite, and serpentinite often weather to produce clay soils that are also chemically extreme to plants (O'Geen et al. 2007). Additionally, some habitat types such as alkali sinks and vernal pools (Comer et al. 2024a, b) are strongly associated with clay soils due to the poor drainage of this soil texture. It was therefore possible that we could find apparent evidence of clay affinity for some taxa where an apparent affinity for soil texture was in fact affinity to other co-occurring soil chemical, hydrologic, or other environmental factors. To allow readers to consider this relative to taxa's affinity to clay, we also noted when collections indicated plants were collected from within vernal pools or from alkali sink habitat, and when records indicated gabbro or serpentine parent material. While the terms "alkali sink", "alkali", and "alkaline" may be used in reference to the soil type in geologic basins of arid regions, we generally found that these terms were applied to vegetation type alone without reference to soil, or were used in reference only to the pH of soil in records. Since we could not always reliably distinguish collectors' specific use of these terms, we did not attempt to apply those terms as indicating clay soils, nor to distinguish alkali sink habitat from alkali-heavy soils or soils with high pH. We instead included the proportion of records referencing these terms for each taxon where they were used in collection notes. Similarly, we did not attempt to interpret mentions of "serpentine" or "gabbro" in voucher notes as meaning clay. In cases where these habitats or parent materials were noted, we included the percentage of the total number of occurrences with references to these habitat types or parent materials (Appendices 1 and S1), but due to the often ambiguous or unclear nature of references, and after observing a strong trend of more references to soil texture than to any one habitat type, we did not attempt to interpret the relative affinity of species to clay soils versus to a specific habitat type. We also noted where records indicated soils with vertic properties, as vertic clay soils entail additional sources of physical stress to plants (Eswaran and Cook 1988; Ahmad 1975; Velde and Barré 2010). We treated soils as vertic if the records referenced "cracked" or "cracking soils", "Vertisols", "vertic properties", "pedoturbation", or otherwise referenced "shrink-swell".

Following examination of each taxon's full records from CCH2, we limited our quantification of clay affinity to taxa based on the following criteria: For taxa with fewer than five records, we have refrained from interpreting clay affinity and excluded those taxa from our final lists of taxa in Appendices 1 and S1. However, if that taxon was included in our initial list based on the Jepson eFlora or the CNPS RPI, we retained that taxon in the appendices and included our findings in them without ranking clay affinity. We ranked clay affinity only for taxa that had a minimum of 5 records where soil texture was addressed, unless the taxon had fewer than 10 records total. Taxa that were included in our initial list based on clay affinity stated in the Jepson eFlora or the CNPS RPI that had 0% of records indicating clay are still listed in Appendices 1 and S1. We did not attempt to rank clay affinity for those taxa, but include them for readers' reference and so that their affinity might be clarified by future researchers. We also note that our results for taxa with 0% of records addressing clay soil do not prove a lack of clay affinity, but rather reflect a lack of support for clay affinity in the herbarium records examined (i.e., such cases may be due to collection notes lacking information on substrate rather than an actual absence of occurrences on clay). There are undoubtedly many taxa for which experts on the taxon or region can attest to clay affinity that have simply not had adequate documentation in vouchers submitted and uploaded to CCH2 for us to capture in our efforts.

To rank clay affinity, we referred to the rankings used by Safford et al. (2005), but modified their framework based on the assumption that clay soils are reported less often by collectors than more recognizable substrates like serpentine. For this reason, we have been narrow in our interpretation of "strict endemism" and broad in our application of "clay tolerance". From the records that stated soil texture, we used the percentage which also referenced clay soils, and we binned collections into broad categories of affinity (clay tolerant: 1% to 29%, weak affinity: 30% to 49%, moderate affinity: 50% to 69%, high affinity: 70% to 89%, endemic: 90% to 99%, and strict endemic: 100%). Information provided in the abbreviated table (Appendix 1) of clay-associated taxa listing these rankings and the additional information in the full table (Appendix S1) on common names, life form, family, and distribution were pulled from the Jepson eFlora. For taxa not covered or taxonomically recognized by the Jepson eFlora, we utilized the California Moss eFlora (Wilson 2024) or Calflora (Calflora Database 2024). Information on special status (CRPR, global rank, state rank, and listing under both California and Federal Endangered Species Acts) were pulled from the Jepson eFlora, the CNPS RPI, and NatureServe (NatureServe 2024). Sources for each taxon's inclusion in our initial list of taxa are included in the full table in Appendix S1.

While work similar to this study used georeferenced coordinates and geologic mapping of serpentine outcrops to clarify locations when inadequate information was provided, we were not able to do similar verifications for records potentially collected on clay soils for several reasons. First, the available mapping of soil texture is aggregated into units from Soil Survey Geographic Database data (Walkinshaw et al. 2023), frequently for multiple soil series in one unit, and the Soil Survey Geographic Database data itself is mapped at a scale of 1:12,000 to 1:63,360 (Soil Survey Staff 2025) and extrapolated from individual soil pits upwards on a large scale. The resolution of soil texture mapping is therefore coarse, with an extremely large margin for error for any use on the scale of individual plant collections. Further, we are also personally aware of several areas with clay soils heterogeneously distributed at a smaller scale than the available mapping's resolution. As CCH2 records predating GPS and those which lack coordinates are frequently georeferenced retroactively by persons other than collectors to provide point coordinates (California Phenology Network 2025), there was substantial risk of compounding any error by using both soil mapping and georeferenced coordinates. While this is problematic for addressing individual records' substrates, these resources do still allow for regional-scale consideration of the distribution of clay soils, and we therefore still provide a figure of the distribution of clay soils (Fig. 1).

Results

We examined 53,534 collections records for 255 taxa, and of those, 240 had sufficient voucher records to consider. Of those taxa, 217 met our minimum threshold for the number of records that included soil texture information to evaluate and rank clay affinity. Based on the results of these reviews, we found taxa had affinities for clay soils that range from clay tolerance to strict endemism to clay soils. We present our results and rankings as evidence of endemism to clay soils in California (Appendices 1 and S1). Of the 217 taxa considered in our ranking, 42 taxa are strictly endemic (100%) to clay soil, 22 taxa are endemic (90–99%), 66 had high affinity (70–89%), and 39 showed moderate affinity (50–69%). A total of 21 taxa had weak affinity (30–49%), while 27 were clay tolerant (1–29%). Twenty-three taxa were excluded from our rankings due to a low number of collections and/or inadequate reference to soil texture in records.

Taxa with clay affinity were not evenly distributed across families (Table 1, Fig. 2). The family with the highest number of taxa with some degree of clay affinity was Asteraceae (39 taxa), followed by Polemoniaceae and Polygonaceae (14 taxa each), Liliaceae and Apiaceae (13 taxa each), Brassicaceae (12 taxa), and Chenopodiaceae (11 taxa). The relative contributions of these and other families to the clay flora included in this study differed somewhat from the contributions of these families to the California flora overall, most notably in Alliaceae, Asteraceae, Chenopodiaceae, Liliaceae, Polemoniaceae, and Themidaceae. The genera that were most well-represented (Table 2) were *Navarretia* (14 taxa), *Atriplex* (10 taxa), *Allium* and *Eriogonum* (9 taxa each), *Phacelia* (8 taxa), *Calochortus* (7 taxa), *Astragalus* (6 taxa), and *Lomatium*, *Layia*, and *Dudleya* (5 taxa each).

The most common life form (Fig. 3) among taxa with clay affinity evaluated was annual herbs (109 taxa), followed by perennial herbs (85 taxa, of which 26 are geophytes), and 14 shrubs (ranging from weak affinity to strict endemism). Our list includes only one annual to perennial herb (of weak affinity), three graminoid taxa (ranging from clay tolerant to strict endemic), one moss taxon (of moderate affinity), one fern taxon (of weak affinity), and one tree taxon (of moderate affinity).

The ecoregion (Table 3, Fig. 4) with the highest number of ranked taxa was the Central Western California region (CW; 96 taxa), followed by the Southwestern California region (SW; 84 taxa), the Great Valley region (GV; 64 taxa), and the Sierra Nevada region (SN; 63 taxa). Of all taxa considered, 105 are found in only one ecoregion. Occurrence density for taxa ranked in this study (Fig. 4A) was greatest in the SW region, with hotspots in the CW, Northwestern California (NW), GV, SN, White and Inyo Mountains (W&I) and Mojave Desert (DMoj) regions. Density of strict endemic, endemic, and high

TABLE 1. CLAY AFFINITY RANKINGS, BY FAMILY. Counts of minimum-rank taxa for each family, by clay affinity ranking. Only families for which we were able to rank at least one minimum-rank taxon are listed.

Family	Clay tolerant	Weak affinity	Moderate affinity	High affinity	Endemic	Strict endemic	Total ranked
Agavaceae	—	—	—	—	1	—	1
Alliaceae	—	—	1	3	1	3	8
Apiaceae	—	2	2	3	—	6	13
Asteraceae	5	2	7	10	10	5	39
Athyriaceae	—	1	—	—	—	—	1
Boraginaceae	2	1	—	2	1	1	7
Brassicaceae	—	1	—	7	—	4	12
Bryaceae	—	—	1	—	—	—	1
Caryophyllaceae	—	—	1	—	—	—	1
Chenopodiaceae	4	—	3	2	—	2	11
Cleomaceae	—	—	—	2	—	—	2
Convolvulaceae	—	—	1	—	1	—	2
Crassulaceae	—	—	1	2	1	1	5
Cupressaceae	—	—	1	—	—	—	1
Cyperaceae	—	—	—	1	—	—	1
Ericaceae	—	—	—	1	—	—	1
Fabaceae	3	1	3	1	—	2	10
Fagaceae	—	1	—	—	—	—	1
Geraniaceae	—	—	—	—	1	—	1
Hydrophyllaceae	3	1	1	2	—	1	8
Lamiaceae	—	—	2	3	2	1	8
Liliaceae	1	—	2	6	1	3	13
Loasaceae	—	—	1	—	—	—	1
Malvaceae	1	—	—	—	1	—	2
Melanthiaceae	—	—	—	1	—	—	1
Namaceae	—	—	—	—	—	1	1
Onagraceae	2	2	2	1	—	—	7
Orobanchaceae	—	—	—	—	—	1	1
Papaveraceae	—	1	—	—	—	—	1
Phrymaceae	1	2	—	1	—	—	4
Plantaginaceae	1	1	1	2	—	—	5
Poaceae	1	—	—	1	—	1	3
Polemoniaceae	1	1	—	4	2	6	14
Polygonaceae	1	2	4	4	—	3	14
Ranunculaceae	—	—	1	1	—	—	2
Rhamnaceae	—	—	1	1	—	—	2
Rosaceae	1	—	2	—	—	—	3
Scrophulariaceae	—	—	—	—	—	1	1
Solanaceae	—	1	—	—	—	—	1
Themidaceae	—	1	1	5	—	—	7
Total	26	21	37	63	22	46	215

affinity taxa (Fig. 4B) was highest in the SW region, with hotspots in the CW, NW, GV, SN, and GV regions. Lower-affinity taxa (clay tolerant, weak affinity, moderate affinity; Fig. 4C) had broader distributions than the higher-affinity taxa, though still highest density in the SW region, with hotspots in the CW, NW, and SN regions.

Most of the taxa we considered here are special-status or rare (Table 4). Of the 240 taxa considered, 162 are listed on the CNPS RPI, 18 have California Endangered Species Act (CESA) status, and 19 have Federal Endangered Species Act (FESA) status. Of those, we were able to rank clay affinity for 142 taxa on the CNPS RPI, 16 with CESA status, and 17 with FESA status. Most taxa either ranked on the CNPS RPI or which have special status under CESA and FESA had clay affinity that was moderate or higher. Of the CNPS RPI ranked taxa, most were ranked at 1B; CESA taxa were mostly listed as endangered, though a slight majority of the FESA taxa were listed only as threatened.

DISCUSSION

Our results show that endemism to clay and clay affinity occur within California's flora across the California, Great Basin, and Desert Floristic Provinces, spans several plant families, and may be as strict as the substrate affinity seen in many serpentine-endemic species. Of the 213 taxa we considered, 30% (64 taxa) are ranked as either endemic or strictly endemic to clay soils. We considered taxa to be strict endemics to clay soils only if 100% of the

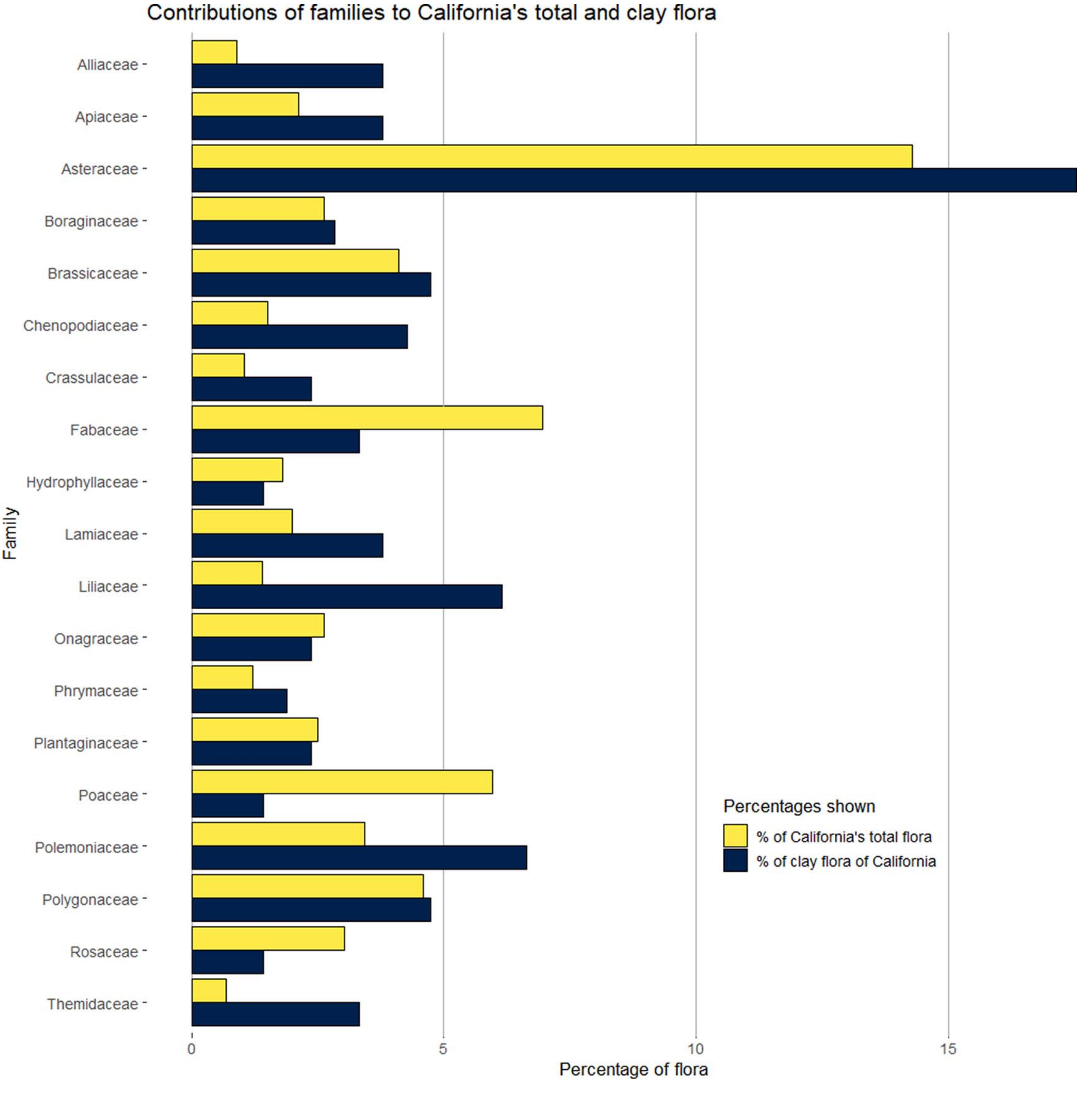

FIG. 2. Contributions of important families for clay affinity, as percentage contributed to both the total California flora (% of California's total flora) and the clay flora of California (% of clay flora of California). Figure includes only families with three or more minimum-rank taxa with some degree of clay affinity.

records indicating soil texture identified clay soils, as we did not expect clay soils to be consistently addressed in voucher records as well as serpentine soils; However, if we applied the percentage bins used by Safford et al. (2005) to our results (i.e., >95% of records indicating the substrate in question being interpreted as strict endemism), the number of strict endemics to clay soils (42 taxa) would increase to 49 of the 217 taxa we ranked.

Most well-studied forms of edaphic endemism in California such as serpentine, gabbro, limestone, and saline soils have primarily focused on extreme soil chemistry. The evidence of clay endemism we have found therefore offers new opportunities for research into extreme physical properties of soil in this context, yet to be explored in California. Geology and soil are driving forces for the distribution of plant species, and the high plant diversity within California reflects its diversity of geology and soil. From this study, we find this pattern not to be coincidental, and advocate for further investigation of the role of soil physical properties like soil texture as a defining element of the range and ecology of species within California's flora.

Of the taxa for which we were able to interpret clay affinity, 50.2% of the 217 taxa were annual

TABLE 2. GENERA WITH TWO OR MORE CLAY-ASSOCIATED TAXA, BY CLAY AFFINITY RANKING. Minimum-rank taxa for each genus, listed by clay affinity ranking; only genera with two or more minimum-rank taxa assessed for clay affinity are shown in table.

Genus	Clay tolerant	Weak affinity	Moderate affinity	High affinity	Endemic	Strict endemic	Total ranked
Acanthomintha	—	—	—	2	2	—	4
Allium	—	—	1	4	1	3	9
Astragalus	2	—	3	—	—	1	6
Atriplex	4	—	3	1	—	2	10
Blepharizonia	—	—	—	1	—	1	2
Bloomeria	—	—	—	2	—	—	2
Brodiaea	—	—	—	3	—	—	3
Calochortus	1	—	2	3	—	1	7
Caulanthus	—	—	—	2	—	—	2
Chorizanthe	—	1	1	1	—	1	4
Cleomella	—	—	—	2	—	—	2
Deinandra	—	—	—	1	1	—	2
Diplacus	1	1	—	1	—	—	3
Dudleya	—	—	1	2	1	1	5
Ericameria	1	—	—	—	1	—	2
Eriogonum	1	—	3	3	—	2	9
Eryngium	—	—	—	1	—	2	3
Fritillaria	—	—	—	2	1	2	4
Horkelia	—	—	2	—	—	—	2
Layia	—	—	—	2	2	1	5
Lepidium	—	—	—	3	—	—	3
Lessingia	—	—	—	2	—	—	2
Lomatium	—	2	1	1	—	1	5
Microseris	—	—	1	—	1	—	2
Monardella	—	—	1	—	—	1	2
Monolopia	—	—	2	—	—	—	2
Navarretia	1	1	—	4	2	6	14
Penstemon	1	—	—	1	—	—	2
Perideridia	—	—	1	—	—	1	2
Phacelia	3	1	1	2	—	1	8
Plagiobothrys	2	—	—	1	—	1	4
Pseudobahia	1	—	—	—	1	—	2
Sanicula	—	—	—	1	—	1	2
Triteleia	—	1	1	—	—	—	2

forbs, 39.2% were perennial forbs, including the 12.0% that were perennial geophytes (bulbs and rhizomatous taxa), and 6.9% were shrubs (or perennial herb-to-shrub taxa). Graminoids made up only 1.4% of our list, annual-to-perennial herbs made up <1%, and mosses, ferns, and trees had only a single taxon. The high number of annual taxa and perennial geophytes is likely linked to these life histories enabling drought avoidance, wherein drought (or soil-related water stress) may be avoided by plants passing periods of drought in dormancy as seeds, bulbs, or rhizomes (Chandler and Bartels 2007). Annual forbs made up a higher proportion of the strict endemics, followed by perennial forbs and perennial bulbs. The proportion of perennial forbs was higher in the strict endemic taxa than in the overall list as well. Similarly, the high number of herbaceous life forms and the low number of woody life forms among taxa with clay affinity is unsurprising given the water limitations and potentially limited nutrient availability of clay soils (Binkley and Vitousek 1989; Fensham et al. 2015).

While we included nonvascular taxa in our efforts on the basis that edaphic affinity has long been noted in bryophytes (e.g., Watson 1918; Briscoe et al. 2009; Rajakaruna et al. 2009), we found only one nonvascular taxon with clay affinity in this study. We suspect this number may be artificially low because there are far fewer records of nonvascular plants than vascular plants in CCH2, even accounting for differences in the number of taxa from each group found within the state (Doyle and Stotler 2006; Consortium of California Herbaria 2024; Jepson Flora Project 2024; Wilson 2024). Though we found only one moss in our effort, there may be interesting future work examining poikilohydry, desiccation tolerance, and/or the lack of both cuticle and true vascular tissue in mosses in the context of clay soils' unique hydrology and chemistry (Vitt et al. 2014).

Some taxa with affinity or endemism to clay soils had many herbarium records collected from clay soil as well as from within vernal pools or in alkali sinks (e.g., *Plagiobothrys acanthocarpus* (Piper) I.M.Johnst., *Gratiola heterosepala* H.Mason & Bacig., *Eryngium*

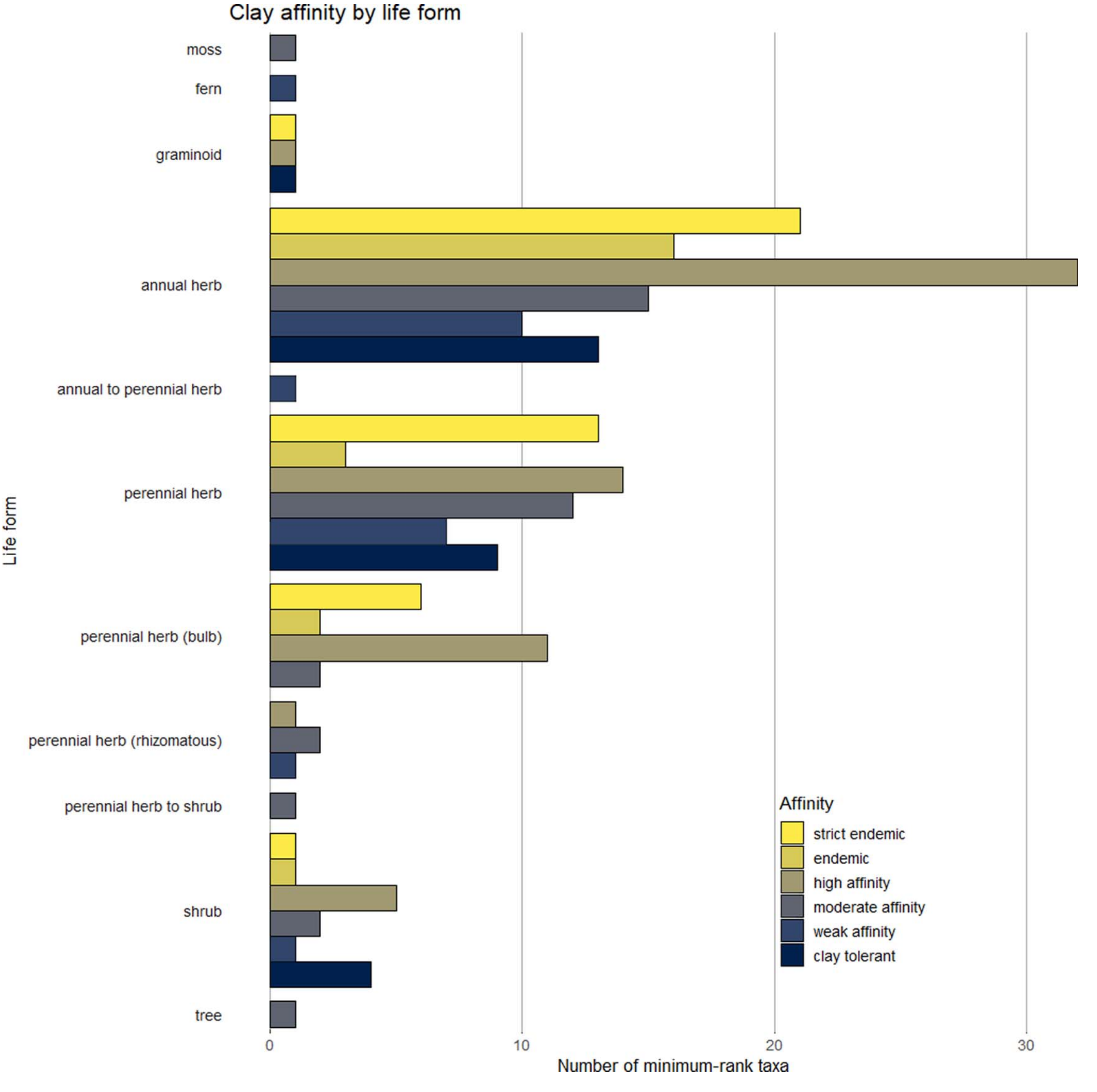

FIG. 3. Clay affinity by life form, for all taxa for which we ranked clay affinity.

pendletonense K.L.Marsden & M.G.Simpson). For those and several other taxa, the high number of clay records combined with a high number of vernal pool or alkali sink records may be due to their affinity for vernal pools' or alkali sinks' hydrologic regime as much as to clay soils (which influence soil hydrology in both habitats). However, we also saw that in some genera which contain taxa with noted affinity to vernal pools (e.g., *Navarretia nigelliformis* Greene subsp. *nigelliformis*) and alkali sinks (*Atriplex parishii* S.Watson) that also had many records on clay, other taxa in the same genus (*N. ojaiensis* Elvin, J.M.Porter & L.A.Johnson, *N. panochensis* D.Gowen & L.A.Johnson, *A. coulteri* (Moq.) D.Dietr.) had many records from clay soils yet no records or apparent affinity to vernal pools or alkali sinks. This supports the importance of soil texture affinity in shaping species distributions and suggests affinity to soil texture alone. However, the task of decoupling a given taxon's apparent affinity to habitat and hydrologic regime versus affinity to clay soils would require experimental work. For this reason, we have refrained from attempting to distinguish clay affinity alone from clay affinity that is potentially incidental to habitat or hydrologic affinity, instead providing the percentage of records associated with habitat types for readers' benefit and consideration (Appendix S1). We also note that such a distinction is likely not well-defined, and that serpentine affinity too, is closely linked with secondary features of many serpentine soils such as high drainage (Alexander et al. 2006), and we hope this paper provides future researchers with a starting point for such experimentation.

TABLE 3. TAXA FOUND IN EACH JEPSON ECOREGION BY CLAY AFFINITY RANKING. Minimum-rank taxa for each family, listed in clay affinity ranking. CA-FP = California Floristic Province, GB = Great Basin Floristic Province, D = Desert Floristic Province. CaR = Cascade Ranges region, CW = Central Western California region, DMoj = Mojave Desert region, DSon = Sonoran Desert region, GV = Great Central Valley region, NW = Northwestern California region, MP = Modoc Plateau region, SN = Sierra Nevada region, SNE = East of the Sierra Nevada region, and SW = Southwestern California region.

Province	Region	Clay tolerant	Weak affinity	Moderate affinity	High affinity	Endemic	Strict endemic	Total ranked
CA-FP	CaR	7	7	8	10	1	1	34
	CW	8	8	18	34	9	19	96
	GV	6	5	11	25	8	9	64
	NW	5	7	12	14	7	6	51
	SN	13	6	12	17	7	8	63
	SW	10	9	15	33	9	8	84
GB	MP	9	6	6	11	2	2	36
	SNE	11	3	4	3	—	2	23
D	DMoj	13	6	7	2	—	1	29
	DSon	5	1	1	1	2	1	11

Similar work on serpentine affinity within California's vascular plants (Safford et al. 2005; Safford and Miller 2020) yielded a higher number of taxa with serpentine affinity (255) than we found for clay within California (216 vascular taxa). Of the taxa in our study, 40 are also ranked in the serpentine database (indicated by * in Appendices 1 and S1). Of those, 23 had more records in CCH2 referencing clay than referenced serpentine (indicated by ** in Appendices 1 and S1). There was a substantial overlap in vascular plant genera and families between our clay affinity list and the serpentine database, though for some taxa it may simply be due to the high number of species within them (e.g., Asteraceae, Fabaceae, *Eriogonum*, *Allium*). The following genera have three or more taxa in both our list and the serpentine database: *Allium*, *Calochortus*, *Eriogonum*, *Fritillaria*, *Lomatium*, *Navarretia*, and *Phacelia*. However, several vascular plant families on our list do not appear at all in the serpentine database (Amaranthaceae, Athyriaceae, Chenopodiaceae, Cleomaceae, Geraniaceae, Loasaceae, Namaceae, and Solanaceae), and our list has a much higher proportion of annual forbs than the serpentine database. We found our list also has overlap with work on gypsum affinity in the Mojave region for some genera (*Atriplex*, *Chorizanthe*, *Eriogonum*, *Lepidium*, and *Phacelia*; Meyer 1986), which is perhaps not surprising given shared characteristics: Both clay and gypsum present complex and challenging hydrology, introduce physical

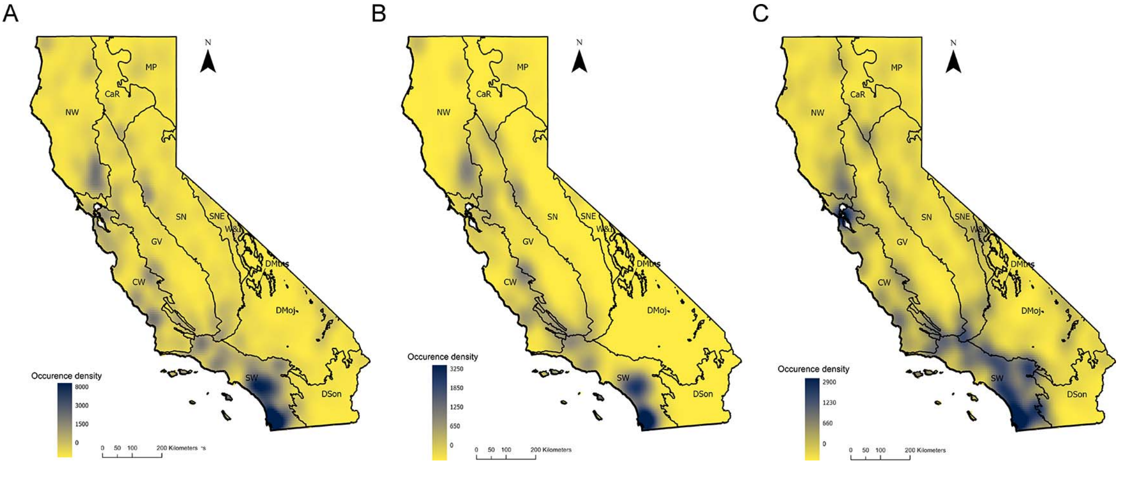

FIG. 4. Distribution of georeferenced CCH2 occurrences with clay affinity, by ecoregion and affinity. A: All taxon occurrences ranked in this study; B: all occurrences for taxa with high affinity, endemism, or strict endemism to clay soils; C: all occurrences for taxa with clay tolerance or weak to moderate affinity to clay soils. CaR = Cascade Ranges region, CW = Central Western California region, Dmtns = Desert Mountains subregion, DMoj = Mojave Desert region, DSon = Sonoran Desert region, GV = Great Central Valley region, NW = Northwestern California region, MP = Modoc Plateau region, SN = Sierra Nevada region, SNE = East of the Sierra Nevada region, SW = Southwestern California region, and W&I = White and Inyo Mountains subregion.

TABLE 4. CLAY-ASSOCIATED TAXA BY CLAY AFFINITY, CALIFORNIA RARE PLANT RANK, FEDERAL, AND STATE STATUS. Number of minimum-rank taxa evaluated for clay affinity with California Rare Plant Ranking, California Endangered Species Act status, or Federal Endangered Species Act status, by clay affinity ranking. CT = CESA "threatened" status; CE = CESA "endangered' status, CR = CESA "critically endangered" status, FT = FESA "threatened" status, and FE = FESA "endangered" status.

	CRPR rank												CESA status				FESA status		
Clay affinity	1B.1	1B.2	1B.3	2B.1	2B.2	2B.3	3	3.2	3.3	4.2	4.3	Total	CE	CR	CT	Total	FE	FT	Total
Strict endemic	14	13	4	1	—	—	—	—	—	1	3	36	1	1	1	3	—	1	1
Endemic	9	2	—	—	—	—	—	—	—	4	2	17	5	—	1	6	3	5	8
High affinity	11	11	1	1	2	2	1	1	—	7	7	44	1	1	1	3	—	3	3
Moderate affinity	5	7	1	—	1	—	—	1	2	4	1	22	2	1	—	3	1	1	2
Weak affinity	3	2	—	—	—	2	—	—	—	2	2	11	—	—	—	—	1	—	1
Clay tolerant	3	2	—	1	3	—	1	—	—	1	1	12	1	—	—	1	2	—	2
Total ranked	45	37	6	3	6	4	2	2	2	19	16	142	10	3	3	16	7	10	17

stress for plant life (especially related to root penetration), and are more common in arid regions (Bridges and Burnham 1980; Poch and Verplancke 1997; Poch 1998; Moore et al. 2014). There is much work to be done untangling affinity to soil texture versus soil chemistry, and on how tolerance of one harsh soil may influence species' adaptability to others.

We are aware of several taxa with very small ranges suggesting those taxa are restricted to clay soils (e.g., *Castilleja ambigua* var. *heckardii* J.M.Egger & Excoffier; Egger and Excoffier 2021) or have strong affinity to clay soil observed by botanists (P. Excoffier, California Native Plant Society, personal communication), but which have not been recorded with voucher specimens. We also acknowledge that in the limited scope of our effort, we have undoubtedly overlooked some taxa with *bona fide* endemism to clay within California. Unavoidably, there are likely numerous non-voucher observations (e.g., private collections, passing observations in the literature) supporting the clay affinity of taxa in many cases which we have not captured in our efforts. Indeed, for some taxa which we have made extensive personal observations, we believe clay affinity is somewhat higher than our results found (e.g., *Caulanthus anceps* Payson, *C. flavescens* (Hook.) Payson., *Eriogonum ordii* S.Watson, and *Monolopia major* DC.), though we believe some have lower affinity than our results suggest (*Chorizanthe biloba* var. *immemora* Reveal & Hardham, *Eriogonum nudum* var. *indictum* (Jeps.) Reveal). Lastly, as we assessed over 50,000 herbarium records for this study, we acknowledge there will be—by nature of herbarium records—misidentified specimens, and with digitization efforts still ongoing throughout the state, it was not feasible to check every specimen addressed in this study. For these reasons, our findings should be treated as a somewhat coarse first indication of clay affinity within California's flora.

Our utilization of the CNPS RPI as a source when compiling our list of taxa to investigate for clay affinity likely introduced some bias to the final list of taxa with clay affinity (Appendices 1 and S1) that we present here. However, the severity of this bias is likely reduced not only because we also conducted a broad search of herbarium records for clay terms to supplement the list derived from the CNPS RPI and the Jepson eFlora, but also because affinity and endemism to abiotic factors is generally associated with rarity (Rabinowitz 1981). It is also true that rarity of species can influence bias in herbarium collections as botanists often tend to make fewer collections of threatened species and are more likely to collect species that are accessible from roads (Daru et al. 2018). So, while a degree of bias towards rare taxa being over-represented within this list is possible, we have made efforts to account for that bias in our sources utilized, and the nature of edaphic endemism and affinity is such that we had already anticipated a larger proportion of rare taxa. Further work on clay affinity will help to improve this issue. In the meantime, our full list of taxa with clay affinity (Appendix S1) provides information for conservation workers on the rarity and special status of clay-associated taxa requiring management, protection, and mitigation efforts.

The topic of clay affinity and endemism warrants further work: There is a need to ground-truth our findings, and for many taxa addressed here that we did not rank for lack of records, further work would greatly clarify the degree of clay affinity. There is also a broad need for botanists to describe substrate in greater detail (rock type, soil texture) when making voucher collections, as the number of records currently addressing substrate for many of these taxa are only sufficient to suggest a pattern of clay affinity or association, and not enough to firmly quantify their affinity. Despite this, our findings show a broad pattern of clay affinity and endemism in the California Floristic Province to a degree comparable to that seen with serpentine. More detailed descriptions of substrate in voucher notes in the future may reveal greater clay affinity for some taxa, or for taxa not included in our efforts and—given the geological diversity of the region—will likely reveal other types of substrate affinity within California. Basic assessments of soil texture can be made in the field relatively quickly. We refer readers to Thien (1979) for a practical guide to conducting soil texture by feel assessments in the field (no specialized equipment or tools needed), and encourage readers to address soil texture and other information regarding substrate (e.g., cracking, visible evaporites, parent material) in their voucher notes whenever possible.

Acknowledgments

We thank Dr. Jenn Yost and Katelin Pearson for their assistance with the CCH2 database, and Marco Iandolini and Jacob Mull for their assistance in assessing herbarium records. We are grateful to the many botanists whose detailed voucher notes made this study possible, and invite readers to submit their own observations on clay affinity for taxa with which they are both familiar and qualified to address at https://www.emmarosefryer.com/clay-affinity for incorporation into any future updates of the database presented here. We thank the reviewers for their thorough review and numerous suggestions which substantially improved this manuscript.

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APPENDIX 1

CLAY-ASSOCIATED TAXA RANKED BY CLAY AFFINITY

MINIMUM-RANK TAXA FOR WHICH CLAY AFFINITY WAS ASSESSED. Clay affinity rankings are based on what percentage of the records for which soil texture was addressed were on clay soils, as follows: clay tolerant = 1% to 29%, weak affinity = 30% to 49%, moderate affinity = 50% to 69%, high affinity = 70% to 89%, endemic = 90% to 99%, and strict endemic = 100%. Taxa for which Clay affinity is marked only as "—" had too few records addressing soil texture to rank affinity. "Records examined" states number of CCH2 herbarium voucher records assessed; "Soil texture addressed" is number of records examined that addressed soil texture in voucher notes. "On clay" gives the subset of herbarium records examined that stated soil texture in the voucher notes (i.e., "Soil texture addressed") for which the soil texture stated was clay or otherwise clay soils. "Vernal pools", "Gabbro", "Serpentine", "Alkali sink or soils", and "Vertic soils" are percentage of all herbarium records assessed that mentioned those habitat or substrate types, so are a percentage of "Records examined". "Life form" and "Family" for taxa state life form and family as stated the Jepson eFlora; in cases where the taxon was not addressed in the Jepson eFlora, this information was pulled from Calflora or the California Moss eFlora. Taxa with an * are those also present in the serpentine database (Safford and Miller 2020), and ** indicates species also present in the serpentine database for which more CCH2 records referenced clay than referenced serpentine.

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Acanthomintha duttonii (Abrams) Jokerst*	—	29	14%	50%	—	—	34%	—	—	Ann. herb	Lamiaceae
Acanthomintha ilicifolia A.Gray**	Endemic	162	39.5%	96.9%	4%	—	—	—	19%	Ann. herb	Lamiaceae
Acanthomintha obovata Jeps.	High affinity	148	48.6%	81.9%	1%	—	11%	4%	9%	Ann. herb	Lamiaceae
Acanthomintha obovata subsp. *cordata* Jokerst	High affinity	55	60.0%	75.8%	—	—	2%	2%	2%	Ann. herb	Lamiaceae
Acanthomintha obovata Jeps. subsp. *obovata*	Endemic	52	51.9%	96.3%	—	—	17%	6%	17%	Ann. herb	Lamiaceae
Achyrachaena mollis Schauer	High affinity	1250	16.7%	84.7%	5%	0%	3%	2%	1%	Ann. herb	Asteraceae
Acmispon rubriflorus (Sharsm.) D.D.Sokoloff	Strict endemic	29	44.8%	100.0%	—	—	—	—	—	Ann. herb	Fabaceae
Adolphia californica S.Watson	High affinity	292	13.0%	76.3%	1%	—	—	—	—	Shrub	Rhamnaceae
Allium anceps Kellogg	Moderate affinity	157	27.4%	67.4%	1%	—	—	2%	—	Per. herb (bulb)	Alliaceae
Allium fimbriatum S.Watson var. *purdyi* (Eastw.) McNeal*	Strict endemic	58	8.6%	100.0%	—	—	52%	—	—	Per. herb (bulb)	Alliaceae
Allium howellii var. *clokeyi* Ownbey & Aase ex Traub	High affinity	77	48.1%	89.2%	—	—	—	—	3%	Per. herb (bulb)	Alliaceae
Allium howellii Eastw. var. *howellii*	High affinity	94	40.4%	71.1%	1%	—	4%	6%	1%	Per. herb (bulb)	Alliaceae
Allium howellii var. *sanbenitense* (Traub) Ownbey & Aase**	Strict endemic	14	50.0%	100.0%	—	—	14%	—	29%	Per. herb (bulb)	Alliaceae
Allium lemmonii S.Watson	High affinity	232	24.1%	83.9%	4%	—	—	<1%	—	Per. herb (bulb)	Liliaceae
Allium munzii (Ownbey & Aase ex Traub) McNeal	Endemic	70	61.4%	90.7%	—	1%	—	—	—	Per. herb (bulb)	Alliaceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Allium peninsulare Greene var. *franciscanum* McNeal & Ownbey*	Strict Endemic	38	2.6%	100.0%	—	—	11%	—	—	Per. herb (bulb)	Alliaceae
Allium unifolium Kellogg**	High Affinity	261	11.1%	72.4%	<1%	—	3%	<1%	—	Per. herb (bulb)	Alliaceae
Ambrosia pumila (Nutt.) A.Gray	Weak affinity	148	17.6%	46.2%	9%	—	—	2%	2%	Per. herb (rhiz.)	Asteraceae
Ammoselinum giganteum J.M.Coult. & Rose	Strict Endemic	6	33.3%	100.0%	—	—	—	—	—	Ann. herb	Apiaceae
Antirrhinum ovatum Eastw.	High Affinity	99	51.5%	72.5%	7%	—	—	—	2%	Ann. herb	Plantaginaceae
Arctostaphylos myrtifolia Parry	High affinity	280	18.6%	71.2%	—	—	<1%	—	—	Shrub	Ericaceae
Artemisia rothrockii A.Gray	—	336	11.9%	0.0%	—	—	—	0%	—	Shrub	Asteraceae
Astragalus atratus var. *mensanus* M.E.Jones	Strict endemic	16	25.0%	100.0%	—	—	—	—	—	Per. herb	Fabaceae
Astragalus canadensis var. *brevidens* (Gand.) Barneby	Clay tolerant	254	13%	9.1%	<1%	—	—	5%	—	Per. herb	Fabaceae
Astragalus cimae M.E.Jones var. *cimae*	—	44	20.5%	0.0%	—	—	—	—	—	Per. herb	Fabaceae
Astragalus claranus Jeps.*	Moderate affinity	30	20.0%	50.0%	—	—	30%	—	—	Ann. herb	Fabaceae
Astragalus lentiginosus var. *idriensis* M.E.Jones	Moderate affinity	108	26.9%	65.5%	—	—	2%	—	2%	Per. herb	Fabaceae
Astragalus preussii A.Gray var. *preussii*	Clay tolerant	133	51.1%	11.8%	2%	—	—	8%	2%	Per. herb	Fabaceae
Astragalus rattanii var. *jepsonianus* Barneby*	Moderate affinity	127	20%	68%	—	—	46%	—	5%	Ann. herb	Fabaceae
Athyrium filix-femina (L.) var. *cyclosorum* Rupr.	Weak affinity	1229	3.9%	31.3%	<1%	—	1%	—	—	Fern	Athyriaceae
Athysanus unilateralis (M.E. Jones) Jeps.	High affinity	140	33.6%	85.1%	1%	—	4%	4%	4%	Ann. herb	Brassicaceae
Atriplex argentea var. *hillmanii* M.E.Jones	Clay tolerant	140	34%	17.0%	1%	—	—	11%	—	Ann. herb	Chenopodiaceae
Atriplex argentea var. *longitrichoma* (Stutz & G.L.Chu & S.C.Sand.) S.L.Welsh	Moderate affinity	42	64.3%	63.0%	—	—	—	7%	24%	Ann. herb	Chenopodiaceae
Atriplex canescens (Pursh) Nutt. var. *canescens*	Clay tolerant	595	31.6%	6.4%	<1%	—	—	4%	—	Shrub	Chenopodiaceae
Atriplex coronata S.Watson var. *coronata*	Moderate affinity	65	23.1%	53.3%	8%	—	—	46%	—	Ann. herb	Chenopodiaceae
Atriplex coulteri (Moq.) D.Dietr.	High affinity	295	18.3%	72.2%	—	—	—	3%	1%	Per. herb	Chenopodiaceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Atriplex depressa Jeps.	Strict endemic	63	20.6%	100.0%	22%	—	—	56%	—	Ann. herb	Chenopodiaceae
Atriplex fruticulosa Jeps.	Moderate affinity	150	15%	69.6%	9%	—	1%	31%	—	Per. herb	Chenopodiaceae
Atriplex gypsophila R.E. Preston	Strict endemic	2	100%	100%	—	—	—	—	—	Ann. herb	Chenopodiaceae
Atriplex parishii S.Watson	Clay tolerant	97	7%	14.3%	25%	—	—	26%	—	Ann. herb	Chenopodiaceae
Atriplex torreyi (S.Watson) S. Watson var. *torreyi*	Clay tolerant	174	28%	20.4%	—	—	—	24%	—	Ann. herb	Chenopodiaceae
Benitoa occidentalis (H.M. Hall) D.D.Keck**	Endemic	100	44.0%	93.2%	—	—	15%	—	3%	Ann. herb	Asteraceae
Beta vulgaris subsp. *Macrocarpa* (Guss.) Thell.	High affinity	14	50.0%	85.7%	—	—	—	29%	—	Per. herb	Chenopodiaceae
Blepharipappus scaber Hook. subsp. *scaber*	Strict endemic	6	83.3%	100.0%	—	—	—	—	—	Ann. herb	Asteraceae
Blepharizonia laxa Greene	High affinity	136	19.9%	81.5%	—	—	5%	1%	—	Ann. herb	Asteraceae
Blepharizonia plumosa (Kellogg) Greene	Strict endemic	85	17.6%	100.0%	—	—	4%	—	5%	Ann. herb	Asteraceae
Bloomeria clevelandii S.Watson	High affinity	122	15.6%	78.9%	11%	—	—	—	—	Per. herb	Themidaceae
Bloomeria humilis Hoover	High affinity	17	52.9%	88.9%	6%	—	—	—	—	Per. herb (bulb)	Themidaceae
Boechera johnstonii (Munz) Al-Shehbaz	Strict endemic	37	5.4%	100.0%	—	—	—	—	—	Per. herb	Brassicaceae
Brodiaea appendiculata Hoover	High affinity	126	7.1%	77.8%	4%	—	—	—	—	Per. herb	Themidaceae
Brodiaea filifolia S.Watson	High affinity	145	27.6%	72.5%	10%	—	—	9%	1%	Per. herb (bulb)	Themidaceae
Brodiaea insignis (Jeps.) T.F.Niehaus	—	36	0.0%	0.0%	—	—	—	—	—	Per. herb (bulb)	Themidaceae
Brodiaea orcuttii (Greene) Baker	High affinity	166	18.7%	77.4%	19%	4%	1%	—	—	Per. herb (bulb)	Themidaceae
California macrophylla (Hook. & Arn.) Aldasoro, C.Navarro, P.Vargas, L.Sáez & Aedo	Endemic	321	11.5%	94.6%	—	<1%	2%	1%	4%	Ann. herb	Geraniaceae
Calochortus argillosus (Hoover) Zebell & P.L.Fiedl.	Strict endemic	87	25.3%	100.0%	—	—	22%	—	—	Per. herb (bulb)	Liliaceae
Calochortus catalinae S.Watson	High affinity	611	18.5%	71.7%	—	—	1%	<1%	—	Per. herb (bulb)	Liliaceae
Calochortus clavatus S.Watson var. *clavatus**	High affinity	72	12.5%	88.9%	—	—	24%	—	—	Per. herb (bulb)	Liliaceae
Calochortus kennedyi Porter var. *kennedyi*	Clay tolerant	125	24.0%	16.7%	—	1%	—	—	—	Per. herb	Liliaceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Calochortus longebarbatus S.Watson var. *longebarbatus*	High affinity	38	15.8%	83.3%	3%	—	—	—	—	Per. herb (bulb)	Liliaceae
Calochortus striatus Parish	Moderate affinity	105	25%	50.0%	1%	—	—	45%	2%	Per. herb (bulb)	Liliaceae
Calochortus weedii Alph. Wood	Moderate affinity	588	16.0%	52.1%	—	1%	—	—	—	Per. herb	Liliaceae
Calystegia subacaulis subsp. *episcopalis* Brummitt	Moderate affinity	92	16.3%	66.7%	—	—	14%	—	—	Per. herb (rhiz.)	Convolvulaceae
Camissoniopsis lewisii (P.H.Raven) W.L.Wagner & Hoch	Clay tolerant	306	40.2%	4.9%	—	—	—	—	—	Ann. herb	Onagraceae
Carex obispoensis Stacey*	High affinity	122	8.2%	80.0%	—	1%	40%	—	—	Per. herb (rhiz.)	Cyperaceae
Castilleja ambigua var. *meadii* J.M.Egger & Ruygt	Strict endemic	8	37.5%	100.0%	38%	13%	13%	13%	13%	Ann. herb	Orobanchaceae
Caulanthus anceps Payson	High affinity	291	35.7%	76.0%	—	—	—	5%	1%	Ann. herb	Brassicaceae
Caulanthus flavescens (Hook.) Payson**	High affinity	189	14.3%	77.8%	—	—	7%	—	4%	Ann. herb	Brassicaceae
Ceanothus decornutus V.T.Parker	—	1	0.0%	0.0%	—	—	100%	—	—	Shrub	Rhamnaceae
Ceanothus maritimus Hoover	Moderate affinity	49	4.1%	50.0%	—	—	2%	—	—	Shrub	Rhamnaceae
Chamaesaracha coronopus (Dunal) A.Gray	Weak affinity	55	23.6%	38.5%	—	—	—	—	—	Per. herb	Solanaceae
Chorizanthe biloba var. *immemora* Reveal & Hardham	Strict endemic	25	8.0%	100.0%	—	—	28%	—	—	Ann. herb	Polygonaceae
Chorizanthe parryi var. *fernandina* (S.Watson) Jeps.	Moderate affinity	83	59.0%	69.4%	—	—	—	—	—	Ann. herb	Polygonaceae
Chorizanthe polygonoides var. *longispina* (Goodman) Munz	High affinity	251	45.0%	76.1%	4%	8%	—	1%	1%	Ann. herb	Polygonaceae
Chorizanthe uniaristata Torr. & A.Gray**	Weak affinity	197	34.5%	30.9%	1%	—	4%	3%	—	Ann. herb	Polygonaceae
Chylismia claviformis subsp. *cruciformis* (Kellogg) W.L. Wagner & Hoch	Weak affinity	183	30.1%	30.9%	—	—	—	4%	—	Ann. to per. herb	Onagraceae
Cleomella hillmanii A.Nelson	High affinity	181	47.0%	80.0%	—	—	—	1%	1%	Ann. herb	Cleomaceae
Cleomella hillmanii A.Nelson var. *hillmanii*	High affinity	104	48.1%	76.0%	—	—	—	1%	2%	Ann. herb	Cleomaceae
Convolvulus simulans L.M.Perry**	Endemic	321	52.3%	97.0%	2%	2%	2%	1%	7%	Ann. herb	Convolvulaceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Cryptantha wigginsii I.M.Johnst.	high Affinity	33	78.8%	84.6%	12%	3%	—	—	6%	Ann. herb	Boraginaceae
Cusickiella quadricostata (Rollins) Rollins	High affinity	67	7.5%	80.0%	—	—	—	—	—	Per. herb	Brassicaceae
Deinandra conjugens (D.D.Keck) B.G.Baldwin	Endemic	98	42.9%	97.6%	5%	—	—	—	15%	Ann. herb	Asteraceae
Deinandra fasciculata (DC.)Greene	Moderate affinity	1597	19.7%	59.4%	2%	<1%	2%	<1%	<1%	Ann. herb	Asteraceae
Deinandra halliana (D.D.Keck) B.G.Baldwin**	High affinity	70	22.9%	81.3%	—	—	3%	11%	14%	Ann. herb	Asteraceae
Delphinium gypsophilum Ewan	Moderate affinity	423	15.4%	55.4%	—	—	<1%	<1%	—	Per. herb	Ranunculaceae
Diplacus douglasii (Benth.) G.L.Nesom*	Weak affinity	405	10.4%	42.9%	0%	1%	14%	—	—	Ann. herb	Phrymaceae
Diplacus pulchellus (Drew ex Greene) G.L.Nesom	Clay tolerant	98	18.4%	27.8%	2%	—	—	—	—	Ann. herb	Phrymaceae
Diplacus pygmaeus (A.L.Grant) G.L.Nesom	High affinity	50	24.0%	75.0%	12%	—	—	2%	—	Ann. herb	Phrymaceae
Doellingeria glabrata (Greene) Semple, Brouillet & G.A.Allen	Moderate affinity	70	2.9%	50.0%	—	—	13%	—	—	Per. herb	Asteraceae
Dudleya blochmaniae (Eastw.) Moran subsp. *blochmaniae***	High affinity	146	10.4%	88.9%	3%	—	12%	—	—	Per. herb	Crassulaceae
Dudleya multicaulis (Rose) Moran	Moderate affinity	194	29.4%	54.4%	—	—	—	—	—	Per. herb	Crassulaceae
Dudleya nesiotica (Moran) Moran	High affinity	36	19.4%	85.7%	—	—	—	—	—	Per. herb	Crassulaceae
Dudleya parva Rose & Davidson	Strict endemic	30	6.7%	100.0%	—	—	—	—	—	Per. herb	Crassulaceae
Dudleya variegata (S.Watson) Moran	Endemic	155	27.7%	93.0%	2%	—	—	1%	1%	Per. herb	Crassulaceae
Enceliopsis nudicaulis var. *corrugata* Cronquist	Moderate affinity	205	14.6%	60.0%	—	—	—	2%	—	Per. herb to shrub	Asteraceae
Epilobium campestre (Jeps.) Hoch & W.L.Wagner	High affinity	655	14.2%	81.7%	27%	—	1%	1%	1%	Ann. herb	Onagraceae
Eremalche parryi subsp. *kernensis* (C.B.Wolf) D.M.Bates	Clay tolerant	259	29.3%	28.9%	1%	—	—	6%	—	Ann. herb	Malvaceae
Ericameria greenei (A.Gray) G.L.Nesom*	Clay tolerant	263	3.8%	10.0%	—	<1%	7%	—	—	Shrub	Asteraceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Ericameria nauseosa var. *washoensis* (L.C.Anderson) G.L.Nesom & G.I.Baird	Endemic	22	63.6%	92.9%	—	—	—	—	27%	Shrub	Asteraceae
Eriodictyon traskiae Eastw. subsp. *traskiae*	Strict endemic	20	35.0%	100.0%	—	—	—	—	—	Shrub	Namaceae
Eriogonum alexanderae (Reveal) Grady & Reveal	Strict endemic	36	58.3%	100.0%	—	—	—	—	—	Per. herb	Polygonaceae
Eriogonum argillosum J.T.Howell**	Strict endemic	35	22.9%	100.0%	—	—	—	—	3%	Ann. herb	Polygonaceae
Eriogonum clavatum Small**	Moderate affinity	190	44.2%	66.7%	—	—	4%	2%	1%	Ann. herb	Polygonaceae
Eriogonum collinum S.Stokes ex M.E.Jones	High affinity	101	45.5%	84.8%	—	—	—	1%	2%	Ann. herb	Polygonaceae
Eriogonum eastwoodianum J.T.Howell	—	53	13.2%	0.0%	—	—	6%	—	—	Ann. herb	Polygonaceae
Eriogonum gossypinum Curran	Moderate affinity	118	24.6%	55.2%	—	—	—	1%	—	Ann. herb	Polygonaceae
Eriogonum heermannii var. *occidentale* S.Stokes	Moderate affinity	44	18.2%	62.5%	—	—	11%	—	—	Shrub	Polygonaceae
Eriogonum kennedyi var. *pinicola* Reveal	—	14	14.3%	100.0%	7%	—	—	—	—	Per. herb	Polygonaceae
Eriogonum microtheca var. *lacus-ursi* Reveal & A.Saunders	Clay tolerant	4	100.0%	25.0%	—	—	—	—	—	Shrub	Polygonaceae
Eriogonum nudum var. *indictum* (Jeps.) Reveal**	High affinity	110	15.5%	76.5%	—	—	11%	—	—	Per. herb	Polygonaceae
Eriogonum ochrocephalum S.Watson var. *ochrocephalum*	—	13	23.1%	0.0%	—	—	—	—	—	Per. herb	Polygonaceae
Eriogonum ordii S.Watson	High affinity	210	47.1%	79.8%	—	—	4%	3%	<1%	Ann. herb	Polygonaceae
Eryngium jepsonii J.M.Coult. & Rose	Strict endemic	31	35.5%	100.0%	10%	—	3%	—	3%	Per. herb	Apiaceae
Eryngium pendletonense K.L. Marsden & M.G.Simpson	High affinity	46	45.7%	85.7%	46%	—	—	—	2%	Per. herb	Apiaceae
Eryngium racemosum Jeps.	Strict endemic	39	43.6%	100.0%	21%	—	—	21%	—	Ann. to per. herb	Apiaceae
Erythranthe exigua (A.Gray) G.L.Nesom & N.S.Fraga	Weak affinity	48	35.4%	41.2%	8%	—	—	—	—	Ann. herb	Phrymaceae
Eschscholzia hypecoides Benth.**	Weak affinity	300	13.3%	35.0%	—	—	2%	—	—	Ann. herb	Papaveraceae
Fritillaria agrestis Greene**	High affinity	166	35.5%	89.8%	1%	—	5%	—	1%	Per. herb (bulb)	Liliaceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Fritillaria biflora Lindl.	High affinity	526	24.1%	89.0%	<1%	2%	8%	—	<1%	Per. herb (bulb)	Liliaceae
Fritillaria liliacea Lindl.**	Strict endemic	151	9.3%	100.0%	3%	—	6%	—	—	Per. herb (bulb)	Liliaceae
Fritillaria pluriflora Torr. ex Benth.**	Endemic	123	39.8%	98.0%	2%	—	11%	—	2%	Per. herb (bulb)	Liliaceae
Fritillaria striata Eastw.	Strict endemic	55	45.5%	100.0%	—	—	—	—	—	Per. herb (bulb)	Liliaceae
Goodmania luteola (Parry) Reveal & Ertter	Weak affinity	146	34.2%	32.0%	6%	—	—	48%	—	Ann. herb	Polygonaceae
Gratiola heterosepala H. Mason & Bacig.	Moderate affinity	79	11.4%	66.7%	42%	—	—	—	—	Ann. herb	Plantaginaceae
Grindelia hirsutula Hook. & Arn.**	Moderate affinity	2452	10.7%	51.0%	0%	—	3%	1%	—	Per. herb	Asteraceae
Harpagonella palmeri A.Gray	Endemic	542	42.1%	92.5%	0%	6%	<1%	—	1%	Ann. herb	Boraginaceae
Hazardia orcuttii (A.Gray) Greene	High affinity	97	6.2%	83.3%	—	—	—	—	—	Shrub	Asteraceae
Hesperocyparis forbesii (Jeps.) Bartel	Moderate affinity	348	9.5%	66.7%	—	—	2%	—	—	Tree	Cupressaceae
Holocarpha macradenia (DC.) Greene	Endemic	124	12.1%	93.3%	—	—	—	—	—	Ann. herb	Asteraceae
Hooveria purpurea (Brandegee) D.W.Taylor & D.J.Keil var. *purpurea*	Endemic	71	45.1%	96.9%	1%	—	—	—	—	Per. herb	Agavaceae
Hordeum intercedens Nevski	High affinity	597	40.7%	87.2%	11%	—	—	14%	3%	Graminoid	Poaceae
Horkelia daucifolia var. *indicta* (Jeps.) Ertter & Reveal	—	7	0.0%	0.0%	—	—	—	—	—	Per. herb	Rosaceae
Horkelia howellii (Greene) Rydb.	—	60	5.0%	100.0%	2%	—	33%	—	—	Per. herb	Rosaceae
Horkelia parryi Greene	Moderate affinity	113	8.0%	55.6%	—	—	—	—	—	Per. herb	Rosaceae
Horkelia sericata S.Watson*	—	176	1.7%	100.0%	—	—	27%	—	—	Per. herb	Rosaceae
Horkelia truncata Rydb.	Moderate affinity	71	16.9%	66.7%	11%	8%	—	—	—	Per. herb	Rosaceae
Isocoma menziesii var. *diabolica* G.L.Nesom	High affinity	47	19.1%	88.9%	—	—	19%	—	—	Shrub	Asteraceae
Isocoma menziesii (Hook. & Arn.) G.L.Nesom var. *menziesii*	Clay tolerant	569	22.8%	22.3%	—	—	—	1%	—	Shrub	Asteraceae
Ivesia kingii S. Watson var. *kingii*	Clay tolerant	110	11.8%	15.4%	—	—	—	25%	—	Per. herb	Rosaceae
Ivesia pickeringii Torr. ex A.Gray*	—	60	3.3%	100.0%	—	—	37%	—	—	Per. herb	Rosaceae
Ivesia webberi A.Gray	—	47	4.3%	50.0%	—	—	—	—	—	Per. herb	Rosaceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Koeleria macrantha (Ledeb.) Schult.	Clay tolerant	2452	12.0%	23.8%	<1%	<1%	3%	<1%	—	Graminoid	Poaceae
Lagophylla diabolensis B.G.Baldwin	Strict endemic	36	22.2%	100.0%	—	—	6%	—	19%	Ann. herb	Asteraceae
Lagophylla dichotoma Benth.	—	34	11.8%	100.0%	—	—	12%	—	—	Ann. herb	Asteraceae
Layia chrysanthemoides (DC.) A.Gray	Endemic	435	12.0%	90.4%	4%	—	1%	3%	<1%	Ann. herb	Asteraceae
Layia heterotricha (DC.) Hook. & Arn.	High affinity	288	37.8%	73.4%	—	—	1%	2%	3%	Ann. herb	Asteraceae
Layia jonesii A.Gray*	Strict endemic	81	18.5%	100.0%	—	—	32%	—	—	Ann. herb	Asteraceae
Layia leucopappa D.D.Keck	Endemic	40	47.5%	94.7%	—	—	—	5%	—	Ann. herb	Asteraceae
Layia munzii D.D.Keck	High affinity	130	21.5%	78.6%	4%	—	—	25%	5%	Ann. herb	Asteraceae
Lepidium jaredii Brandegee	High affinity	72	25.0%	77.8%	1%	—	—	39%	—	Ann. herb	Brassicaceae
Lepidium jaredii Brandegee subsp. *jaredii*	High affinity	13	61.5%	87.5%	—	—	—	38%	31%	Ann. herb	Brassicaceae
Lepidium jaredii subsp. *album* Hoover	High affinity	19	78.9%	86.7%	—	—	—	—	37%	Ann. herb	Brassicaceae
Leptosyne calliopsidea (DC.) A.Gray	Weak affinity	449	24.1%	49.1%	1%	—	1%	5%	—	Ann. herb	Asteraceae
Lessingia hololeuca Greene*	High affinity	170	10.6%	83.3%	1%	—	16%	2%	—	Ann. herb	Asteraceae
Lessingia nana A.Gray	High affinity	98	11.2%	78.6%	1%	4%	—	—	3%	Ann. herb	Asteraceae
Logfia arizonica (A.Gray) Holub	Endemic	259	43.2%	90.9%	1%	—	—	—	—	Ann. herb	Asteraceae
Lomatium bicolor var. *leptocarpum* (Torr. & A.Gray) Schlessman	Moderate affinity	276	16.3%	66.7%	3%	—	—	<1%	<1%	Per. herb	Apiaceae
Lomatium hendersonii (J.M. Coult. & Rose) J.M.Coult. & Rose	High affinity	58	17.2%	70.0%	—	—	—	2%	—	Per. herb	Apiaceae
Lomatium ravenii var. *paiutense* K.M.Carlson & Mansfield	Weak affinity	45	33.3%	46.7%	—	—	—	—	—	Per. herb	Apiaceae
Lomatium ravenii Mathias & Constance var. *ravenii*	Strict endemic	9	77.8%	100.0%	—	—	—	—	—	Per. herb	Apiaceae
Lomatium roseanum Cronquist	Weak affinity	14	64.3%	44.4%	—	—	—	—	—	Per. herb	Apiaceae
Lomatium stebbinsii Schlessman & Constance	—	20	0.0%	0.0%	—	—	—	—	—	Per. herb	Apiaceae
Lupinus formosus Greene var. *formosus*	Clay tolerant	438	18.7%	29.3%	—	—	<1%	—	—	Per. herb	Fabaceae
Madia radiata Kellogg	High affinity	156	44.9%	84.3%	1%	—	3%	4%	3%	Ann. herb	Asteraceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Mentzelia pterosperma Eastw.	Moderate affinity	59	39.0%	69.6%	—	—	—	—	—	Ann. herb	Loasaceae
Microseris acuminata Greene	Moderate affinity	160	13.1%	61.9%	11%	—	—	3%	—	Ann. herb	Asteraceae
Microseris laciniata subsp. *detlingii* K.L.Chambers	Endemic	34	76.5%	96.2%	—	—	—	—	6%	Per. herb	Asteraceae
Monardella australis subsp. *occidentalis* Elvin, R.A. Burgess & A.C.Sanders	Moderate affinity	7	100.0%	57.1%	—	—	—	—	—	Per. herb	Lamiaceae
Monardella venosa (Torr.) A.C.Sanders & Elvin	Strict endemic	22	50.0%	100.0%	—	—	9%	—	36%	Ann. herb	Lamiaceae
Monolopia major DC.	Moderate affinity	260	13.5%	65.7%	<1%	—	4%	<1%	1%	Ann. herb	Asteraceae
Monolopia stricta Crum	Moderate affinity	249	29.3%	58.9%	—	—	—	6%	2%	Ann. herb	Asteraceae
Navarretia cotulifolia (Benth.) Hook. & Arn.	Strict endemic	169	12.4%	100.0%	6%	—	4%	7%	2%	Ann. herb	Polemoniaceae
Navarretia divaricata Greene	Clay tolerant	640	8%	25.0%	2%	—	1%	—	—	Ann. herb	Polemoniaceae
Navarretia eriocephala H. Mason	Strict endemic	65	10.8%	100.0%	6%	—	2%	3%	—	Ann. herb	Polemoniaceae
Navarretia filicaulis (Torr. ex A.Gray) Greene	High affinity	155	6%	88.9%	—	3%	12%	—	—	Ann. herb	Polemoniaceae
Navarretia gowenii L.A.Johnson	Strict endemic	7	71%	100.0%	—	—	14%	—	43%	Per. herb	Polemoniaceae
Navarretia heterandra H.Mason	Endemic	161	31.7%	92.2%	11%	—	2%	1%	1%	Ann. herb	Polemoniaceae
Navarretia jepsonii V.L.Bailey ex Jeps.*	High affinity	101	17.8%	88.9%	2%	—	47%	1%	—	Ann. herb	Polemoniaceae
Navarretia nigelliformis Greene subsp. *nigelliformis*	Endemic	58	44.8%	92.3%	14%	—	14%	2%	—	Ann. herb	Polemoniaceae
Navarretia nigelliformis subsp. *radians* (J.T. Howell) A.G.Day	Strict endemic	64	39.1%	100.0%	11%	—	6%	2%	6%	Ann. herb	Polemoniaceae
Navarretia ojaiensis Elvin, J.M.Porter & L.A.Johnson	Strict endemic	27	55.6%	100.0%	—	—	—	—	—	Ann. herb	Polemoniaceae
Navarretia panochensis D. Gowen & L.A.Johnson	Strict endemic	11	90.9%	100.0%	—	—	—	—	64%	Ann. herb	Polemoniaceae
Navarretia pubescens (Benth.) Hook. & Arn.**	High affinity	683	10%	80.6%	1%	—	4%	—	1%	Ann. herb	Polemoniaceae
Navarretia setiloba Coville	High affinity	83	54.2%	88.9%	4%	1%	1%	2%	1%	Ann. herb	Polemoniaceae
Navarretia viscidula Benth.	Weak affinity	246	8.9%	45.5%	2%	—	2%	—	—	Ann. herb	Polemoniaceae
Neoholmgrenia andina (Nutt.) W.L.Wagner & Hoch	Moderate affinity	168	15.5%	57.7%	4%	—	—	1%	—	Ann. herb	Onagraceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Oenothera caespitosa Gillies ex Hook. & Arn.	Clay tolerant	926	17%	26.6%	<1%	<1%	—	<1%	—	Per. herb	Onagraceae
Oreocarya tumulosa Payson	Weak affinity	183	8.2%	40.0%	—	—	—	—	—	Per. herb	Boraginaceae
Oxytropis oreophila A.Gray	Weak affinity	176	14%	40.0%	—	—	—	—	—	Per. herb	Fabaceae
Paronychia echinulata Chater	Moderate affinity	4	75.0%	66.7%	—	—	—	—	—	Ann. herb	Caryophyllaceae
Pedicularis rigginsiae D.J.Keil	—	7	0.0%	0.0%	—	—	—	—	—	Per. herb	Orobanchaceae
Penstemon heterodoxus var. *shastensis* (D.D.Keck) N.H.Holmgren	Clay tolerant	105	4.8%	20.0%	—	—	—	—	—	Per. herb	Plantaginaceae
Penstemon janishiae N.H.Holmgren	High affinity	104	28.8%	70.0%	—	—	—	—	—	Per. herb	Plantaginaceae
Pentachaeta lyonii A.Gray	Endemic	53	18.9%	90.0%	2%	—	—	—	—	Ann. herb	Asteraceae
Perideridia bolanderi subsp. *involucrata* T.I.Chuang & Constance	Strict endemic	31	32.3%	100.0%	—	—	6%	—	—	Per. herb	Apiaceae
Perideridia pringlei (J.M.Coult. & Rose) A.Nelson & J.F.Macbr.**	Moderate affinity	221	33.9%	61.3%	<1%	—	10%	—	<1%	Per. herb	Apiaceae
Phacelia ciliata Benth.	High affinity	598	25.3%	78.1%	1%	<1%	1%	4%	1%	Ann. herb	Hydrophyllaceae
Phacelia distans Benth.**	Clay tolerant	4106	23.9%	8.2%	<1%	<1%	1%	<1%	—	Ann. herb	Hydrophyllaceae
Phacelia gymnoclada Torr. ex S.Watson	High affinity	150	44.0%	72.7%	—	—	—	5%	—	Ann. herb	Hydrophyllaceae
Phacelia monoensis Halse	Strict endemic	45	40.0%	100.0%	—	—	—	—	9%	Ann. herb	Hydrophyllaceae
Phacelia neglecta M.E.Jones	Clay tolerant	154	21%	12.1%	—	—	—	1%	—	Ann. herb	Hydrophyllaceae
Phacelia parishii A.Gray	Weak affinity	72	34.7%	48.0%	1%	—	—	22%	10%	Ann. herb	Hydrophyllaceae
Phacelia pulchella var. *gooddingii* (Brand) J.T.Howell	Clay tolerant	123	37%	28.9%	—	—	—	2%	2%	Ann. herb	Hydrophyllaceae
Phacelia thermalis Greene	Moderate affinity	104	36%	62.2%	8%	—	—	—	2%	Ann. herb	Hydrophyllaceae
Pickeringia montana var. *tomentosa* (Abrams) I.M.Johnst.	High affinity	119	7.6%	77.8%	—	3%	—	—	—	Shrub	Fabaceae
Plagiobothrys acanthocarpus (Piper) I.M.Johnst.	High affinity	501	25.1%	89.7%	30%	<1%	<1%	5%	2%	Ann. herb	Boraginaceae
Plagiobothrys chorisianus var. *hickmanii* (Greene) I.M.Johnst.	Clay tolerant	101	6.9%	28.6%	21%	—	—	—	—	Ann. herb	Boraginaceae
Plagiobothrys infectivus I.M.Johnst.	Strict endemic	61	31.1%	100.0%	11%	—	5%	—	8%	Ann. herb	Boraginaceae
Plagiobothrys scriptus (Greene) I.M.Johnst.	Clay tolerant	58	19.0%	18.2%	14%	—	—	—	—	Ann. herb	Boraginaceae

CONTINUED

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Plagiobryoides vinosula (Cardot) J.R.Spence	Moderate affinity	62	25.8%	56.3%	—	—	—	—	—	Moss	Bryaceae
Plantago erecta E.Morris**	Weak affinity	2530	21.5%	47.5%	2%	1%	5%	<1%	<1%	Ann. herb	Plantaginaceae
Pogogyne floribunda Jokerst	High affinity	69	20.3%	85.7%	26%	—	—	—	6%	Ann. herb	Lamiaceae
Pseudobahia bahiifolia (Benth.) Rydb.	Clay tolerant	97	11.3%	9.1%	2%	—	1%	—	—	Ann. herb	Asteraceae
Pseudobahia peirsonii Munz	Endemic	94	53.2%	92.0%	—	—	—	—	1%	Ann. herb	Asteraceae
Pyrrocoma lucida (D.D. Keck) Kartesz & Gandhi	—	57	7.0%	50.0%	5%	—	—	2%	—	Per. herb	Asteraceae
Quercus dumosa Nutt.	Weak affinity	1151	7.7%	39.3%	—	<1%	1%	—	—	Shrub	Fagaceae
Ranunculus canus Benth.	High affinity	476	11.8%	80.4%	1%	—	—	0%	—	Per. herb	Ranunculaceae
Salsola damascena Botsch.	—	22	0.0%	0.0%	—	—	—	—	—	Shrub	Chenopodiaceae
Sanicula hoffmannii (Munz) R.H.Shan & Constance*	High affinity	122	7.4%	77.8%	—	—	12%	—	—	Per. herb	Apiaceae
Sanicula maritima Kellogg ex S.Watson**	Strict endemic	45	46.7%	100.0%	—	—	11%	—	—	Per. herb	Apiaceae
Scrophularia peregrina L.	Strict endemic	16	31.3%	100.0%	—	—	—	—	—	Ann. herb	Scrophulariaceae
Scutellaria holmgreniorum Cronquist	Moderate affinity	355	27.6%	54.1%	<1%	—	—	—	3%	Per. herb (rhiz.)	Lamiaceae
Sibaropsis hammittii S.Boyd & T.S.Ross	Strict endemic	33	63.6%	100.0%	—	30%	—	—	6%	Ann. herb	Brassicaceae
Sidalcea keckii Wiggins**	Endemic	78	17.9%	92.9%	1%	—	12%	—	1%	Ann. herb	Malvaceae
Spergularia platensis (Cambess.) Fenzl var. *platensis*	—	3	0.0%	0.0%	67%	—	—	—	—	Ann. herb	Caryophyllaceae
Sphenopholis interrupta subsp. *californica* (Vasey) Scribn.	Strict endemic	9	100.0%	100.0%	—	—	—	—	11%	Graminoid	Poaceae
Stenotus acaulis (Nutt.) Nutt.	Clay tolerant	559	11.4%	25.0%	—	—	—	<1%	—	Per. herb	Asteraceae
Stephanomeria pauciflora (Torr.) A.Nelson	Clay tolerant	1369	22.2%	8.2%	1%	—	—	1%	1%	Per. herb	Asteraceae
Streptanthus cordatus var. *piutensis* J.T.Howell	Strict endemic	32	40.6%	100.0%	—	<1%	—	—	—	Per. herb	Brassicaceae
Stylocline citroleum Morefield	—	46	4.3%	100.0%	—	—	—	—	—	Ann. herb	Asteraceae
Taraxia ovata (Nutt.) Small	Moderate affinity	399	10.8%	69.8%	1%	—	—	—	—	Per. herb	Onagraceae
Tetrapteron graciliflorum (Hook. & Arn.) W.L.Wagner & Hoch	Weak affinity	392	22.7%	47.2%	1%	—	5%	—	<1%	Ann. herb	Onagraceae
Thelypodium brachycarpum Torr.*	Weak affinity	141	8.5%	41.7%	—	—	10%	11%	—	Per. herb	Brassicaceae

Continued

Taxon	Clay affinity	Records examined	Soil texture addressed	On clay	Vernal pools	Gabbro	Serpentine	Alkali sink or soils	Vertic soils	Life form	Family
Tidestromia eliassoniana (Sánch. Pino & Flores Olv.) Sánch. Pino	—	5	40.0%	0.0%	—	—	—	—	40%	Ann. herb	Amaranthaceae
Trifolium piorkowskii Rand. Morgan & A.L.Barber	—	6	0.0%	0.0%	83%	—	—	—	—	Ann. herb	Fabaceae
Triteleia crocea (Alph. Wood) Greene*	Weak affinity	171	6.4%	36.4%	—	—	19%	—	—	Per. herb	Themidaceae
Triteleia laxa Benth.	Moderate affinity	1438	11.0%	63.3%	<1%	—	3%	—	—	Per. herb	Themidaceae
Triteleia piutensis E.Kentner & K.E.Steiner	—	1	0.0%	0.0%	—	—	—	—	—	Per. herb	Themidaceae
Tropidocarpum californicum (Al-Shehbaz) Al-Shehbaz	Strict endemic	13	38.5%	100.0%	8%	—	—	46%	—	Per. herb	Brassicaceae
Veratrum insolitum Jeps.	High affinity	108	9.3%	80.0%	—	—	9%	—	—	Per. herb	Melanthiaceae
Wyethia reticulata Greene	Strict endemic	54	11.1%	100.0%	—	13%	6%	—	—	Per. herb	Asteraceae