

FLOWERS IN THE GARDEN: WHAT NEXT FOR CALIFORNIA FLORISTICS?

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ABSTRACT

As much as 79.5% of the California Floristic Province and 73% of the State of California remains poorly inventoried, judging from a review of local and regional floras. The Cascade Range, the Sierra Nevada, the Great Valley, and the Modoc Plateau have been especially neglected. The southern Sierra Nevada, portions of the Diablo Range, the Warner Mountains, the Little San Bernardino Mountains, and most of the major mountain ranges of northwestern California merit special attention. Most local and regional floras have been descriptive. Detailed and informative analyses of floristic patterns and processes depend on fine-scale samples of phytogeographic and floristic regions. Future studies should include comparative analyses, using appropriate exploratory statistical methods that examine overall relationships. Such approaches may reveal patterns deserving further inquiry. Studies of biogeographic processes (that have shaped California's flora) and local or regional patterns of diversity will benefit from new approaches that include molecular analyses and application of cladistic methods.

The California flora is well known for its species diversity and endemism (Raven and Axelrod 1978; Stebbins and Major 1965). Much of this diversity is coincidental with political boundaries superimposed on a natural phytogeographic region, the California Floristic Province (Howell 1957). The province is characterized by a Mediterranean climate, considerable topographic and geologic diversity, and a geochronological history that involved elements of the Arcto-Tertiary and Madro-Tertiary Geofloras (Raven and Axelrod 1978).

The first statewide vascular flora of California (Brewer et al. 1876; Watson 1880) resulted from William Brewer's participation in the Geological Survey of California (Farquhar 1949). The 2-volume "Botany" of the Survey was supplanted by Jepson's *A Flora of California* (Jepson 1909–1943; Dempster 1979), which included identification keys, morphological descriptions, ecological and geographic distributions, citation of synonyms and specimens, and discussions of taxonomic affinities. Jepson (1925) and subsequent regional or statewide treatments (Abrams 1940–1951; Ferris 1960; Hickman 1993; Mason 1957; Munz 1974; Munz and Keck 1968) were primarily designed for brevity and identification purposes. Consequently, the difference in information content between Jepson's flora

and subsequent statewide treatments (perhaps best called manuals, fide Lawrence 1951) is a function of scale. Because detailed analyses of floristic patterns (and their relationship to abiotic and biotic processes) depend on specimen-based data sets (Pielou 1979; Myers and Giller 1988), floras are more informative than manuals. Unfortunately, economics of field and herbarium studies often restrict the size of floristic studies. Floras based on political boundaries present an analogous problem, because they rarely coincide with natural physiographic units.

Since the mid-19th century, California's flora has received much attention from systematic, ecological, and geographic perspectives. The purpose of this paper is to review progress in the inventory of California's flora, relative to geographic distribution. I restricted my review to published scientific studies in which (1) authors claimed systematic sampling techniques throughout their study areas and (2) voucher specimens and herbarium repositories were clearly cited. The survey was confined to the years 1960–1993, which represent 34 years of published work subsequent to Munz and Keck (1959). Unpublished theses, reports by local government agencies, reports by environmental consultants, and other literature not readily in the public domain were excluded. Some earlier literature citations were added retrospectively for purposes of discussion. Descriptive studies of vegetation were excluded, because published data are often restricted to species occurring above a specified frequency. An informative and more extensive list of references for the California flora (including many unpublished reports and theses) can be found in Smith (1992).

I arranged floras by classifying them in the hierarchical system used in *The Jepson Manual* (Hickman 1993), which recognizes 3 floristic provinces and 10 major subdivisions. Because these categories more closely approximate natural physiographic units (Fenneman 1931) than political units (e.g., counties), they are more informative for purposes of floristic comparison. I was unable to accurately estimate areas of subdivisions directly, but they sufficiently coincide with the 10 floristic regions of Raven and Axelrod (1978) so as to permit a general estimate of area in km². I extracted area estimates from floras in Table 1 and calculated their combined proportion of floristic regions, after correcting for overlap. My estimates for the Sierra Nevada, the Great Valley, Central Western California, and Southwestern California should be used with caution, because I was unable to clearly define subdivision boundaries within several politically defined floras (e.g., Hoover 1970; Twisselmann 1967). I also surveyed literature from 1978–1993, using Raven and Axelrod (1978) as a benchmark, for synthetic analyses of patterns at local and regional levels.

Table 1 includes 73 references pertaining to 63 local or regional

TABLE 1. CLASSIFICATION OF 73 REFERENCES PERTAINING TO 63 LOCAL OR REGIONAL FLORAS OF CALIFORNIA. Numbers in () or [] are km². Numbers in [] represent sums of estimates from references/total area for each province or subdivision. Numbers in () represent estimates of individual references. ^a Combined area of 9085 km² for North Coast and North Coast Ranges was obtained from Smith and Wheeler 1990–1991. ^b 2000 km² was estimated for the 3 subdivisions of Sierra Nevada from parts of Twisselmann 1967 (21,165). ^c 6000 km² was estimated from parts of Hoover 1970 (5800), Twisselmann 1967 (21,165), and Smith 1976 (5600). ^d 27,570 km² was estimated from parts of Hoover 1970 (5800), Howell 1970 (1370), Thomas 1961 (3590), Howitt and Howell 1964, 1973 (8610), Smith 1976 (5600), and Twisselmann 1956 (7050), 1967 (21,165). ^e 13,050 km² was estimated from parts of Beauchamp 1986 (10,935), Boughey 1968 (1800), Fletcher 1983 (57), Raven et al. 1986 (985), Smith 1976 (5600) and Twisselmann 1967 (21,165). ^f 6800 km² was estimated from parts of Beauchamp 1986 (10,935) and Twisselmann 1967 (21,265).

California Floristic Province [66,850/324,000]

Northwestern California [9630/55,000]

North Coast: Hardham and True 1972 (4); Hektner and Foin 1977 (7); Smith and Wheeler 1990–1991^a.

Klamath Ranges: Ferlatte 1974 (455).

North Coast Ranges: Heckard and Hickman 1985 (55); King 1985 (2.5);

Murphy and Heady 1983 (21); Smith and Wheeler 1990–1991^a.

Cascade Ranges [780/34,370]

Cascade Range Foothills: No references.

High Cascade Range: Cooke 1940, 1941, 1949 (260);

Gillett et al. 1961 (520).

Sierra Nevada [3131/43,380]

Sierra Nevada Foothills: Jockerst 1983 (7); Twisselmann 1967^b.

High Sierra Nevada: Smiley 1921 (area not estimated); Hunter and

Johnson 1983 (60); Knight et al. 1970 (13); Lavin 1983 (500);

Palmer et al. 1983 (80); Savage 1973 (50); Smith 1973, 1983 (480);

Twisselmann 1967^b; Howald 1981 (1).

Tehachapi: Twisselmann 1967^b.

Great Valley [6012.5/59,390]

Sacramento Valley: Broyles 1987 (5); Jockerst 1983 (7);

Schlising and Sanders 1983 (0.5).

San Joaquin Valley: Twisselmann 1956, 1967^c; Hoover 1970

and Keil et al. 1985^c; Smith 1976^c.

Central Western California [31,750/47,920]

Central Coast: Barbour 1970, 1972 (6.5); Coulter 1970, 1978 (0.5);

Fletcher 1983 (57); Genetti and Engles 1984 (15); Howell et al. 1958 (115);

Howell 1970^d; McClintock et al. 1990 (12); Peñalosa 1963 (15);

Thomas 1961^d.

San Francisco Bay Area: Bowerman 1944 (142.5); Howell 1970^d;

Ripley 1980 (8); Sharsmith 1945 (3885); Thomas 1961^d;

Howitt and Howell 1964^d, 1973; Wetzel 1971 (10).

South Coast Ranges: Bickford and Rich 1984 (15.5);

Ferren et al. 1984 (4); Fletcher 1983 (57); Genetti and Engles 1984 (15);

Griffin 1974 (7.5); Hoover 1970^d and Keil et al. 1985;

Howitt and Howell 1964^d, 1973; Smith 1976^d; Twisselmann 1956, 1967^d.

Southwestern California [15,550/47,500]

South Coast: Boughey 1968^e; Ferren 1985 (1); Fletcher 1983^e;

Raven et al. 1986^e; Smith 1976^e; Beauchamp 1986^e.

Channel Islands: Junak et al. 1995 (249), Philbrick 1972 (2.6)

and Junak et al. 1993; Raven 1963 (145); Thorne 1967, 1969 (194);

Wallace 1985 (904).

TABLE 1. CONTINUED

Transverse Ranges: Magney 1986 (4); Smith 1976 ^e ; Twisselmann 1967 ^e .
Peninsular Ranges: Boughey 1968 ^e ; Beauchamp 1986 ^e ;
Lathrop and Thorne 1978 (1150), 1983 (0.5), 1985 (181).
Great Basin Floristic Province [3037/22,600]
Modoc Plateau: Applegate 1938 (225).
East of Sierra Nevada: Forbes et al. 1988 (31); Howald and Orr 1981 (1);
Lavin 1983 (500); Lloyd and Mitchell 1973 (2280)
and Morefield et al. 1988.
Desert Floristic Province [42,191/87,180]
Mojave Desert: DeDecker 1984 (30,000; Castagnoli et al. 1983;
Hart et al. 1979; Pavlik 1985 (50); Peterson 1986 (1066);
Thorne et al. 1981 (3291); Twisselmann 1967 ^f .
Sonoran Desert: Beauchamp 1986 ^f ; McLaughlin et al. 1987 (2050).

floras. California has an area of 411,000 km² (Raven and Axelrod 1978). After correction for overlap, the area covered by floras in Table 1 was estimated to be 112,080 km², representing 27% of the state's area. The area of the California Floristic Province, which includes small portions of Oregon and Baja California, is 324,000 km² (Raven and Axelrod 1978). The area of this province covered by floras in Table 1, after correction for overlap and excluding those covering the Great Basin and Desert Provinces, was estimated to be 66,850 km² (20.6% of the Province).

Northwestern California is represented by 7 floras, covering 17.5% of the subdivision's area. Studies of the Trinity Alps (Ferlatte 1974) and Snow Mountain (Heckard and Hickman 1984, 1985) are notable for their analyses of floristic affinities. Several important physiographic units, including the Siskiyou and Yolla Bolly Ranges, have not been systematically surveyed, although 6 unpublished theses were cited by Smith and Sawyer (1988).

The Cascade Ranges are represented by only 2 floras, covering 2.3% of the subdivision's area (Cooke 1940–1977; Gillett et al. 1961). The recent discovery of *Neviusia* (Shevock et al. 1992) clearly suggests that this region deserves special attention.

Surprisingly, the Sierra Nevada does not appear adequately represented. Only 10 floras, covering 9% of the subdivision's area, have surveyed this most prominent feature of California's landscape. Four of them treated relatively small but natural physiographic units (Jokerst 1983; Palmer et al. 1983; Savage 1973; Smith 1973, 1983) in the northern Sierra Nevada. Twisselmann (1967) covered the southern Sierra Nevada and Tehachapi Mountains of Kern County. Smiley's (1921) study, whose area was not determined, represents a notable, early attempt to analyze origins and relationships of the higher elevation flora. Shevock (1988) presents a strong case for further inventories.

The flora of the Great Valley is poorly documented, with 6 floras covering 10% of the subdivision's area. Most of the inventoried area is represented by the southern San Joaquin Valley (Hoover 1970; Twisselmann 1956, 1967; supplemented by Keil et al. 1985). Unfortunately, because of agriculture and urbanization, a synthesis of the Great Valley flora will have to be based primarily on historic herbarium records and studies of small, undeveloped areas.

Central Western California, perhaps the best studied region in California, is treated by 26 references that cover 66% of the subdivision's area. The Diablo Range between Pacheco Pass and the Temblor Range (between Sharsmith 1945 and Twisselmann 1956) is a major physiographic unit remaining to be inventoried. The flora of the Santa Lucia Range needs synthesis, although parts are covered in at least 3 references (Hoover 1970; Howitt and Howell 1964, 1973).

Fifteen floras, based on 17 references, cover 33% of Southwestern California. Although most of the western Transverse Ranges are treated by relatively recent floras (Raven et al. 1986; Smith 1976; Magney 1986; Twisselmann 1967), floras of the eastern Transverse Ranges (San Gabriel and San Bernardino Mountains) have not been reviewed and updated since Parish (1917–1918). The San Jacinto Mountains, in the Peninsular Ranges, were last treated by Hall (1901). The contiguous Santa Rosa Mountains apparently remain to be systematically surveyed. Wallace (1985) provided a thorough checklist for all California islands based on selected specimens. Smith (1976) included the four northern Channel Islands. Only San Clemente, Santa Catalina, Santa Barbara, and Santa Cruz islands have published floras based on extensive field studies. Because of urbanization, a thorough floristic inventory of the lower Los Angeles, San Gabriel, and Santa Ana River drainages will depend almost exclusively on historic herbarium collections.

Six floras cover 13.5% of the Great Basin Province, but the White Mountains (Lloyd and Mitchell 1973; Morefield et al. 1988) contribute to most of the estimate. The best documented flora for the Modoc Plateau region appears to be Applegate (1938), supplemented partly by Smith et al. (1993). Although the floristic boundary between the Modoc Plateau and the Cascade Range is unclear (Hickman 1993), the Warner Mountains clearly represent a distinct physiographic unit, floristically related to Great Basin ranges, and apparently unstudied (Raven and Axelrod 1978).

The Desert Province of Hickman (1993) is composed of only 2 subdivisions, but includes 3 distinct floristic regions, the Inyo, Mojave, and Colorado (Stebbins and Major 1965; Raven and Axelrod 1978). Hickman's Mojave subdivision (which approximates the Inyo and Mojave regions) is treated by 5 floras that cover as much as 38,000 km² (66% of 57,730 km²). However, much of the region

covered by DeDecker (1984) has been incompletely sampled; exclusion of her treatment, but including Peterson (1986), reduces the estimate to 9,100 km² (16%). No flora has been published for the Little San Bernardino Mountains, which are contiguous to 3 California floristic provinces (Raven and Axelrod 1978). The Sonoran Desert subdivision (Colorado region) is treated by only 2 floras (4,250 km² or 15% of area), and no flora exists for most mountain ranges and intervening basins of eastern Riverside and Imperial Counties and southeastern San Bernardino County.

Most floras in Table 1 are descriptive but some discuss floristic affinities in general terms or address particular species assemblages. Notably, Peterson (1986) used Jaccard's Coefficient (Sneath and Sokal 1973) to determine patterns of overall floristic similarity among 12 desert mountain ranges, based on several unpublished reports and theses. This coefficient is limited in its application to floristic data, but represents a useful exploratory tool for further analysis. McLaughlin (1986) investigated 50 local floras using factor analysis, which revealed objective circumscriptions of 7 floristic "elements" in the southwest. Raven (1967) analyzed the relationship between area and species number for Channel Island floras, based on migration and extinction equilibria (MacArthur and Wilson 1967). This approach, also used by Harper et al. (1978) to analyze relationships among 15 insular, montane floras of the Great Basin, represents a model for discussion of dispersal patterns and other factors that may influence floristic composition. These kinds of statistical methods provide effective and repeatable methods for analyzing the affinities of floristic regions at several levels of geographic scale.

Most synthetic analyses since Raven and Axelrod (1978) have focused on regional endemism (Axelrod 1982; Philbrick 1980; Smith and Sawyer 1988), with special attention to serpentine substrates (Kruckeberg 1984) and vernal pools (Jain 1976). Richerson and Lum (1980) examined relationships among species richness, climate, and topography. A few studies have tabulated distribution of life forms (Peterson 1986; McLaughlin 1986), but comparative studies are few, despite their importance to understanding dispersal and habitat requirements (Stebbins 1982). Some studies discussed hypotheses concerning the migration and origin of species comprising local and regional floras (Heckard and Hickman 1984; Stebbins 1982). Molecular analyses offer considerable promise in analyzing such problems, as exemplified by cpDNA restriction site variation among disjunct races of *Tolmiea* and *Tellima* in glacial refugia of the Pacific Northwest (Soltis et al. 1989, 1991). Such analyses, complemented by area cladograms (Mickey 1981), may contribute to understanding some of California's floristic complexity.

Like the living collections found in botanic gardens, manuals for plant identification only provide limited views of the natural vari-

ation, ecological and geographic distribution, and evolutionary relationships among native and naturalized plant taxa. Significant progress in the study of the California flora will depend on inventories of current herbarium collections, systematic sampling of poorly known geographic areas, refined methods of analyses, and publication of results in accessible media. Detailed and informative analyses of floristic patterns and processes depend on fine-scale samples of phytogeographic and floristic regions. Such analyses will continue to rely on local and regional floras using specimen-based data sets. Judging from citations in Smith (1992), much can be accomplished by extracting data from unpublished documents. However, future floristic studies and analyses, including citation of voucher specimens, can and should be made more accessible through printed or electronic media.

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