

BIOREGIONS: AN ECOLOGICAL AND EVOLUTIONARY PERSPECTIVE AND A PROPOSAL FOR CALIFORNIA

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Bioregions are natural assemblages of plants and animals with discernible but dynamic boundaries existing simultaneously along both spatial and temporal trajectories. I argue that the designation of bioregions should be based on the study of biogeography and must adhere to the tenets of this discipline; they are not spatial designations of political convenience. Bioregions are defined by physiographic and climatic limits that define the natural communities of organisms in space and time through interactions with the physiological and behavioral capabilities of these organisms. Plants are less vagile than animals and therefore lend themselves better to describing such natural communities. Despite the fluctuation of biotic communities in both time and space, and the anthropogenic bias inherent in defining their composition, such natural assemblages do exist on the landscape and they are of scientific interest and have useful management applications. I propose sixteen bioregions for the state of California and include definitions of geographic boundaries, dominant plant communities, and lists of vertebrate species typical of these bioregions.

INTRODUCTION

My purpose in describing a set of biotic provinces for California is two-fold: (1) to establish such sub-divisions with a firm biological basis, grounded in the biogeographic literature; and (2) to provide a biogeographic framework for the conservation of California's faunal resources and natural biodiversity, while facilitating wise use of its natural resources. My particular emphasis is on vertebrate wildlife resources, and these proposed bioregions were initially-developed to provide the basis for a bioregional revision of California's statewide Wildlife Habitat Relationships System (WHR) (Airola 1988) in order to improve the system's accuracy and utility.

Barry (1991) developed a detailed system of 24 ecological regions for California consistent with, as are those proposed here, the more coarse scale biotic provinces of Bailey (1976, 1978) and Udvardy (1975). Both Udvardy and Bailey integrated broad scale continental climatic and physiographic attributes along with extensive vegetational zones, such as temperate forest, steppe, and desert, to identify their provinces. Barry's (1991) system of ecological regions is considerably more extensive and refined, including marine and island ecological regions as well as a system of subregions. Barry's (1991) efforts are commendable in their completeness and detail and set a new standard for describing the range of ecological variability present within the Pacific

Southwest. His system is, however, considerably more elaborate than required by most wildlife managers, and at a finer scale than generally manifests in patterns of vertebrate fauna diversity. The more simplified system described below is most closely aligned with Barry (1991) at the level of his ecological regions, but with fewer regions and no subregions. See his descriptions of comparable ecological regions for more complete details on the physiography, climate, flora, and fauna of these biotic provinces. Mason (1970) provided a subdivision of California based primarily on physiography, Hickman (1993) described the floristic provinces, and Moyle (1976), Moyle and Williams (1990), and Moyle and Ellison (1991) described aquatic ecosystems of the state based on the distributions of native fishes and their habitats. Keeler-Wolf (1990) detailed numerous unique botanic assemblages found within California, most of which are too limited in distribution to be included in a coarse-scale system of the states bioregions.

Conceptual Background

Our awareness that nature organizes itself into biotic assemblages according to specific ecological principles in specific regions of the planet is long-standing. Living organisms are shaped by and are in synchronization with their environment. They breed, grow, and function in relation to the natural cycles and seasons where they dwell. Furthermore, living organisms are integral components of that place, functioning in concert with other organisms to shape their environment. For example, both Clark's Nutcracker (*Nucifraga columbiana*) and the pinyon jay (*Gymnorhinus cyanocephalus*) are important distributors of viable seed for pinyon pine (*Pinus edulis*) in the southwest and act as a powerful selective force in the establishment of new stands (VanderWall and Balda 1977, Ligon 1978). These stands in turn provide bird habitat for nesting and foraging. Another example of such biotic interdependence can be found in the important role that small mammals play in the distribution of mycorrhizal fungi which are essential for nutrient uptake of trees in the families Pinaceae (most conifers), Fagaceae (oaks), and Betulaceae (birch and alder) (Maser et al. 1978, 1986, Maser and Maser 1988). This critical symbiotic relationship between fungus and tree is essential for tree growth and subsequent stand formation. Such stands provide the dead and down woody material for cover and nesting, and the nuts and cones for forage, that in turn support the small mammal community.

Dry and wet seasons, daily light and climatic cycles, and the complex interrelationships of living organisms all contribute to the uniqueness of a given place and determine what species of plants and animals exist there. Yet few resource managers to date have sought this knowledge of place, beyond the narrow focus of local habitats, and applied it in the management of natural resources (e.g., Leopold 1949). Local phenomena can translate into causal mechanisms, often interconnecting and reciprocal, with related phenomena at levels of space and time right up through broad landscapes and beyond. Such information is essential to manage for the long-term viability of rare or threatened species and to wisely manage for the long-term sustainability of other resources that are commercially harvested. When and how

should elements of a forest be harvested and how much of it should remain? What are the impacts of management activities on other species, the stability of the natural community, and local and regional biodiversity? These questions are place-specific and require knowledge of the natural assemblage of plants and animals of a particular region and how they interact. They are, in a word, bioregional questions (Berg and Mills 1981), and a bioregional focus is required to manage natural resources knowledgeably and wisely while preserving the integrity of natural systems.

At least since the 19th century and the work of Schouw (1823), Swainson (1835), Sclater (1858), and Wallace (1869, 1876, 1880), investigators have studied plant and animal distributions to discover geographic patterns. As a result, the science of biogeography has a long and distinguished tradition and an extensive and detailed literature. Interest in this research domain has remained high to the present, and biogeographic literature is reviewed and updated in light of new knowledge and concepts with great regularity (e.g., Dansereau 1957, Darlington 1957, Udvardy 1969, MacArthur 1972, Pielou 1979, Brown and Gibson 1983). Any effort to describe bioregions or other biogeographic constructs would be remiss if it were not grounded in this extensive literature.

The Domains of Biogeography and the Importance of Hierarchy and Scale

Biogeography is the study of form-making (speciation, and the evolution of higher taxa) along the simultaneous continua of space and time (Fig. 1). Croizat's (1964) powerful metaphor "space, time, form: the biological synthesis" captures the essence of biogeography (and evolutionary biology) because it integrates the three primary trajectories of life on Earth into a single, unified, dynamic process of perpetual transformation. Viewed in this way, organic life is a constantly changing process expressed simultaneously across geographic space and on the time line of history. Implicit within Croizat's metaphor are the closely related concepts of hierarchy and scale (but see Brooks 1988). Both time and space, by virtue of how human consciousness and language employ them, are innately hierarchical; smaller increments combine to form larger increments. These hierarchical constructs cannot help but involve scale in conceptual and practical applications. The scale denotes the increments from small to large or from one order of magnitude to the next in any hierarchical construct. Hierarchy theory has been increasingly invoked to describe biotic processes (Allen and Starr 1982, Salthe 1985, O'Neill et al. 1986, Brooks and Wiley 1988). From milliseconds to epochs and from meters to hundreds of kilometers, as the scales of space and time are expanded, the variety of evolving life forms changes constantly. New forms occur, interact, and replace older forms along spatial and temporal trajectories.

The fine time scale pertains to small intervals of time (i.e., decades) and is often referred to as the ecological time scale. Here, biogeography addresses the spatial relationships of extant plant and animal populations with each other and with contemporary attributes of the physical environment (Fig. 2). Much of the subdiscipline of community ecology focuses on questions based in ecological time. At this end of

the scale, form-making is minimal and difficult or impossible to detect. The fine time scale is the domain of population ecology, population genetics, and geographical ecology (see MacArthur 1972), where species distributions appear relatively static in time and their populations (and metapopulations) fluctuate spatially in response to changes in the environment (Andrewartha and Birch 1954), changes in relative numbers of individuals within populations (e.g., McCullough 1979), or both (Horn 1968). At the fine end of the temporal scale, the spatial aspects of populations and species are defined by the concept of ecological niche (Grinnell 1917; see also James et al. 1984). However, even at this end of the continuum an awareness of scale is vital to understanding processes (Wiens et al. 1986, Wiens 1989).

As one approaches the other extreme of the time continuum, which involves large increments of time and is referred to as the evolutionary or geologic time scale, one enters the realm of historical biogeography. Here, the focus shifts to the origins of contemporary distribution patterns based on evidence from pattern congruency among unrelated taxa, geologic history, paleoecological studies, and the fossil record. Form-making is manifested clearly and relationships of forms within presumably related lineages must be established (e.g., Hennig 1979, Wiley 1981; see also the evolutionary species concept of Frost and Hillis 1990) before one can examine spatial relationships with confidence. Once phylogenetic relationships are established, historical biogeography involves the reconstruction of past attributes of the physical environment in order to derive hypotheses to explain similarities in distributions among different contemporary lineages. The spatial scale of historical biogeography generally involves large regions or continents, and the temporal scale is on the order of ages and epochs (e.g., Wright and Frey 1965, Rosen 1978, Gray and Boucot 1978).

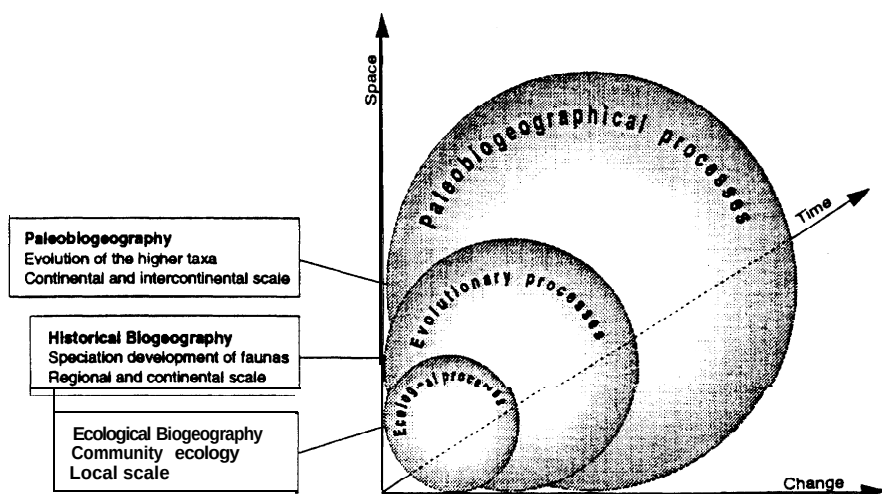


Figure 1. Biogeographical processes may be studied by reference to three main bodies of research which are closely interrelated along the scales of space, time, and change; based on Blonde (1987).

Investigators with a focus at opposing ends of this space-time continuum might have difficulty communicating with one another without a common understanding of how these apparently divergent biological processes are related hierarchically. In fact, the lack of such an integrated overview might explain why ecologists and historical biogeographers often seem to be talking past one another (Blonde1 1987, Brooks 1988). This same integrated overview is invaluable when considering the formation, establishment, and turnover (i.e., the dynamics) of the spatially explicit biotic assemblages that constitute the contemporary natural communities of the planet.

Biomes, Ecosystems, Provinces, Communities, Assemblages, and Associations: Real Biological Entities or Constructs of Convenience?

The biological layer of the planet has been subdivided innumerable, ways by phytogeographers and zoogeographers (see introduction, and Holdridge 1947, 1967, Dice 1952, Shelford 1963, Kuchler 1964, Udvardy 1975, Bailey 1976). Most of these subdivisions are based on the geography of vegetation cover which is somewhat more fixed in space than are animal species. At least that is how it appears in ecological time. The reality is that plants, over generations, shift spatially (e.g., Axelrod 1977). Given that fact, how real can a spatially explicit assemblage of plant species actually be? The plant species composition can change with climatic and geologic changes and the species themselves can change (i.e., evolve) into new organisms. Even at the fine end of the time scale, the question of whether a plant community is a group of interdependent organisms, or is actually comprised of many forms whose individual ranges are

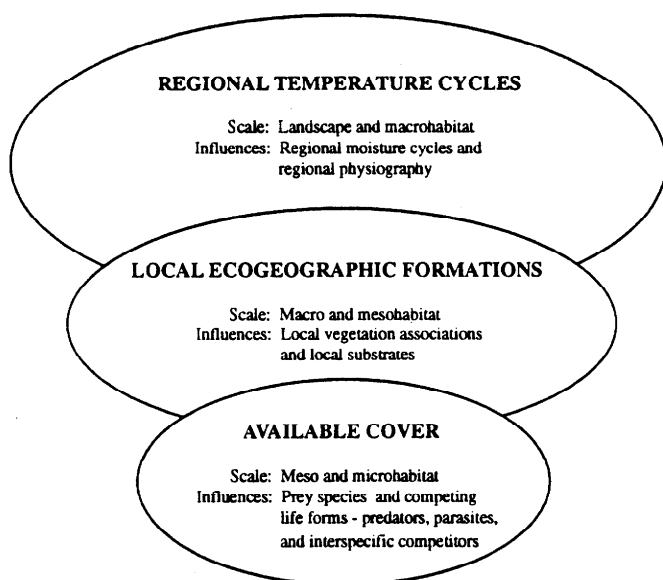


Figure 2. tierarchical relationships of phenomena determining the distributions of species in three dimensional space (after Welsh 1976).

somewhat similar because of similar physiological limits is an old debate in ecology (Gleason's individualistic concept of plant associations versus Clement's concept of vegetation communities; see Brown and Gibson [1983] for discussion and citations).

Certain plant types do group consistently together into recognizable assemblages in similar areas of the world (e.g., chaparral communities of California, Chile, and the Mediterranean). In the final analysis these natural assemblages have spatial integrity and temporal duration (but with fuzzy and fluctuating "boundaries") useful for describing the biotic organization of the planet. It is important however, that any such constructs be clearly defined in terms of both temporal and spatial scale. On a very fine scale the boundaries of individual species are not fixed and fluctuate in space and time (e.g., Schmidt 1950, Keve and Udvardy 1951, Lindroth 1956, Scudday 1977). However, toward the opposite end of these scales, intermediate to long-term (e.g., geologic time), and in larger (e.g., continental) space, certain consistent combinations of plants and animals (= biotic communities) fluctuate together spatially in response to geotectonic activity and climatic shifts within the biosphere (e.g., Raven and Axelrod 1974, Axelrod 1975, 1976, 1979, Holman 1976, VanDevender and Mead 1978, Savage 1960, 1982).

If we define our objectives to be a reasonably stable construct of plants over an intermediate period of time (say on the order of hundreds of years) we can be fairly certain (the greenhouse effect notwithstanding) that our biotic constructs will serve the purpose of providing stable areas for resource management purposes. Once we have agreed that these are somewhat anthropogenic constructs of convenience because they are both dynamic in space and time, and somewhat dependent upon the choice of species used to define biotic boundaries, then we can go forward with our goal of defining such constructs based on utility. Despite their fuzzy, ever-changing boundaries, and our anthropocentric biases, unique, real, and relatively stable biotic assemblages do exist on the landscape and they are of scientific interest and have useful management applications.

The Biogeography of California

California and the proximate political entities of Oregon, Nevada, Arizona and northern Mexico, have an extensive and diverse geography that make this region the most biologically complex on the North American continent. For example, the highest and lowest elevations in the lower 48 states are both in California, within 150 miles (240 km) of one another (Death Valley at -282 ft [-92.5 m], and Mt. Whitney at 14,495 ft [4,756 m]). Such great variation in geography contributes to a diversity of biotas matched by few temperate regions on the planet. These biotic assemblages range from lowland desert, coastal scrub, interior grassland and chaparral, through coastal and interior woodland and forest, to montane forest, and sub-alpine and alpine tundra types. This rich biodiversity has presented a formidable challenge to workers interested in the distributions of plants and animals. Research in this region has resulted in many important contributions to the science of biogeography (e.g., Merriam 1890, 1894; Grinnell 1914, 1917; Gleason 1917, 1926; Miller 1948, 1958;

Whittaker 1960; Savage 1960; Raven and Axelrod 1974; Brown 1978; Axelrod 1975, 1976, 1979). The wealth of research contains detailed analyses of the biotic assemblages of this Region and their development through time. As a consequence, these works provide a strong foundation for defining bioregional provinces based on pertinent research in community ecology, evolutionary biology and paleobotany.

METHODS

Bailey (1976,1978) and Udvardy (1975) proposed coarse biogeographic divisions for North America based on generalized climate, physiography, and plant assemblage distributions. Their province-level systems provided a good basis for distinguishing the general outlines of many of the bioregions that cover California and adjacent political entities (Figs. 3 and 4). However, given my geographically limited and more refined objectives, considerable modifications and additions to the provinces of Udvardy (1975) and Bailey (1976, 1978) were required. My approach allowed me to take into account the complex physiography and unique biotic attributes of certain regions of the state (e.g., the San Francisco Bay and Sacramento/San Joaquin River Delta region) that Bailey and Udvardy were not able to address given their coarse scale.

To establish more precise boundaries I followed the approach of Welsh (1988) which integrated climatic data, physiography, and the distributions of vegetational associations (Munz and Keck 1949) to define a matrix of ecogeographic formations for a region of Baja California, Mexico (Fig. 5). For the present effort, I focused at a scale intermediate to the high resolution of Welsh (1988) and the coarse resolution of Udvardy (1975) and Bailey (1976, 1978). Instead of using Welsh's (1988) concept of ecogeographic formations, which would constitute fine scale subunits of the entities here defined, I employed the term ecogeographic region (bioregion for short) for the biotic subdivisions of California described below.

Where possible, I first used physiographic formations such as natural drainages (ridgelines) or coastlines which provide a more definitive boundary. Welsh (1988:5) noted that..."biogeographic assemblages generally represent gradients with regard to space, time, and biotic form and boundaries between assemblages are therefore at best approximate and variable, changing continuously, and varying somewhat for each biotic form (see Udvardy 1969). Therefore, I have used ecotones to establish approximate boundaries between ecogeographic formations". For this effort, where the physiography was insufficient, I used ecotones between vegetational assemblages to delineate bioregional boundaries.

I used a detailed map of the physiography of California and environs (Nystrom 1966), and the plant formation descriptions and distributions of both Kuchler (1977), and Mayer and Laudenslayer (1988), to further refine the provinces of Bailey (1976, 1978) (Fig. 3) and Udvardy (1975) (Fig. 4). I first defined the major physiographic provinces within the state using Nystrom's (1966) map, then using natural drainage patterns (op. cit.), and Kuchler's (1977) vegetation formation distributions, I subset these physiographic entities where appropriate using either vegetational ecotones or

watershed divisions, or both. These entities were then cross-checked with the vegetation type maps in Mayer and Laudenslayer (1988) for distributional consistency as a check to assure that these initial bioregional boundaries were consistent with those

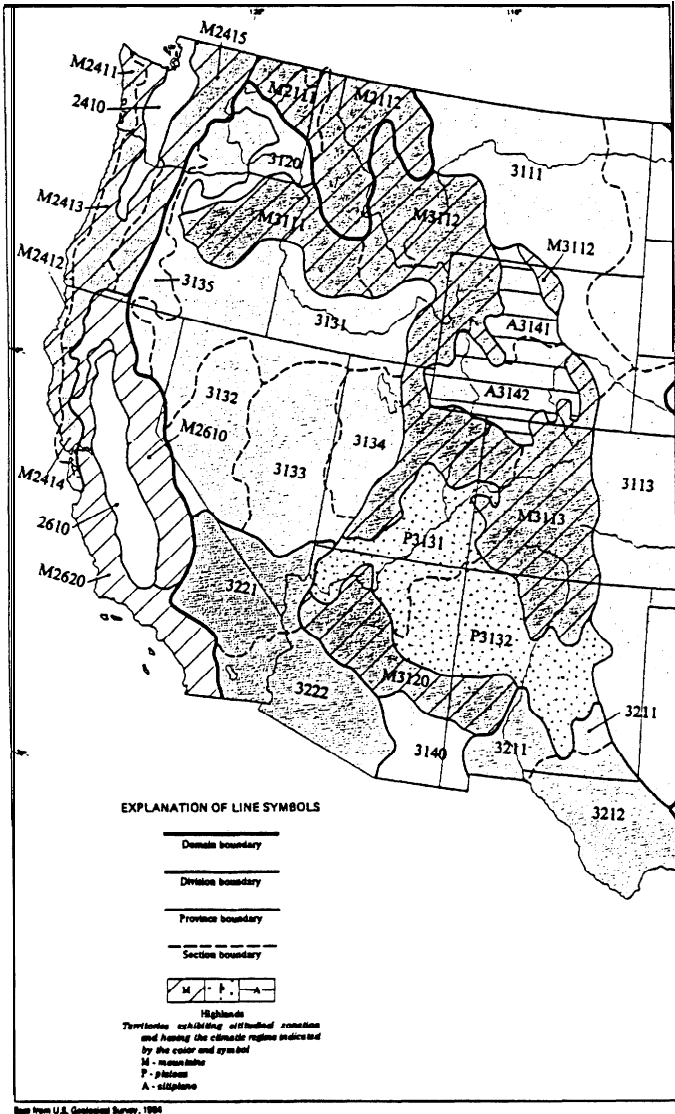


Figure 3. Ecoregions of California (Bailey 1976). M2412 = Redwood forest, M2413 = Cedar-Hemlock-Douglas for Forest, M2414 = California Mixed Evergreen Forest, M2610 = Sierran Province Forest, M2620 = California Chaparral Province, 3131 = Sagebrush-Wheatgrass, 3132 = Grama-Galleta + Juniper-Pinyon Woodland Mosaic, 3135 = Ponderosa Shrub Forest, 3221 = Creosote Brush, 3222 = Creosote Bush-Bur Sage. Consult original publication for details beyond California.

identified using a second independent phytogeographic analysis of the state. However, the Great Central Valley (Sacramento plus San Joaquin valleys) and the Sierra Nevada are both extensive ecoclines with respect to their biota, and were divided somewhat arbitrarily near their mid-points using natural drainages.

These ecotonal boundaries were then finalized by comparison with the distributions of those native vertebrate taxa with the lowest vagility, the reptiles and amphibians, using the ranges depicted in Stebbins (1985). I selected those ecotones that reflect the greatest degree of faunal change within these taxa consistent with the phytogeographic gradient. Using the reptiles and amphibians (minus the marine forms) as model organisms to fine-tune bioregional boundaries has several advantages: (1) they are a large, and diverse fauna representing some four orders, 28 families, and 130 species (27 salamanders, 25 frogs, 3 turtles, 37 lizards, and 38 snakes); and (2) they are, as a

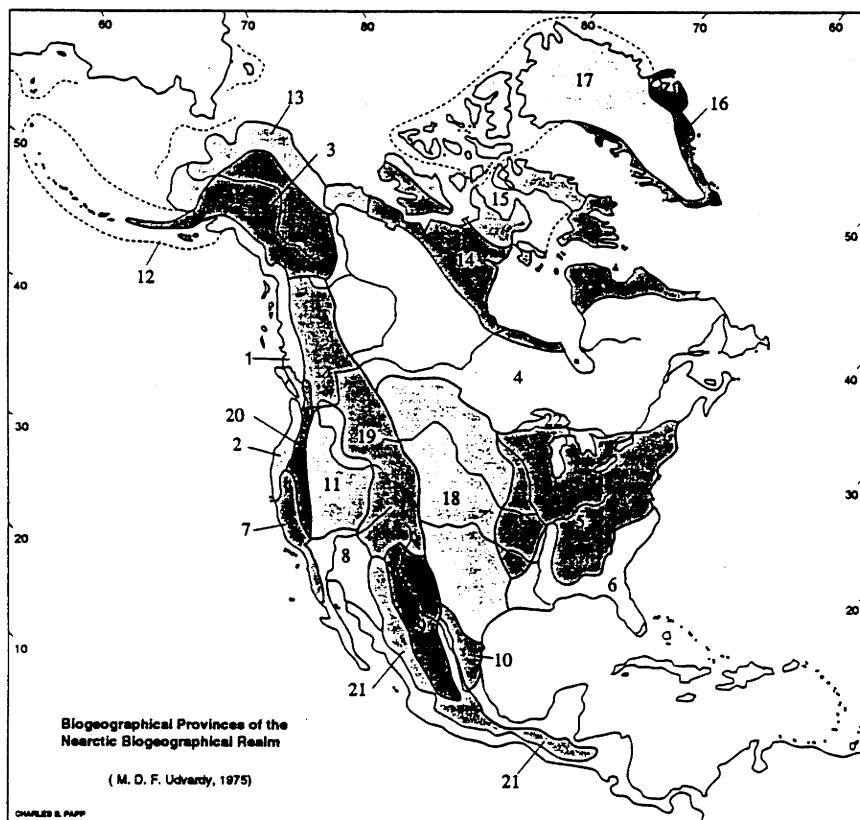


Figure 4. Biogeographical provinces of the Nearctic Biogeographical Realm from Udvardy (1975); 2 = Oregonian Province, 7 = Californian Province, 8 = Sonoran Province, 11 = Great Basin Province, 20 = Sierra - Cascade Province. Consult original publication for details beyond California.

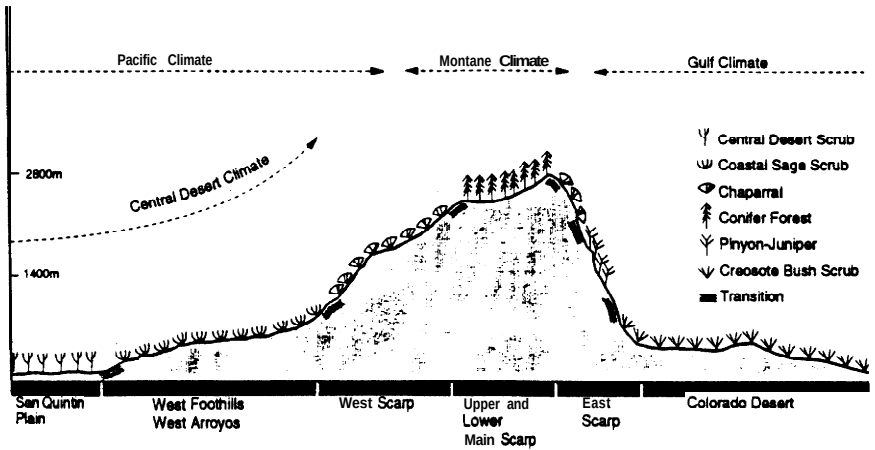


Figure 5. The ecogeographic formations of the Sierra San Pedro Martir, Baja California, Mexico at latitude 31°N . An ecogeographic formation is comprised of a topographic element (e.g., western foothills, east scarp), a climatic element, and a vegetation association; from Welsh (1988).

rule, sedentary species whose presence (or absence) closely reflects local environmental conditions over extended time.

Under each bioregion described below, Kuchler's (1977) vegetation types are listed first under dominant and secondary vegetations; Mayer and Laudenslayer (1988) types are listed second and referred to as California wildlife habitat relationships (WHR) types. The following WHR types are common throughout the state: fresh emergent wetland, pasture, riverine, lacustrine, cropland, orchard, urban, and eucalyptus (see Mayer and Laudenslayer 1988 for details). For a crosswalk between Kuchler (1977), Mayer and Laudenslayer (1988), and other vegetation classification systems of California see Mayer and Laudenslayer (1988: Table 6). Climate descriptions are based on Kahrl (1971) and Barry (1991). Soil descriptions are from Bailey (1976). Common names of vertebrates follow Laudenslayer et al. (1991) and Stebbins (1985). The lists of resident vertebrates are intended to characterize the fauna of each bioregion and, with the exception of the reptiles and amphibians, were compiled after the boundaries were first determined using the method described above. They are neither complete lists of resident animals, or composed entirely of animals endemic to a particular bioregion. All counties referenced below are within California.

Land classification systems such as proposed here are important and useful for stratifying natural variability and placing resource use and management in a broader biogeographic context. However such systems are inherently anthropocentric and should be viewed as models, based on ecological theory, to be constantly evaluated and verified (Whittier et al. 1988, and cites therein).

THE BIOREGIONS OF CALIFORNIA

I delineated sixteen bioregions for the state of California and adjacent environs (Fig. 6).

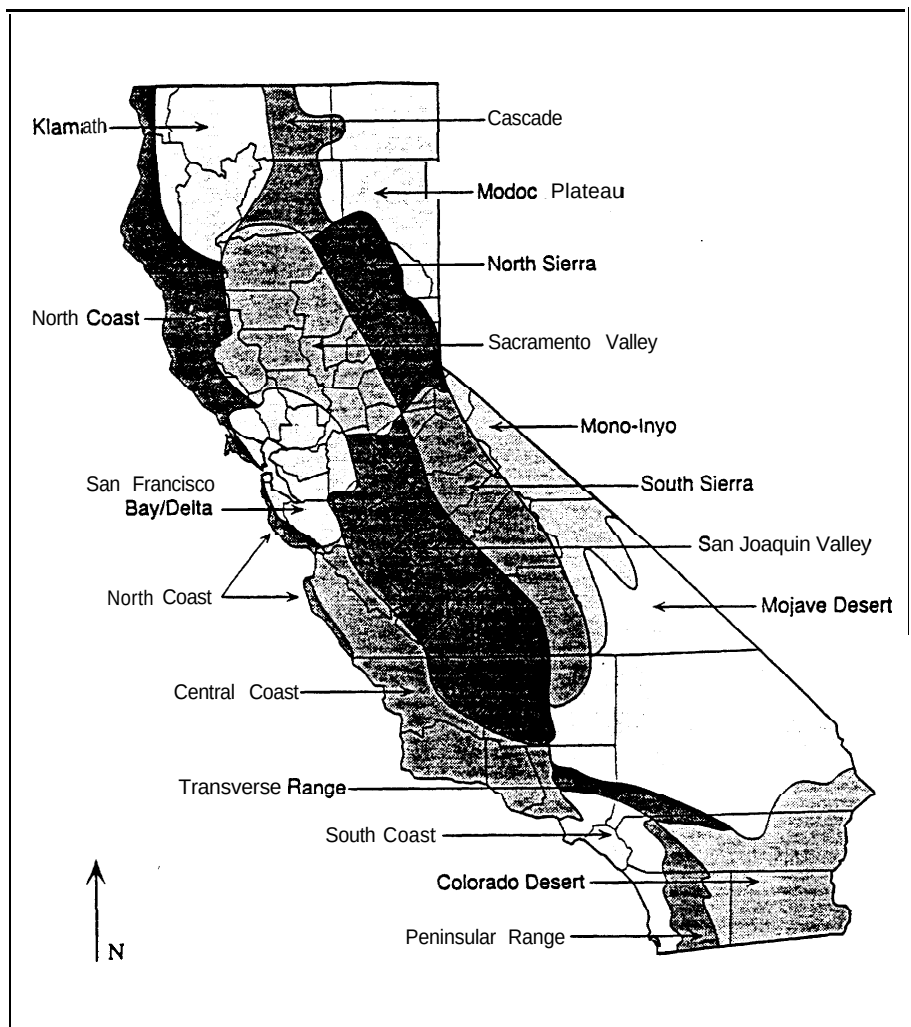


Figure 6. Approximate boundaries of the sixteen proposed bioregions of California. Fine lines are county boundaries.

North Coast Bioregion

This bioregion is comparable to the southern part of Udvardy's (1975) Oregonian Province, and is synonymous with Bailey's (1976, 1978) combined redwood forest and California mixed evergreen forest sections of his Pacific Forest Province. In California, it encompasses the area from southwestern Oregon to the southern extent of the mixed hardwood forest with redwood in southern Monterey County. The North Coast Bioregion is delineated by the Pacific Ocean on the west and the Klamath Bioregion on the east, as defined by the transition from redwood forest and mixed evergreen forest with rhododendron to Klamath forest types which occurs along the higher interior ridgelines of Del Norte, Humboldt, and south-central Trinity counties (i.e. Southfork Mountain). In western Tehama and Glenn counties the ecotone between the North Coast and the adjacent bioregion is defined by the transition from Coast Range montane forest to the dry interior of the Sacramento Valley Bioregion as represented by chaparral and oak-digger pine plant communities. All of Mendocino County is in this bioregion. In Lake County south to Mount St. Helena, an area that is predominantly ecotonal, the natural drainages define bioregional affinities. Interior drainages are part of the Sacramento Valley Bioregion, and coastal drainages (e.g., the Russian River) are part of the North Coast Bioregion. Those portions of Napa and Sonoma counties that drain toward the San Francisco Bay Delta are part of that bioregion (see below). From central Sonoma County south to San Luis Obispo County, the North Coast Bioregion consists of those lands west of the highest ridgeline dividing areas that drain directly into the Pacific Ocean from those areas that drain toward the interior. The bioregion does not include those creeks and rivers that flow into Monterey Bay from the Pajaro River south and are part of the Central Coast Bioregion. The bioregion includes parts of western Marin and San Mateo counties, most of Santa Cruz County, and western Monterey County south of Monterey to the southern extent of the mixed hardwood and redwood forest.

Climate: humid temperate, marine; highest rainfall in winter; coldest month from -3° to 18°C , warmest month $<22^{\circ}\text{C}$; northern area precipitation is 30-120 inches/year, average 75 inches/year; southern area precipitation is 30-70 inches/year, average 40 inches/year.

Dominant soils: brown forest, gray-brown podzolic (alfisols).

Dominant vegetation: redwood forest, mixed evergreen forest with rhododendron, Coast Range montane forest, mixed hardwood and redwood forest, and mixed hardwood forest. **WHR types:** redwood, Douglas-fir, montane hardwood-conifer, montane hardwood, coastal oak woodland.

Secondary vegetation: chaparral, blue oak-digger pine, coastal prairie-scrub mosaic, coastal cypress and pine forests, grand fir-sitka spruce forest, and northern seashore communities. **WHR types:** mixed chaparral, chamise-redshank chaparral, blue oak-digger pine, coastal scrub, perennial grassland, wet meadow, closed-cone pine-cypress, ponderosa pine, lodgepole pine, mixed chaparral, chamise-redshank chaparral, montane chaparral, alpine dwarf shrub, annual grassland, blue oak

woodland, valley oak woodland, montane riparian, valley foothill riparian, saline emergent wetland, estuarine, marine.

Examples of resident vertebrates: California slender salamander, southern torrent salamander, red-bellied newt, northern red-legged frog, Pacific and California giant salamanders, marbled murrelet, Vaux's swift, red-shouldered hawk, Townsend's warbler, mountain beaver, red tree vole, coast mole, shrew-mole, Roosevelt elk.

Klamath Bioregion

This Bioregion is part of Udvardy's (1975) Oregonian Province and is comparable to the southern part of Bailey's (1976, 1978) cedar-hemlock-Douglas-fir forest section of his Pacific Forest Province. It encompasses southwestern Oregon, interior of the coast, south to southern Trinity County (vicinity of Yolla Bolly Mountain). The western boundary is defined by the transition from redwood forest and mixed evergreen forest with rhododendron into mixed evergreen forest with chinquapin and Klamath montane forest with Douglas-fir which occurs along the higher interior ridgelines of Del Norte and Humboldt counties, and south-central Trinity County. The eastern boundary is defined by the ecotone between the Klamath montane forest of this bioregion and the Sierran montane forest, sagebrush steppe (central Siskiyou County), and northern yellow pine forest (in western Shasta County) of the Cascade Bioregion. The Klamath Bioregion interfaces with the Sacramento Valley Bioregion in west central Shasta and northwestern Tehama counties where the Klamath montane forest with yellow pine interdigitates with blue oak-digger pine, and chaparral. The Klamath Bioregion ends in south-central Trinity County where the Klamath montane forest with Douglas-fir, Klamath montane forest with yellow pine, and the mixed evergreen forest with chinquapin interdigitate with the Coast Range montane forest of the North Coast Bioregion.

Climate: dry summers, rainy winters; coldest month from -3° to 18°C , warmest month $>22^{\circ}\text{C}$; precipitation is 20-80 inches/year, average 60 inches.

Dominant soils: brown forest, gray-brown podzolic (alfisols), and some immature soils, Sierra-Nevada rock types-mesozoic eugeosynclinal formations intruded by mesozoic granite.

Dominant vegetation: mixed evergreen forest with chinquapin, Klamath montane forest with Douglas-fir, Klamath montane forest with yellow pine. WHR types: Douglas-fir, montane hardwood with conifer, montane hardwood, Klamath mixed conifer, red fir, white fir, ponderosa pine, subalpine conifer.

Secondary vegetation: Oregon oak forest, northern yellow pine. WHR types: Sierran mixed conifer, lodgepole pine, Jeffrey pine, aspen, closed-cone pine cypress, alpine dwarf shrub, bitterbrush, wet meadow, montane chaparral, mixed chaparral, chamise-redshank chaparral, perennial grassland, montane riparian.

Examples of resident vertebrates: Del Norte salamander, Siskiyou Mountain salamander, tailed frog, Northern spotted owl, pileated woodpecker, William's sapsucker, Hammond's flycatcher, Nashville warbler, black-capped chickadee, red crossbill, Pacific fisher, western pocket gopher, bushy-tailed woodrat, shrew-mole.

Cascade Bioregion

This Bioregion is synonymous with the north central portion of Udvardy's (1975) Sierra-Cascade Province, and portions of the northern third of Bailey's (1976, 1978) Sierran Forest Province. It extends from British Columbia through Washington, Oregon, and northern California, to Battle Creek and Lassen National Park in Shasta County. In the east, Sierran montane forest predominates on lower slopes and interdigitates with the yellow pine-shrub forest, sagebrush steppe, and juniper-shrub savanna of the Modoc Plateau Bioregion. In the west, the adjacent Klamath Bioregion is defined by the ecotone between Klamath forest types (see above) and Sierran montane and Northern yellow pine forests.

Climate: dry summers, rainy winters; coldest month from -10° to 18°C , warmest month $>22^{\circ}\text{C}$; precipitation is 20-80 inches/year, average 60 inches.

Dominant soils: mostly immature, some volcanic types.

Dominant vegetation: Sierran montane forest, upper montane-subalpine forests with alpine communities and barren terrain in the higher elevations. WHR types: white-fir, subalpine conifer, eastside pine, ponderosa pine, red fir, sierran mixed conifer, montane hardwood-conifer.

Secondary vegetation: northern yellow pine forest, yellow pine-shrub forest, Oregon oak forest, chaparral, and sagebrush steppe. WHR types: Klamath mixed conifer, montane chaparral, mixed chaparral, chamise-redshank chaparral, low sage, bitterbrush, sagebrush, lodgepole pine, juniper, aspen, closed-cone pine-cypress, montane hardwood, blue oak-digger pine, wet meadow, montane riparian.

Examples of resident vertebrates: long-toed salamander, Shasta salamander, tailed frog, Cascade frog, Oregon alligator lizard, mountain kingsnake, rubber boa, northern spotted owl, red crossbill, Clark's nutcracker, mountain chickadee, water shrew, pika, snowshoe hare, mountain beaver, hoary marmot, northern flying squirrel, red fox, Pacific fisher, marten.

Modoc Plateau Bioregion

This Bioregion is part of the Intermountain Sagebrush Province (Bailey 1976, 1978) or the Great Basin Province (Udvardy 1975) that constitutes the high desert steppe between the Cascade-Sierra Nevada ranges and the Rocky Mountains to the east. In California, this Bioregion extends from south-central Oregon east of the Cascade and North Sierra Bioregions south to eastern Plumas, Sierra, and Nevada counties, and east into Nevada. It is distinguished from the Cascade and North Sierra Bioregions by the ecotone between the Sierran montane, northern Jeffrey pine, and upper montane-subalpine forests of those Bioregions and the sagebrush steppe, yellow pine-shrub, and juniper-shrub savanna communities that characterize the Great Basin. This Bioregion contains island-like mountain ranges with vegetation characteristic of adjacent montane Bioregions (e.g., Warner Mountains).

Climate: dry summers, cold, harsh winters; precipitation averages 15 inches/year
Dominant soils: Warner basalt, heavy clay soils, with loamy to sandy soils occurring in the undulating lower elevation terraces.

Dominant vegetation: sagebrush steppe, yellow pine-shrub forest, juniper-shrub savanna. WHR types: low sage, bitterbrush, sagebrush, juniper, eastside pine.

Secondary vegetation: desert saltbush, chaparral, northern Jeffrey pine, upper montane-subalpine forest, sierran montane forest. WHR types: alkali desert scrub, montane chaparral, mixed chaparral, chamise-redshank chaparral, Jeffrey pine, subalpine conifer, white fir, montane hardwood-conifer, aspen, alpine dwarf shrub, wet meadow, montane riparian.

Examples of resident vertebrates: Great Basin spadefoot toad, northern leopard frog, northern sagebrush lizard, short-homed lizard, pinyon jay, sandhill crane, vesper sparrow, gray flycatcher, pronghorn, pygmy rabbit, Great Basin pocket mouse.

North Sierra Bioregion

This Bioregion is synonymous with the south-central portion of Udvardy's (1975) Sierra-Cascade Province, and central one third of Bailey's (1976, 1978) Sierran Forest Province. This Bioregion extends from Battle Creek and Lassen National Park in Shasta County, along the Sierran massif south to the south fork of the American River and the south rim of the Lake Tahoe Basin in El Dorado County. It's western boundary is defined by the Sacramento valley and it extends east to the Great Basin steppe (Modoc Plateau Bioregion). This Bioregion is dominated by Sierran montane forest, and at higher elevations, upper montane-subalpine forests. In the northeast, Sierran montane forest predominates on lower slopes and interdigitates with the sagebrush steppe, yellow pine-shrub forest, and juniper-shrub savanna of the Modoc Plateau Bioregion. The west and southwest boundary of the North Sierra Bioregion is defined by the ecotone between northern and Sierran yellow pine forests and the blue oak-digger pine and chaparral communities of the Sacramento Valley. On the east and southeast, the boundary of the North Sierra Bioregion is defined by the ecotone between northern Jeffrey pine, yellow pine-shrub, and upper montane-subalpine forests, and the Great Basin plant communities of juniper-pinyon woodland, sagebrush steppe, and juniper-shrub savanna.

Climate: cold, harsh winters, dry summers; coldest month from -15°C to 18°C , warmest month $>22^{\circ}\text{C}$; precipitation = 40-95 inches/year, average 65 inches.

Dominant soils: mostly immature soils, some mollisols.

Dominant vegetation: Sierran montane forest, upper montane-subalpine forests, Sierran yellow pine forest, with alpine communities and barren terrain in the higher elevations. WHR types: white fir, sub-alpine conifer, ponderosa pine, red fir, lodgepole pine, sierran mixed conifer, montane hardwood-conifer, montane hardwood, montane chaparral.

Secondary vegetation: northern yellow pine forest, yellow pine-shrub forest, northern Jeffrey pine forest, blue oak-digger pine forest, chaparral. WHR types: Jeffrey pine,

eastside pine, blue oak-digger pine, montane chaparral, mixed chaparral, chamise-redshank chaparral, aspen, juniper, alpine dwarf shrub, closed-cone pine-cypress, bitterbrush, wet meadow, montane riparian.

Examples Of resident vertebrates: foothill yellow-legged frog, mountain yellow-legged frog, Californiamountain kingsnake, rubber boa, black-backed woodpecker, pine grosbeak, Clark's nutcracker, mountain chickadee, pika, hoary marmot, lodgepole chipmunk, montane vole, mountain beaver, Pacific fisher, wolverine.

South Sierra Bioregion

This Bioregion is synonymous with the southern third of Udvardy's (1975) Sierra-Cascade Province, and southern third of Bailey's (1976, 1978) Sierran Forest Province. This Bioregion is dominated by Sierran montane forest, and at higher elevations, upper montane-subalpine forests. In the north the boundary is defined as the south fork of the American River and the south shore of Lake Tahoe (North Sierra Bioregion). In the south the boundary is defined as the Kern River drainage. The west and southwest boundary of the South Sierra Bioregion is defined by the ecotone between Sierran yellow pine and Sierran montane forests and the blue oak-digger pine and chaparral communities of the San Joaquin valley. On the east, the boundary of the South Sierra Bioregion is defined by the ecotone between northern Jeffrey pine and upper montane-subalpine forests, and the Great Basin plant communities of the Mono-Inyo and Mojave Bioregions, including juniper-pinyon woodland, sagebrush steppe, and juniper-shrub savanna.

Climate: Mediterranean with cold winters and dry summers: coldest month from -15° to 18°C , warmest month $>22^{\circ}\text{C}$; precipitation is 20-65 inches/year, average 45 inches.

Dominant soils: mostly immatures, some mollisols.

Dominant vegetation: Sierran montane forest, upper montane-subalpine forests, Sierran yellow pine forest, with alpine communities and barren terrain in the higher elevations. WHR types: white fir, subalpine conifer, ponderosa pine, red fir, lodgepole pine, sierran mixed conifer, montane hardwood-conifer, montane hardwood, montane chaparral.

Secondary vegetation: northern Jeffrey pine, pinyon-juniper woodland, chaparral, giant sequoia. WHR types: Jeffrey pine, pinyon-juniper, mixed chaparral, chamise-redshankchaparral, aspen, closed-cone pine-cypress, alpine dwarf shrub, bitterbrush, wet meadow, montane riparian.

Examples Of resident vertebrates: Mount Lyell salamander, limestone salamander, mountain yellow-legged frog, Yosemite toad, California mountain kingsnake, rubber boa, black-backed woodpecker, pine grosbeak, Clark's nutcracker, red crossbill, mountain bluebird, mountain chickadee, pika, hoary marmot, Pacific fisher, lodgepole chipmunk, montane vole, mountain beaver, red fox, wolverine.

Mono-Inyo Bioregion

This Bioregion is biotically very similar to the Modoc Plateau Bioregion, but with some unique characteristics resulting from its more southern latitude and extreme physiography. This Bioregion is also part of the Intermountain Sagebrush Province (Bailey 1976, 1978) or the Great Basin Province (Udvardy 1975) that constitutes the high desert steppe between the Cascade-Sierra Nevada ranges and the Rocky Mountains to the east. The Mono-Inyo Bioregion encompasses that part of California from the latitude of south Lake Tahoe south along the eastern flank of the Sierran massif to the Mojave Desert, and is contiguous through lower elevations with the Great Basin Steppe Desert of Nevada to the east. Along the eastern flank within California, this Bioregion includes mountain ranges with montane vegetation similar to the South Sierra Bioregion (e.g., White and Inyo Mountains). The western boundary of the Mono-Inyo Bioregion is defined by the ecotone between the juniper-pinyon woodland and steppe vegetations of this Bioregion and the upper montane-subalpine and northern Jeffrey pine forests of the Sierra Nevada.

Climate: dry steppe with cold, harsh winters and dry summers; coldest month from -15° to 18°C, warmest month >22°C; precipitation = 5-30 inches/year, average 15 inches.

Dominant soils: immature soils, some mollisols to audisols (southern).

Dominant vegetation: sagebrush steppe, juniper-pinyon woodland. WHR types: low sage, bitterbrush, sagebrush, pinyon-juniper.

Secondary vegetation: Great Basin subalpine forest, blackbush scrub, desert saltbush, northern Jeffrey pine forest, upper montane-subalpine forest, alpine communities, barren terrain. WHR types: subalpine conifer, alkali desert scrub, Jeffrey pine, eastside pine, aspen, wet meadow.

Examples of resident vertebrates: Inyo Mountain slender salamander, striped whipsnake, gray flycatcher, black-throated sparrow, broad-tailed hummingbird Inyo shrew, Merriam's shrew, Townsend's ground squirrel, sagebrush vole.

Sacramento Valley Bioregion

This Bioregion is part of Udvardy's (1975) Californian Province and Bailey's (1976, 1978) California Grassland Province. This Bioregion begins in the blue oak-digger pine forests in the vicinity of Lake Shasta, and extends south through the California Prairie grasslands of the Sacramento Valley to the marshlands of the Sacramento/San Joaquin River Delta to Putah Creek (southern Yolo County line) and the American River in Sacramento County. This bioregion includes the watersheds of Lake Berryessa and Clear Lake. From the American River south, and east of State Highway 99, this Bioregion extends south to the main fork of the Mokelumne River (northern San Joaquin County). The eastern boundary of the Bioregion is defined by the ecotone of the blue oak-digger pine and chaparral of the valley uplands with the yellow pine of the Sierran foothills. On the west side of the valley, in Shasta, Tehama,

Glenn. and Colusa counties, this Bioregion is defined by the ecotone between the chaparral and blue oak-digger pine forest of the valley and the Klamath montane forest with yellow pine and northern yellow pine forest of the Klamath Bioregion, and the Coast Range montane forest of the North Coast Bioregion. From northwestern Colusa County south, the Bioregion boundary is defined by the topography (ridgelines) that divide the drainages between those flowing eastward into the Sacramento River and those flowing westward into the Pacific Ocean.

Climate: Mediterranean with dry summers and rainy winters: coldest month from -5° to 18°C , warmest month $>22^{\circ}\text{C}$; precipitation = 20-30 inches/year, average 20 inches.

Dominant soils: immature soils, some mollisols to audisols (southern).

Dominant vegetation: California prairie, blue oak-digger pine forest, riparian forest.

WHR types: annual grassland, blue oak-digger pine, valley oak woodland, valley foothill riparian.

Secondary vegetation: tule marsh, chaparral, Sierran yellow pine; WHR types: blue oak woodland, valley foothill riparian, mixed chaparral, chamise-redshank chaparral, montane chaparral, montane hardwood-conifer, montane hardwood.

Examples of resident vertebrates: red-legged frog, foothill yellow-legged frog, giant garter snake, yellow-billed magpie, tricolored blackbird, yellow-billed cuckoo, acorn woodpecker, scrub jay, red-tailed hawk, California kangaroo rat, black-tailed jackrabbit, beaver.

San Francisco Bay/Delta Bioregion

This Bioregion is also part of Udvardy's (1975) Californian Province. According to Bailey (1976, 1978) this area transects three provinces: California grassland, California mixed evergreen, and California chaparral. I have chosen to treat this very complex region as a single Bioregion because I consider its hydrologic role to be preeminent. The Delta is probably the single most intricate and important biological "entity" in the state of California because it is the interface between significant freshwater systems (e.g., Sacramento and San Joaquin rivers) of the State and the marine ecosystem of San Francisco Bay. It functions, like all estuarine wetlands, as both a filtration system between marine and freshwater ecosystems, and a great nursery where organisms from both realms carry on critical procreative aspects of their life cycles. The San Francisco Bay/Delta Bioregion extends from the Pacific Ocean east to the edge of the tule marsh zone in the great central valley which is most conveniently defined by State Highway 99. This highway, from the American River in the north to the Stanislaus River in the south, was built on solid ground east of the Delta and thus defines a reasonable geologic boundary for the eastern extent of the Delta marshlands. This Bioregion includes eastern Marin County, and those parts of Sonoma, Napa, and Solano counties that drain into the Bay or Delta. It also includes southern Yolo County from Putah Creek south, and west of the Sacramento River, and all areas east of the Sacramento River to State Highway 99. The southern boundary

is defined by the Stanislaus River and the southern San Joaquin County line, and includes San Joaquin and northeast Stanislaus counties. In the Diablo' Range the Bioregion boundary follows the highest ridgeline south, from the southeast corner of Alameda County, to the transverse ridge that divides the Coyote Creek drainage from the Pajaro River drainage. The boundary follows this ridgeline west across the highest part of the Santa Clara Valley where the drainage is defined north to San Francisco Bay or south to the Pajaro River, to the ridgeline of the Santa Cruz Mountains that divides coastal from interior (San Francisco Bay) drainages. It includes all of Alameda, San Francisco, and Contra Costa counties, and east San Mateo County, and those portions of Santa Clara County that drain into San Francisco Bay.

Climate: Mediterranean with maximum rainfall in winter; coldest month from -3° to 18°C , warmest month may exceed 22°C ; precipitation = 20-50 inches/year, average 35 inches.

Dominant soils: brown forest, gray-brown podzolic (alfisols) and some immature soils (eastward).

Dominant vegetation: tule marsh, California prairie, riparian forest, coastal prairie-scrub mosaic, coastal salt marsh. WHR types: fresh emergent wetland, perennial grassland, saline emergent wetland, coastal scrub, valley oak woodland, coastal oak woodland, annual grassland, estuarine.

Secondary vegetation: mixed hardwood forest, redwood forest, chaparral, blue-oak-digger pine forest, valley oak savanna. WHR types: montane hardwood-conifer, montane hardwood, redwood, mixed chaparral, blue oak woodland, blue oak-digger pine, chamise-redshank chaparral, montane chaparral, valley foothill riparian, marine.

Examples of resident vertebrates: sturgeon, striped bass, Delta smelt, red-legged frog, Alameda whipsnake, giant garter snake, silvery legless lizard, black rail, Clapper rail, meadowlark, loggerhead shrike, salt-marsh harvest mouse, mink, otter, beaver (extirpated).

San Joaquin Valley Bioregion

This Bioregion is part of Udvardy's (1975) Californian Province and Bailey's (1976, 1978) California Grassland Province. It extends from the Mokelumne River, east of State Highway 99, and from the Stanislaus River and the San Joaquin County line west of this Highway, south (including valley bottom grasslands and oak woodland uplands) to the crest of the Tehachapi Mountains south of the Kern River drainage. This Bioregion is bounded on the east side by the blue oak-digger pine and chaparral ecotones with the yellow pine montane forest of the Sierran Bioregion. On the south (from the Kern River drainage southward) and-west sides, this Bioregion is defined by the topography (ridgelines) of the Tehachapi Mountains and coast ranges (the Caliente and Diablo ranges) that effect the direction of drainages toward either the San Joaquin River or toward the Mojave and Central Coast Bioregions. The eastern versant of the Diablo Range, and the entire Temblor Range are within this Bioregion.

Climate: Mediterranean (dry), with warm, dry summers, cool winters; coldest month between 0° and 18°C, warmest month >22°C; precipitation = <10 inches/year.

Dominant soils: alfisols to aridisols.

Dominant vegetation: California Prairie, blue oak-digger pine forest, San Joaquin salt bush, chaparral. WHR types: annual grassland, alkali desert scrub, blue oak-digger pine.

Secondary vegetation: tule marsh, riparian forest, valley oak savanna. WHR types: fresh emergent wetland, blue oak woodland, valley oak woodland, mixed chaparral, chamise-red shank chaparral, valley foothill riparian.

Examples of resident vertebrates: blunt-nosed leopard lizard, silvery legless lizard, San Joaquin coachwhip, giant garter snake, white-faced ibis, yellow-billed magpie, tri-colored blackbird, yellow-billed cuckoo, meadowlark, loggerhead shrike, tule elk, pronghorn, San Joaquin Valley kit fox, giant kangaroo rat, short-nosed kangaroo rat, Buena Vista Lake shrew, San Joaquin antelope squirrel.

Central Coast Bioregion

This Bioregion is part of Udvardy's (1975) California Province and Bailey's (1976, 1978) California Chaparral Province. It extends from southern Santa Clara County, including the Pajaro River drainage and all creeks and rivers draining into Monterey Bay, south along the eastern versant of the Santa Lucia Mountains of Monterey County and the western versant of the Diablo and Caliente ranges, including Santa Barbara and Ventura counties, to western Los Angeles County. The Pacific Ocean defines the northwestern boundary at Monterey Bay, and the ridgelines separating the Salinas River drainage from interior (San Joaquin Valley) and Pacific coast drainages south of Monterey to the Monterey County line, determines both the eastern and western boundaries north of San Luis Obispo County. From northern San Luis Obispo County, the western boundary is the Pacific Ocean, and the eastern boundary is defined by the western versant of the interior Coast Ranges south to the Tehachapi Mountains. South of the Tehachapi Mountains, in Los Angeles County, the eastern boundary is defined by the limits of the chaparral formation in the Sierra Pelona where it meets the Joshua tree scrub and Mojave Creosote bush of the Mojave Bioregion and the Pinyon-Juniper woodland and mixed hardwood forest of the Transverse Range Bioregion (San Gabriel Mountains). The Santa Monica Mountains of western Los Angeles County form the southern extent of this bioregion.

Climate: Mediterranean with dry summers and rainy winters; coldest month between -3° and 18°C, warmest month >22°C; precipitation = 10-45 inches/year, average 25 inches.

Dominant soils: mostly immatures.

Primary vegetation: blue oak-digger pine, southern oak forest, chaparral, California prairie, valley oak savanna, mixed hardwood forest. WHR types: blue oak-digger pine, blue oak woodland, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, annual grassland, valley oak woodland, montane hardwood,

montane hardwood-conifer, coastal scrub.

Secondary vegetation: coastal prairie-scrub mosaic, coastal sagebrush, coastal cypress and pine forests, juniper-pinyon woodland. WHR types: perennial grassland, closed-cone pine-cypress, pinyon-juniper, ponderosa pine, montane chaparral, wet meadow, valley foothill riparian, montane riparian, wet meadow.

Examples of resident vertebrates: Black-bellied slender salamander, Gabilan slender salamander, San Lucia slender salamander, coast homed lizard, black legless lizard, California thrasher, rufous-crowned sparrow, California condor, Cassin's kingbird, red-shouldered hawk, white-eared pocket mouse, narrow-faced kangaroo rat.

South Coast Bioregion

This Bioregion is part of Udvardy's (1975) California Province and Bailey's (1976, 1978) California Chaparral Province. It extends from the base of the Santa Monica and San Gabriel Mountains (including the San Fernando Valley) in Los Angeles County south into northern Baja California, Mexico. its northern and eastern boundaries are defined by the lower limits of the chaparral belts of the Transverse, Santa Monica, and Peninsular Range Mountains.

Climate: Mediterranean with dry summers and rainy winters; coldest month from 0° to 18°C; precipitation = 20-40 inches/year, average 25 inches.

Dominant soils: mostly immatures.

Dominant vegetation: Coastal sagebrush, southern oak forest, chaparral. WHR types: coastal scrub, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, annual grassland.

Secondary vegetation: coastal salt marsh, valley oak savanna. WHR types: saline emergent wetland, valley oak woodland, closed-cone pine-cypress. montane riparian. valley foothill riparian, estuarine, marine.

Examples of resident vertebrates: Pacific slender salamander, arroyo southwestern toad, orange-throated whiptail, coast homed lizard, silvery legless lizard, red diamond rattlesnake, Clapper rail, least Bell's vireo, California gnatcatcher, Costa's hummingbird, Cassin's kingbird, California vole, Pacific kangaroo rat.

Transverse Range Bioregion

This bioregion is comprised of the San Gabriel and San Bernardino Mountains (Transverse Ranges) of southern California. This Bioregion divides the South Coast Bioregion from the desert Bioregion to the north and east. The Transverse Range Bioregion (along with the Peninsular Range Bioregion) comprises the boundary between Udvardy's (1975) Californian and Sonoran Provinces, and the boundary between Bailey's (1976, 1978) California Chaparral and American Desert Provinces. The Transverse Range extends along the San Gabriel Mountains from central Los Angeles County eastward and includes the San Bernardino Mountains of western San Bernardino County and the Little San Bernardino Mountains of central Riverside

Countv. San Gorgonio Pass in northwestern Riverside County separates the Transverse Range Bioregion from the Peninsular Range Bioregion.

The lower elevational limit of chaparral defines the boundary of this Bioregion with the Southcoast Bioregion. The chaparral, juniper-pinyon woodland and southern Jeffrey pine forest define its boundary with the desert Bioregions to the north and east, while the mixed hardwood forest and juniper-pinyon woodland define its northwestern boundary with the chaparral of the Central Coast Bioregion in central Los Angeles County.

Climate: Mediterranean with dry summers and rainy winters; coldest month from 0° to 18°C, warmest month may exceed 22°C; precipitation = 20-40 inches/year, average 30 inches.

Dominant soils: mostly immatures.

Dominant vegetation: mixed hardwood forest, chaparral, southern Jeffrey pine forest, southern yellow pine forest, juniper-pinyon woodland. WHR types: montane hardwood-conifer, montane hardwood, montane chaparral, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, Jeffrey pine, pinyon-juniper.

Secondary vegetation: Coulter pine forest, southern montane subalpine forest. WHR types: subalpine conifer, lodgepole pine, ponderosa pine, alpine dwarf shrub, annual grassland, wet meadow, montan riparian, valley foothill riparian.

Examples Of resident vertebrates: Pacific slender salamander, Monterey salamander, Mountain yellow-legged frog, California treefrog, southwestern toad, California spotted owl, Costa's hummingbird, Stephens' kangaroo rat, Peninsular bighorn sheep, Merriam's chipmunk.

Peninsular Range Bioregion

This Bioregion is comprised of the San Jacinto, Santa Rosa, and Laguna Mountains of California and the Sierra Juarez and Sierra San Pedro Martir of Baja California (the Peninsular Range). This Bioregion divides the South Coast Bioregion from the Colorado Desert Bioregion to the east. The Peninsular Range Bioregion (along with the Transverse Range Bioregion to the north) comprises the boundary between Udvardy's (1975) Californian and Sonoran Provinces, and the boundary between Bailey's (1976, 1978) California Chaparral and American Desert Provinces. The Peninsular Range Bioregion extends from San Gorgonio Pass in northwestern Riverside County southeast into northern Baja California, ending where the Sierra San Pedro Martir meets the central desert at the latitude of El Rosario. The lower elevational limit of chaparral defines the boundary of this Bioregion with the Southcoast Bioregion. The chaparral, juniper-pinyon woodland and southern Jeffrey pine forest define its boundary with the Colorado Desert Bioregion to the east.

Climate: Mediterranean with dry summers and rainy winters; coldest month from 0° to 18°C, warmest month may exceed 22°C; precipitation = 10-40 inches/year, average 20 inches.

Dominant soils: mostly immatures.

Dominant vegetation: mixed hardwood forest, chaparral, southern yellow pine forest, southern Jeffrey pine forest, juniper-pinyon woodland. WHR types: montane hardwood-conifer, montane hardwood, montane chaparral, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, Jeffrey pine, pinyon-juniper.

Secondary vegetation: southern montane subalpine forest. WHR types: subalpine conifer; lodgepole pine, ponderosa pine, alpine dwarf shrub, annual grassland, wet meadow, montane riparian, valley foothill riparian.

Examples of resident vertebrates: Pacific slender salamander, large-blotched salamander, California treefrog, southwestern toad, granite spiny lizard, granite night lizard, barefoot gecko, banded rock lizard, California spotted owl, Costa's hummingbird. Peninsular bighorn sheep, Merriam's chipmunk, spiny pocket mouse, western yellow bat.

Mojave Desert Bioregion

This Bioregion encompasses the southern end of Udvardy's (1975) Great Basin Province and the northern end of his Sonoran Province; it encompasses the creosote bush section of Bailey's (1976, 1978) American Desert Province. This Bioregion begins in the north in the vicinity of the White-Inyo Mountains and the southern Sierra Nevada where the boundary is defined by the ecotone between the Mojave creosote bush or Joshua tree scrub of the Mojave desert and the juniper-pinyon woodland and chaparral of the adjacent montane regions and the sagebrush steppe of the Mono-Inyo Bioregion (Owens Valley). The west and southwest boundaries are defined by the ecotones of these same desert vegetation communities with the chaparral and juniper-pinyon woodlands of the Central Coast and Transverse Range Bioregions. The boundary between this Bioregion and the Colorado Desert Bioregion to the south is defined by the ecotone, in Riverside and southeastern San Bernardino counties, between the Mojave creosote bush and Joshua tree scrub of this Bioregion and the Sonoran creosote bush vegetation of the Colorado Desert Bioregion. To the east, this Bioregion extends into Nevada and Arizona.

Climate: very dry all seasons, high summer temperatures, mild winters; precipitation less than 10 inches/year.

Dominant soils: sedimentary, metamorphic, and volcanic types of varying ages (aridisols).

Dominant vegetation: Mojave creosote bush, Joshua tree scrub, desert saltbush. WHR types: desert scrub, Joshua tree, alkali desert scrub, desert wash.

Secondary vegetation: Juniper-pinyon woodland, blackbush scrub, Mojave montane forest. WHR types: pinyon-juniper, desert succulent shrub, desert riparian, palm oasis.

Examples of resident vertebrates: Mojave fringe-toed lizard, desert night lizard, Mojave rattlesnake, rosy boa, Mojave patch-nosed snake, western shovel-nosed snake, southwestern black-headed snake, Mojave sidewinder, Bendire's thrasher, Gambel's quail, black-tailed gnatcatcher, cactus wren, Mojave ground squirrel, kit fox, badger.

Colorado Desert Bioregion

This Bioregion is part of Udvardy's (1975) Sonoran Province and comprises the Creosote Bush-Bur Sage section of Bailey's (1976, 1978) American Desert Province. This Bioregion extends to the south and east into western Arizona, northeastern Baja California and northwestern Sonora, Mexico. The Transverse and Peninsular Range Bioregion bounds the Colorado Desert Bioregion on the west, where the ecotone between the chaparral and juniper-pinyon woodlands of these montane areas and the desert vegetation of the Colorado Desert define the boundary. On the north, the boundary of the Colorado Desert Bioregion is defined by the ecotone between the Mojave creosote bush and Joshua tree scrub vegetations of the Mojave Bioregion and the Sonoran creosote bush of the Colorado Desert.

Climate: very dry all seasons, high summer temperatures, mild winters; precipitation less than 10 inches/year.

Dominant soils: aridisols, extensive areas of desert pavement.

Dominant vegetation: Sonoran creosote bush. WHR types: desert scrub, desert succulent shrub, desert wash.

Secondary vegetation: cactus scrub, oasis scrub woodland, Salton Sea saltbush, alkali scrub woodland, desert saltbush, hot sandy desert. WHR types: alkali desert scrub, desert riparian, palm oasis.

Examples of resident vertebrates: Colorado Desert fringe-toed lizard, Coachella valley fringe-toed lizard, flat-tailed homed lizard, Clark's spiny lizard, Colorado shovel-nosed snake, western diamondback rattlesnake, Colorado Desert sidewinder, gila woodpecker, great-tailed grackle, white-winged dove, verdin, Le Conte's thrasher, Phainopepla, black-tailed gnatcatcher, Abert's towhee, cactus wren, California leaf-nosed bat, spiny pocket mouse.

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LITERATURE CITED

- Airola, D.A. 1988. Guide to the California wildlife habitat relationships system. California Resources Agency, Dept. Fish and Game. Rancho Cordova, CA. 74 p.
- Allen, T.H., and T.B. Starr. 1982. Hierarchy: perspectives for ecological complexity. Univ. of Chicago Press, Chicago, Illinois. 310 p.
- Andrewartha, H.G. and L.C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois. 782 p.
- Axelrod, D.I. 1975. Evolution and biogeography of madrean-Tethyan sclerophyllous vegetation. *Ann. Missouri Bot. Gard.* 62:280-334.
- _____. 1976. History of coniferous forests, California and Nevada. *Univ. Calif. Pub. Bot.* 70:1-62.
- _____. 1977. Outline history of California vegetation. Pages 139-193 in M.G. Barbour and J. Major, eds. *Terrestrial vegetation of California*. John Wiley and Sons, Inc., New York.
- _____. 1979. Age and origin of the Sonoran Desert vegetation. *Calif. Acad. Sci. Occas. Pap.* 132: 1-74.
- Bailey, R.G. 1976. Ecoregions of the United States. USDA Forest Service, Ogden, UT 84401. Map.
- _____. 1978. Descriptions of the ecoregions of the United States. USDA Forest Service. Intermtn. Region, Ogden, Ut. 77 p.
- Barry, W.J. 199 1. Ecological regions of California. Unpublished report, prepared for California Interagency Natural Areas Coordinating Committee, California Department of Parks and Recreation, 15 July, 33 p.
- Berg, P., and S. Mills (eds.). 198 1. Bioregions. *Coevolution Quart.* No. 32. 144 p.
- Blondel, J. 1987. From biogeography to life history theory: a multithematic approach illustrated by the biogeography of vertebrates. *J. of Biogeography* 14:405-422.
- Brooks, D.R. 1988. Scaling effects in historical biogeography: a new view of space, time, form. *Syst. Zool.* 37:237-244.
- _____, and E.O. Wiley. 1988. *Evolution as entropy: toward a unified theory of biology*. 2nd Edition. Univ. of Chicago Press, Chicago, Il. 415 p.
- Brown, J.H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Nat. Mem.* 2:209-227.
- _____, and A.C. Gibson. 1983. *Biogeography*. The C.V. Mosby Company, St. Louis, Missouri. 643 p.
- Croizat, L. 1964. Space, time, form: the biological synthesis. Published by the author, Caracas, Venezuela. 881 p.
- Dansereau, P.M. 1957. *Biogeography; an ecological perspective*. Ronald Press. New York. 394 p.
- Darlington, P.J. 1957. *Zoogeography: the geographical distribution of animals*. John Wiley and Sons, Inc., New York. 675 p.
- Dice, L.R. 1952. *Natural communities*. University of Michigan Press, Ann Arbor. 547 p.
- Frost, D.R., and D.M. Hillis. 1990. Species in concept and practice: herpetological applications. *Herpetologica* 46:87-104.
- Gleason, H.A. 19 17. The structure and development of the plant association. *Bull. Torrey Bot. Club* 53:7-26.
- _____. 1926. The individualistic concept of plant associations. *Bull. Torrey Bot. Club.* 53:7-26.
- Gray, J., and A.J. Boucot (eds.). 1978, *Historical biogeography, plate tectonics, and the changing environment*. Oregon State University Press, Corvallis. 500 p.

- Grim-tell, J. 1914. The Colorado River as a hindrance to the dispersal of species. Univ. Calif. Pub. Zool. 12:100-107.
- _____. 1917. The niche-relationship of the California thrasher. Auk 34:427-433.
- Hennig, W. 1979. Phylogenetic systematics. 3rd ed. Tr. D.D. Davis and R. Zanderl. University of Illinois Press, Urbana, Il. 263 p.
- Hickman, J.C. 1993. The Jepson manual: higher plants of California. Univ. California Press, Berkeley, CA. 1400 p.
- Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. Science 105:367-368.
- _____. 1967. Life zone ecology. Tropical Science Center, San Jose Costa Rica. 124 p.
- Holman, J.A. 1976. Paleoclimatic implications of "ecologically incompatible" herpetological species (late Pleistocene: southeastern United States). Herpetologica 32:290-295.
- Horn, H.S. 1968. Regulation of animal numbers: a model counter-example. Ecology 49:776-778.
- James, F.C., R.F. Johnston, N.O. Warner, G.J. Niemi. and W.J. Boecklen. 1984. The Grinnellian niche of the wood thrush. American Naturalist 124:17-30.
- Kahrl, W.L. 1979. The California Water Atlas. State of California Publ. Sacramento, CA. 118 p.
- Keeler-Wolf, T. 1990. Ecological surveys of Forest Service research natural areas in California. USDA Forest Service, Pacific Southwest Research Station GTR-PSW 125. 177 p.
- Keve, A., and M.D.F. Udvardy. 1951. Increase and decrease of the breeding range of some birds in Hungary. International Ornithological Congress, Proceedings 11:468-476.
- Kuchler, A.W. 1964. Potential natural vegetation of the coterminous United States. Am. Geogr. Soc. Spec. Pub. 36. 31 p. + map.
- _____. 1977. The map of the natural vegetation of California. Pages 909-938 in M.G. Barbour and J. Major, eds. Terrestrial vegetation of California. John Wiley and Sons, New York.
- Laudenslayer, W.F., Jr., and W.E. Grenfell, Jr. 1991. A checklist of the amphibians, reptiles, birds, and mammals of California. Calif. Fish and Game 77(3):109-141.
- Leopold, A. 1949. A Sand County Almanac. Oxford University Press, New York, New York, USA. 226 p.
- Ligon, D.J. 1978. Reproductive interdependence of pinyon jays and pinyon pines. Ecol. Monographs 48(2): 111-126.
- Lindroth, C.H. 1956. Movements and changes of area at the climatic limit of terrestrial animal species. Pages 226-230 in K.G. Wingstrand, ed. Bertil Hamstrom zoological papers in honor of his 65th birthday. Zoological Institute, Lund, Sweden.
- MacArthur, R.H. 1972. Geographical ecology; patterns in the distribution of species. Harper and Row, Publishers, Inc., New York.
- Maser, C., and Z. Maser. 1988. Interactions among squirrels, mycorrhiza fungi, and coniferous forests in Oregon. Great Basin Natl. 48(3):358-369.
- _____, J.M. Trappe. and DC. Ure. 1978. Implications of small mammal mycophagy to the management of western coniferous forests. Trans. Forty-Third North American Wildlife Conf. 43:78-88.
- _____, Z. Maser, J.W. Witt, and G. Hunt. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Can. J. Zool. 64: 2086-2089.
- Mason, H.L. 1970. Report of the subcommittee on the scenic, scientific, and educational values of the natural landscape of California. Dept. Parks and Recreation report. 36 p.
- Mayer, K.E., and W.F. Laudenslayer, Jr. (eds). 1988. A guide to the wildlife habitats of California. California Department of Forestry and Fire Protection, 166 p.
- McCullough, D.R. 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor. Michigan, USA. 271 p.

- Merriam, C.H. 1890. Results of a biological survey of the San Francisco Mountain region and the desert of the Little Colorado, Arizona. *North American Fauna* 3:1-136.
- _____. 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Natl. Geogr. Mag.* 6:229-238.
- Miller, R.R. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. *Univ. Mich. Mus.* 2001. *Misc. Pub.* 42:1-80.
- _____. 1958. Origin and affinities of the freshwater fish fauna of western North America. Pages 187-222 in C.L. Hubbs, ed. *Zoogeography*. *Am. Assoc. Advancement Sci. Pub.* 51, Washington, D.C.
- Moyle, P.B. 1976. *Inland Fishes of California*. Univ. Calif. Press, Berkeley 405 p.
- _____, and J.E. Williams. 1990. Biodiversity loss in the temperate zone: decline of the native fish of California. *Cons. Biol.* 4(3):275-284.
- _____, and J.P. Ellison. 1991. A conservation-oriented classification system for the inland waters of California. *Calif. Fish and Game* 77(4):161-180.
- Munz, P.A. and D. Keck. 1949. *California plant communities*. El Aliso 2:87-105.
- Nystrom, A.J. & Co. 1966. Raised relief map of the physiography of California. Field Enterprises, Inc. Chicago, IL.
- O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. A hierarchical concept of ecosystems. *Monographs in Population Biology* 23, Princeton Univ. Press, Princeton, New Jersey. 253 p.
- Pielou, E.C. 1979. *Biogeography*. John Wiley and Sons, Inc., N.Y. 351 p.
- Raven, P.H., and D.I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61:539-673.
- Rosen, D. 1978. Vicariant patterns and historical explanations in biogeography. *Syst. Zool.* 27:159-188.
- Saithe, S.N. 1985. Evolving hierarchical systems: Their structure and representation. Columbia Univ. Press, New York. 343 p.
- Savage, J.M. 1960. Evolution of a peninsular herpetofauna. *Syst. Zool.* 9:184-212.
- _____. 1982. The enigma of Central American herpetofauna: dispersal or vicariance. *Ann. Missouri Bot. Gard.* 69:464-597.
- Schmidt, K.P. 1950. The concept of geographic range with illustrations from amphibians and reptiles. *The Texas Journal of Science* 1950:326-334.
- Schouw, F. 1823. *Grunzuge einer allgemeinen Pflanzegeographie*. Berlin. 524 p.
- Slater, P.L. 1858. On the general geographical distribution of the members of the class Aves. *Zool. J. Linn. Soc.* 2: 130-145.
- Scudday, J.F. 1977. Some recent changes in the herpetofauna of the northern Chihuahuan Desert. Pages 513-522 in R.H. Wauer and D.H. Riskind, eds. *Trans. symp. on the biological resources of the Chihuahuan Desert region*. USDI, National Park Service, Trans. and Proc. 3.
- Shelford, V.E. 1963. *The ecology of North America*. Univ. of Illinois Press, Urbana, Illinois. 610 p.
- Stebbins, R.C. 1985. *A field guide to western reptiles and amphibians*. Houghton-Mifflin Co. Boston, Mass. 336 p.
- Swainson, W. 1835. *A treatise on the geography and classification of animals*. Longman, Green, London. 367 p.
- Udvardy, M.D.F. 1969. *Dynamic zoogeography, with special reference to land animals*. Van Nostrand Reinhold Co., New York. 445 p.
- _____. 1975. A classification of the biogeographical provinces of the world. IUCN Occasional paper no. 18. International Union for conservation of nature and natural resources. Morges, Switzerland. 49 p.

- VanderWall, S.B., and R.P. Balda. 1977. Coadaptions of the Clark's nutcracker and the pinyon pine for efficient seed harvest and dispersal. *Ecol. Monogr.* 47:89-111.
- VanDevender, T.R., and J.I. Mead. 1978. Early Holocene and late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. *Copeia* 1978:464-475.
- Wallace, A.R. 1869. *The Malay Archipelago: the land of orangutan, and the bird of paradise.* Harper Co., New York. 638 p.
- Wallace, A.R. 1876. *The geographical distribution of animals.* MacMillan Co., London. 2 vols.
- _____. 1880. *Island life, or the phenomena and causes of insular faunas and floras.* MacMillan Co., London. 563 p.
- Welsh, H.H., Jr. 1976. *Ecogeographic distribution of the herpetofauna of the Sierra San Pedro Martir Region, Baja California Norte, Mexico.* M.S. Thesis, Humboldt State University, Arcata, California. 169 p.
- _____. 1988. *An ecogeographic analysis of the herpetofauna of the Sierra San Pedro Martir Region, Baja California, with a contribution to the biogeography of the Baja California herpetofauna.* *Proc. Calif. Acad. Sci.* 46(1):1-72.
- Whittaker, R.H. 1960. *Vegetation of the Siskiyou Mountains, Oregon and California.* *Ecol. Monogr.* 30:279-338.
- Whittier, T.R., R.M. Hughes, and D. P. Larsen. 1988. Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Can. J. Fish. and Aquat. Sci.* 45:1264-1278.
- Wiens, J.A. 1989. *Spatial scale in ecology.* *Functional Ecology* 1989:385-397.
- _____. J.F. Addicott, T. Case, and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. Pages 45-153 in J. Diamond and T.J. Case, eds. *Community Ecology.* Harper and Row, New York.
- Wiley, E.O. 1981. *Phylogenetics, the theory and practice of phylogenetic systematics.* Wiley-Interscience, New York. 439 p.
- Wright, H.E., and D.G. Frey. 1965. *The Quaternary of the United States.* Princeton Univ. Press, Princeton, New Jersey. 922 p.

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