PART THREE

BIOTA

ELEVEN

Biodiversity

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Introduction

If California were a country, it would be among the largest of global economies, most important innovators of popular culture, leaders of technological advancement, producers of food crops, and generators of groundbreaking science. But surrounding Hollywood and Silicon Valley is a more ancient and irreplaceable wealth: California's biodiversity. Compared to the world's countries, California ranks about seventeenth in breeding bird richness and thirty-ninth in mammal richness. Compared to the rest of the United States, California ranks first in plant and animal species richness as well as single-state endemic species richness. Although it comprises only 3% of U.S. land area, California houses more than 30% of all plant and vertebrate species in the U.S. and ranks in the top five states for richness of every group of vertebrates except freshwater fishes (Figures 11.1 and 11.2).

This remarkable biodiversity was once matched by California's indigenous cultural diversity. Before the arrival of Europeans, California was one of the most culturally diverse places on earth, with more languages than any other U.S. state and an estimated 35% of all languages spoken in what is now the U.S. and Canada (Hinton 1998). California's remarkable biodiversity and former linguistic diversity are closely linked to the state's physical diversity. It has the greatest range of latitude and elevation of any state in the continental U.S., the greatest diversity of soils in the U.S. (Amundson et al. 2003), and the greatest range of mean annual rainfall (from >255 centimeters in Humboldt County to <5 centimeters in Death Valley) and temperature (from <0°C in the high Sierras to >21°C in the southeast desert) of any state in the U.S. (NOAA 2005). The range of California's microclimates is so great that several times each year California registers both the nation's highest and lowest daily temperatures on the same day (NOAA 2005). The interaction between microclimate and soil types makes for a spectacular mosaic of habitats, resulting in high levels of beta diversity and endemism. Finally, much of California is included in one of the world's five Mediterranean-climate regions, all of which are recognized for their exceptionally high plant diversity (Cody 1986).

California's spectacular biodiversity took millions of years to evolve and assemble, but its future is uncertain. California

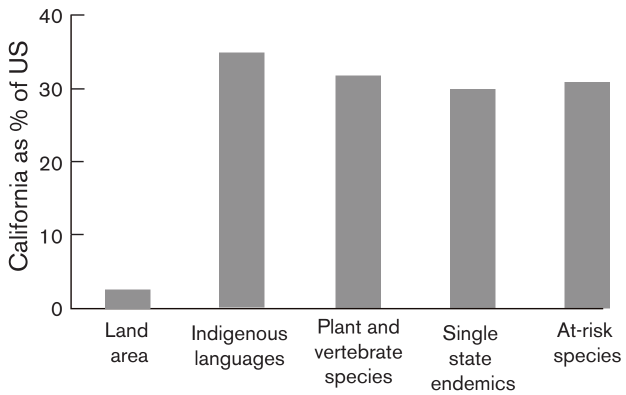

FIGURE 11.1 California's current biodiversity measures and historical cultural diversity as a percentage of U.S. totals (bars). California is the third largest state in the U.S. but ranks first in number of indigenous languages, number of plant species, number of vertebrate species, number of single state endemic species, and number of at-risk species. Sources: Biodiversity data: Parasi 2003. Language data: Hinton 1988.

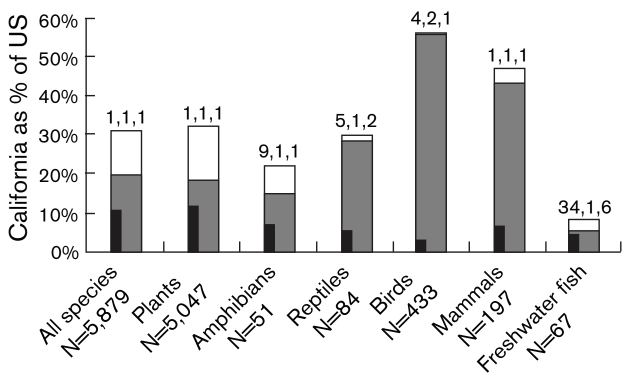

FIGURE 11.2 California's species richness as a percentage of U.S. totals for all plant and vertebrate species and by taxonomic group. Total bar is for all species in the state; the filled portion represents nonendemic species and the open portion represents state endemic species. The black line in each bar indicates percentage of federally endangered or threatened species. Numbers above the bars are national ranks for richness of species, number of endemic species, and number of threatened species, respectively. Values for freshwater fish endemism differ from those in Chapter 33, "Rivers," which reports California as having 63% endemic freshwater fishes and 19% shared with one other state. This is because we use only full species data, while the authors of Chapter 33 use data for evolutionary significant units (ESUs) and distinct population segments, some of which have yet to receive full species status. Invertebrate numbers are less well known and not included in the figure. The estimated thirty-four thousand California invertebrates are thought to make up 30% of U.S. invertebrates, ranking California first in richness. California's thirty-two endangered invertebrates make up over half of the U.S. total.

Photo on previous page: Winter storm clearing at Rancho Del Oso, Big Basin State Park, with Waddell Creek flowing near flood stage after two days of heavy rains. Visible in this one scene are redwood forest, Monterey pine forest, coastal estuary, willow/alder riparian forest, oak woodland, maritime chaparral, and coastal scrub. Photo: Ed Dickie (eddickie.com).

has more threatened species (1,822) than any other U.S. state and a higher percentage of species threatened (31%) than any other state except Hawaii (see Figure 11.1). In California, as elsewhere, the two largest threats to biodiversity are habitat loss and invasive species (responsible for 63% and 38% of California extinctions, respectively) (Table 11.1; see Chapter 13, "Biological Invasions"). Most (72%) of California's extinct species have been terrestrial mainland species, while 19% and 9% of California's extinctions have been in freshwater systems and on marine islands, respectively. However, scaled to area, freshwater systems have extinction densities six times greater than the terrestrial mainland, and marine islands have extinction densities ninety times greater than the terrestrial mainland. There have been no recorded marine extinctions in the state, and no species extinctions in California have clearly been attributed to pollution or overexploitation to date.

Fortunately, California has experienced very little permanent biodiversity loss; only about thirty-two California species, fewer than 0.1%, are known to have gone extinct in the past two hundred years (see Table 11.1). Furthermore, well-established and effective conservation actions exist that can protect the majority of the state's threatened species and assist in the successful reintroduction of extinct California species persisting outside the state. For example, the successful eradication of damaging invasive mammals from California's islands is a globally significant conservation victory that has protected many of the state's most vulnerable terrestrial species (Keitt et al. 2011; see Chapter 34, "Managed Island Ecosystems"). The successful eradication of pike (*Esox lucius*) from Lake Davis and invasive trout (Salmonidae) from many high Sierra lakes (Knapp et al. 2007) show that invasive species eradication can be an effective tool for the conservation of California's freshwater systems (see Chapter 13, "Biological Invasions"). California's network of terrestrial protected areas covers a remarkable 46% of the state (Calands 2013), and our understanding of protected area design and management for biodiversity conservation is steadily improving. Although many areas critical for the survival of threatened species remain unprotected, tools are available to identify and prioritize those lands, as are innovative approaches to protecting them (Leverington et al. 2010, Apronen et al. 2012, Bull et al. 2013, Spatz et al. 2014).

California's global leadership in the development of effective environmental protection strategies has led to significant pollution reductions in the past twenty-five years (Parrish et al. 2011). Although damaging toxins continue to be identified (e.g., atrazine, brodifacoum), a 2013 ban on lead ammunition, to help protect critically endangered species (California Assembly Bill number 711), demonstrates California's continued leadership in effective environmental regulation. Finally, the successful reintroduction of locally extinct marsh sandwort (*Arenaria paludicola*), Owens pupfish (*Cyprinodon radiosus*), Roosevelt (*Cervis canadensis roosevelti*) and tule elk (*Cervis canadensis nannodes*), bald eagles (*Haliaeetus leucocephalus*), island fox (*Urocyon littoralis*), and California condors (*Gymnogyps califonianus*) to the wild demonstrates that even the most endangered of California's species can be saved.

This chapter provides an overview of five major groups of California's biological diversity. We begin with plants and go on to the state's diversity of invertebrates, HERPETOFAUNA (reptiles and amphibians), birds, and mammals. We summarize the evolutionary diversification, biogeography, and conservation context for each taxonomic assemblage. Nonvascu-

TABLE 11.1

California species globally extinct in the past hundred years, the ecosystem in which each occurred, and the driver of each extinction

Note: H = Habitat loss; I = Invasive species; U = Unknown

					Driver[C]		
Taxa[A]	Common name	Family	Species	Ecosystem[B]	H	I	U
Fish (2)	Thicktail chub	Cyprinidae	*Gila crassicauda*	freshwater	1	1	
	Clear lake splittail	Cyprinidae	*Pogonichthys ciscoides*	freshwater	1	1	
Invertabrates (10)	Sooty crayfish	Astacidae	*Pacifastacus nigrescens*	freshwater		1	
	Pasadena freshwater shrimp	Atyidae	*Syncaris nigrescens*	freshwater	1		
	Central valley grasshopper	Acrididae	*Conozoa hyalina*	terrestrial continental	1		
	Xerces blue butterfly	Lycaenidae	*Glaucopsyche xerces*	terrestrial continental	1	1	
	Mono lake diving beetle	Dytiscidae	*Hygrotus artus*	freshwater	1		
	Antioch dunes shieldback katydid	Tettigoniidae	*Neduba extincta*	terrestrial continental	1		
	Voluntina Stonemyia fly	Tababanidae	*Stonemyia volutina*	terrestrial continental			1
	Castle lake caddis fly	Rhyacophilidae	*Rhyacophila amabilis*	freshwater		1	
	Yorba Linda weevil	Curculionidae	*Trigonoscuta yorbalindae*	terrestrial continental			1
	Fort Ross weevil	Curculionidae	*Trigonoscuta rossi*	terrestrial continental			1
Plants (20)	Bakersfield smallscale	Chenopodiaceae	*Atriplex tularensis*	terrestrial continental	1		
	Single-flowered mariposa lily	Liliaceae	*Calochortus monanthus*	terrestrial continental			1
	Point Reyes paintbrush	Orobanchaceae	*Castilleja leschkeana*	terrestrial continental			1
	Pitkin Marsh paintbrush	Orobanchaceae	*Castilleja uliginosa*	terrestrial continental			1
	Lost thistle	Asteraceae	*Cirsium praeteriens*	terrestrial continental	1		
	Hoover's cryptantha	Boraginaceae	*Cryptantha hooveri*	terrestrial continental			1
	Mariposa daisy	Asteraceae	*Erigeron mariposanus*	terrestrial continental			1
	San Nicolas Island desert-thorn	Solanaceae	*Lycium verrucosum*	terrestrial island		1	
	Mendocino bush-mallow	Malvaceae	*Malacothamnus mendocinensis*	terrestrial continental			1
	Parish's bush-mallow	Malvaceae	*Malacothamnus parishii*	terrestrial continental	1		
	Santa Cruz Island monkeyflower	Phrymaceae	*Mimulus brandegeei*	terrestrial island		1	

(continued)

TABLE 11.1 *(continued)*
Note: H = Habitat; I = Invasive; U = Unknown

Taxa[A]	Common name	Family	Species	Ecosystem[B]	Driver[C] H	I	U
	Santa Catalina Island monkeyflower	Phrymaceae	*Mimulus traskiae*	terrestrial island		1	
	Whipple's monkeyflower	Phrymaceae	*Mimulus whipplei*	terrestrial continental			1
	Merced monardella	Lamiaceae	*Monardella leucocephala*	terrestrial continental	1		
	Pringle's monardella	Lamiaceae	*Monardella pringlei*	terrestrial continental	1		
	Hairless popcorn-flower	Boraginaceae	*Plagiobothrys glaber*	terrestrial continental			1
	Mayacamas popcorn-flower	Boraginaceae	*Plagiobothrys lithocaryus*	terrestrial continental			1
	Ballona cinquefoil	Rosaceae	*Potentilla multijuga*	terrestrial continental	1		
	Cunningham Marsh cinquefoil	Rosaceae	*Potentilla uliginosa*	terrestrial continental	1		
	Parish's gooseberry	Grossulariaceae	*Ribes divaricatum*	terrestrial continental	1	1	

SOURCE: Data from International Union for the Conservation of Nature (IUCN) Redlist, Natureserve, Wikipedia, and CDFW websites (accessed April 2014).

A. Known extinction in past one hundred years/number of species in California: plants 20/5,879; invertebrates 10/34,000; fish 2/67; reptiles, amphibians, birds, and mammals = 0.

B. Ecosystems from which species have gone extinct: terrestrial continental = 23, freshwater = 6, terrestrial island = 3, marine water = 0.

C. Proximate drivers of California global extinctions: habitat destruction = 15, invasive species = 9, overexploitation and pollution = 0, unknown = 12 (multiple causes can contribute to extinction of one species).

lar plants, algae, fungi, and other taxa are not covered in this chapter, but their relative richness could also be quite high in California and linked to the state's physical diversity (e.g., Moeller et al. 2014). California's diversity of freshwater fishes is explored in detail in Chapter 33, "Rivers," rather than here. Marine diversity is described in the context of the several distinct marine ecosystem types occurring at and off the California coast (Chapter 16, "The Offshore Ecosystem"; Chapter 17, "Shallow Rocky Reefs and Kelp Forests"; Chapter 18, "Intertidal"; and Chapter 19, "Estuaries: Life on the Edge"). Finally, the importance of California's biological diversity to the functioning of California's ecosystems, including their services to its human populace, is explored in Chapter 15, "Introduction to Concepts of Biodiversity, Ecosystem Functioning, Ecosystem Services, and Natural Capital."

California has been subdivided somewhat differently for different taxa in ways that reflect both the state of knowledge and the characteristic scales and patterns of diversity and turnover in the state. The taxonomic sections that follow in this chapter describe the biogeographic distribution of species following conventions most common for that taxon. We elected this approach rather than a common ecoregional subdivision across all sections so that the reader can easily move between this volume and taxon-specific resources organized according to taxon-specific conventions. Thus the six regions used here to describe invertebrates differ slightly from the five ecoregions around which mammal biogeography is organized, and so on. Furthermore, the number of species and their relationships to each other change over time. Molecular techniques make it possible to more easily and clearly separate subspecies into full species and to identify cryptic species that are morphologically similar but genetically distinct. Molecular techniques have also made it possible to more accurately reconstruct evolutionary relationships and moved taxonomy into the framework of phylogenetic systematics. For plants, for example, the newest flora for California—*The Jepson Manual*, second edition (Baldwin et al. 2012)—has followed this framework and radically changed Californian plant taxonomy. Species definitions have changed as well, for a variety of reasons, so that even when old names persist they may have new meanings. For example, the annual herb hillside collinsia (*Collinsia sparsiflora* var. *collina*) is now a Californian endemic because its Oregonian relatives are no longer considered to belong to the same species.

Flora

California has long been recognized as the botanically richest part of the United States, as well as one of the world's most significant regions for plant diversity. Together with its sheer numbers of plant species and varieties, California is outstanding for its plant endemism—its wealth of species and varieties found nowhere else. Indeed, the majority of the state—everything but its deserts—is considered, together with small parts of adjoining Oregon and Baja California, a globally unique Floristic Province united by the shared evolutionary histories of its plant lineages. Many of the plant lineages centered in California appear to be relatively young and rapidly evolving, and since the advent of modern evolutionary biology in the mid-twentieth century, these lineages have attracted considerable attention from biosystematists interested in plant adaptation and speciation. California has thus been considered a "model system" for studying plant diversity.

In many ways, however, our understanding remains far from complete. California's large size and its rugged, climatically and geologically diverse landscape might seem obvious explanations for its botanical richness. Curiously, though, many of the diverse Californian plant lineages show only modest ecological differentiation, suggesting that something besides the state's variety of climates and soils must have given rise to their diversification. Interestingly, California is not nearly as rich in endemic animal species, except in a few groups notable for their low mobility and (again) lack of strong ecological or morphological divergence. Today, California's climate most resembles the other four Mediterranean-climate regions, with distinct wet winters and long dry summers and high interannual variability in rainfall (Cody and Mooney 1978, Cowling et al. 1996 see Chapter 2, "Climate"). Recent molecular and paleontological evidence suggests that the origins of high plant diversity arose before the onset of the modern Mediterranean-climatic pattern, 1.8 million years ago.

In the section we review plant species richness and endemism in California, including comparisons of the state with other states, the state with the Floristic Province, and the Floristic Province with the other Mediterranean-climate regions of the world. We briefly explore patterns of plant diversity within California, which are provided in more detail in Chapter 12, "Vegetation," and we review old and new evidence on the causes of California's plant diversity.

Evolutionary Diversification

Overall, 4,266 full species of plants are now considered native to the state of California, including approximately 1,307 that are endemic to the state (Baldwin et al. 2012) (see Figure 11.1). In the past, splitting of taxa was more common and numbers were thus higher (e.g., Raven and Axelrod 1978). Because the new revisions are so recent, this chapter will often draw on older figures (e.g., see Figures 11.1 and 11.2), except where noted. We are unaware of any cases in which the broad patterns of plant diversity in California have been altered by these recent taxonomic changes. In a comprehensive assessment of plant and animal diversity within the United States (that did not incorporate more recent taxonomic revisions and so has slightly different numbers than above) no other state approached California's botanical richness, with an estimated 4,839 native plant species, of which 1,416 or 30% are endemic to the state (Stein et al. 2000; see Figure 11.2). The next highest states are Texas with 4,458 species, of which 251 (6%) are endemic; Florida with 2,995 species, of which 155 (5%) are endemic; and Hawaii with 1,207 species, of which, unsurprisingly given its isolation as an ocean island, 1,048 (87%) are endemic.

Californian endemism is also high in freshwater fish (29%) and amphibians (34%) as well as in a few animal families: for example, the often flightless Acridid grasshoppers (51%), nest-building Megachilid bees (53%), and tiny Phalangogid harvestmen (60%) (Harrison 2013). However, overall endemism rates are much lower in most major group of animals (mammals, 9%; birds, 0.5%; reptiles, 6%; insects, an estimated 15%) (see Figure 11.2; Stein et al. 2000). These numbers do not change greatly if endemism to the Floristic Province is considered. In a comprehensive new analysis, Burge et al. (2016) listed 1,884 (33%) endemic plant species out of 5,782 total native plant species in the California Floristic Province (CFP), as compared with 1,736 CFP endemics among the 5,332 total plant species in the state of California. Thus, while the state's deserts add numerous species to the flora, nearly all of these are also found outside the state. These authors also found that southwestern Oregon added 90 total species and 40 endemics to the Province, while northwestern Baja added 227 total species and 107 endemics. An analysis taking into account the recent taxonomic changes (Baldwin et al. 2012) revised the earlier estimates downward slightly to approximately 4,500 total species of native plants including 1,931 (42%) endemics in the Floristic Province. Of these, now higher totals are contributed by Baja California of 969 plant species including 338 endemics, and by Oregon of 220 total species including 14 endemics (Harrison 2013).

The farewell-to-spring genus (*Clarkia*) and the monkey-flowers (*Mimulus*) illustrate radiations that took place in California in response to multiple, interacting forces. Clarkias radiated in the time of pre-Mediterranean climate and include forty-two species, of which thirty-six are found only in the California Floristic Province. Evolutionary studies on narrowly endemic *Clarkia* species initially focused on the role of nonadaptive changes, such as random chromosomal rearrangements, that could occur in small populations and lead them to become new species. Newer studies suggest that not only chromosomal rearrangements but also natural selection, spatial isolation, and breeding system changes all play roles whose relative importance is not yet clear (Gottlieb 2003). The monkey-flower genus is one of the most ecologically diverse groups of Californian neoendemics, with species occupying not only Mediterranean but also desert and alpine climates, and species restricted to wetlands, serpentine, dunes, peat bogs, geyser margins, and other unusual substrates. Diversity in flower color and shape, seasonality, growth form, and breeding systems is also high. Ecological speciation plays an undeniable role in *Mimulus*, and the genus is a model system for examining how environmental challenges (drought stress, extreme soils) interact with genetic mechanisms (e.g., chromosome duplication, allelic incompatibility, linkage structure) and reproductive strategies (e.g., seasonality, pollinators, mating system) to facilitate speciation (Beardsley et al. 2004, Hall et al. 2010, Wu et al. 2007).

Biogeography

Biogeographers divide the world based not on current climate, vegetation, or species, but rather on the shared ancestry and biogeographic history that are believed to unite the plant lineages within a region; the most widely used system recognizes Floristic Kingdoms, Regions, and Provinces (e.g., Takhtajan 1986). The California Floristic Province broadly coincides with where Mediterranean-type climate occurs in North America. It extends from south-central Oregon through the nondesert parts of California to northwestern Baja California

(Raven and Axelrod 1978, Conservation International 2011, Baldwin et al. 2012; see Figure 11.1).

All five of the world's Mediterranean-climate regions fall among the planet's top twenty-five hotspots of diversity and endangerment, defined by having >1,500 endemic plant species as well as >75% loss of native vegetation (Myers et al. 2000). Strikingly, these Mediterranean-climate regions are almost the only such hotspots outside of the tropics, as well as among the few not similarly rich in animal endemism. After adjusting for differences in area, by far the richest flora among the Mediterranean-climate regions of the world belongs to the Cape region of South Africa, which is so evolutionarily distinctive that it is considered its own Floristic Kingdom—the top level in the biogeographic classification hierarchy. Next is southwestern Australia, followed by the Mediterranean Basin; California lies fourth, ahead of only Central Chile (Cowling et al. 1996, Harrison 2013). These patterns are almost exactly opposite of what might be predicted based on topographic and geologic heterogeneity.

Patterns of Plant Diversity and Endemism in California

In a now classic analysis, G. Ledyard Stebbins and Jack Major (1965) asked what gave rise to California's botanical uniqueness by determining where in the state the greatest numbers of endemics (species found nowhere else) were found. These authors pioneered the distinction between "paleoendemics" (taxonomically isolated species thought to belong to ancient lineages that are RE TS of past wetter climates) and "neoendemics" (species with many close relatives nearby, thought to belong to young and rapidly evolving lineages). Paleoendemics include redwoods (*Sequoia sempervirens*), giant sequoias (*Sequoiadendron giganteum*), and many other trees, shrubs, and herbs with their closest relatives often occurring in the southeastern U.S. or temperate Asian forests. These occur mainly in the wetter parts of the state, including the Klamath and North Coast regions and the coastal fog belt. Neoendemics include the species-rich plant genera most strongly centered in California and most often studied by those interested in plant speciation—shrubs such as manzanitas (*Arctostaphylos*) and California-lilac (*Ceanothus*) and herbs such as *Madia*, *Clarkia*, *Limnanthes*, and *Navarretia*. Neoendemics are most common in the Mediterranean-type climates of the central Coast Ranges, mid-elevation Sierran foothills, and southern Californian coast, and least abundant in the deserts and Central Valley. Rapid plant evolution, these authors concluded, was promoted by a fluctuating climate and a rugged landscape where short distances separated dramatically different plant habitats.

Recent, comprehensive analyses also find that the Coast Ranges are the richest part of the state for endemic plants (Thorne et al. 2009, Kraft et al. 2010). The highest concentrations of neoendemics are found in the Central Coast (particularly the San Francisco Bay area), the southern part of the North Coast region, and the Sierra Nevadan foothills. The neoendemics with the smallest ranges are found at low elevations in the Coast Ranges and at higher elevations in the Sierra and Transverse Ranges. The youngest neoendemics, as judged by molecular evidence, occur in the deserts. However, neither the means nor the heterogeneity in topography or climate variables—the drivers of plant diversification hypothesized by Stebbins and Major—are good predictors of endemic diversity (Kraft et al. 2010).

Clearly, new evidence about California's floristic history continues to come from not only molecular genetics but also paleobotany; there has been a steady growth in the quality of evidence from traditional macrofossils, fossil pollen in marine sediment cores, radiometric dating techniques, and global and regional climate reconstructions using isotope ratios. In particular, the details of how California's vegetation changed during Pleistocene glacial-interglacial cycles are now much better known (Millar 1996; see Chapter 8, "Ecosystems Past: Vegetation Prehistory"). In striking contrast to animals, the timing of genetic divergence in plants appears inconsistent both among lineages and with the timing of emergence of montane and water barriers that could provide geographic isolation leading to speciation (Calsbeek et al. 2003). For example, the well-studied tarweed lineage (Asteraceae, Madiinae) contains many neoendemics, mostly summer-flowering annuals with sticky foliage. Relationships among the fifteen species of *Calycadenia*, as well as among the six species in one subgroup of *Layia*, indicate gradual speciation in response to geographic isolation. But the patterns in other *Layia*, as well as within the genus *Holocarpha*, are more suggestive of ecological speciation, in which adaptation to a novel environment leads to isolation from the ancestor. Serpentine-restricted *Layia discoidea* is closely related to, but highly differentiated from, widespread *L. glandulosa*; the sand dune endemic *L. carnosa* is likewise differentiated from its widespread ancestor *L. gaillardiodes*.

Serpentine is the most distinctive and widespread special substrate for plants in California. Derived from oceanic crustal rocks, serpentine is excessively rich in magnesium and poor in calcium and nutrients compared with most continental rocks and soils. Long, discontinuous strings of serpentine outcrops wind from the Klamath Mountains down through the Coast Ranges and along the Sierran foothills. About two hundred plant species are confined to serpentine in California, the majority in the Klamath-Siskiyou and North Coast Ranges (Safford et al. 2005). Californian serpentine plants have often served as model subjects for studying plant ecology, adaptation, and speciation (Huenneke et al. 1990, Brady et al. 2005, Kay et al. 2011, O'Dell and Rajakaruna 2011). The jewelflower (*Streptanthus*), dwarf wild flax (*Hesperolinon*), and wild onion (*Allium*) genera are among those richest in serpentine endemics in California. Elsewhere in the world, rich floras in serpentine are found in Cuba, New Caledonia, southeast Asia, and the eastern Mediterranean region. Other edaphic (soil) environments that support unique plant species and varieties in California (albeit to a lesser extent than serpentine) are gabbro in the Sierra Nevadan foothills and Peninsular Ranges, limestone in the Klamath-Siskiyou region and central Sierra Nevada, gypsum and alkali soils in the deserts, and granite talus in the Sierras.

Vernal pools are another significant habitat for Californian endemic plants (as well as their animal associates). These winter-wet, summer-dry wetlands are found in flat or gentle terrain where drainage is impeded by bedrock, fine clays, or chemical precipitates. More than one hundred plant species and varieties are strongly associated with vernal pools, and over thirty of these are strict vernal pool endemics. Some of the typical vernal pool genera, like calicoflowers (*Downingia*), meadowfoam (*Limnanthes*), goldfields (*Lasthenia*), and stickyseeds (*Blennosperma*), are pollinated by specialized solitary bees in the family Andrenidae. Since the vernal pool habitat is so closely tied to the young Mediterranean climate, the evolutionary radiation of these genera is thought to be relatively recent (Meyers et al. 2010).

Conservation Context

Although California has an estimated 612 globally threatened plant species, only 20 California plant species are globally extinct (CNPS 2014). Causes of extinction were attributed to 12 species (8 land conversion and 4 invasive species). Three of the 19 species were Channel Island endemics, although the Channel Islands make up only 0.2% of California land area. California and the larger California Floristic Province have benefited from a number of plant conservation successes. For example, the Eureka Valley evening primrose (*Oenothera avita eurekensis*) and the Eureka dune grass (*Swallenia alexandrae*) were listed as endangered species in the 1970s due to habitat destruction caused by off-road vehicle recreation and camping on and around their dune habitat. Protection of the dunes first by the Bureau of Land Management and later by the Death Valley National Park allowed both species to recover, and they were proposed for de-listing in 2014.

Another spectacular example is the recovery of native flora on Guadalupe Island, Mexico (part of the California Floristic Province), after invasive goats were eradicated. Prior to goat eradication, there were fewer than two hundred individuals of the Guadalupe Island Pines (*Pinus radiata* var. *binata*), fewer than two thousand Guadalupe Island Cypress (*Cupressus guadalupensis guadalupensis*), and fewer than one thousand Guadalupe Island palms (*Brahea edulis*). More significant than the low numbers was the complete absence of seedlings. Within just a few years of goat eradiation, the number of all three species increased tenfold as, for the first time in over one hundred years, all seedlings weren't consumed by goats. Moreover, seven endemic species thought to be extinct were rediscovered: the western tansymustard (*Descurainia pinnata*), coyote tobacco (*Nicotiana attenuata*), dense false gilia (*Allophyllum gilioides*), Guadalupe savroy (*Satureja palmeri*), redflower currant (*Ribes sanguineum*), buckbush (*Ceanothus crassifolius*), and common woolly sunflower (*Eriophyllum lanatum* var. *grandiflorum*) (Aguirre-Muñoz et al. 2011). The hard and thoughtful work of the California Native Plant Society has laid the groundwork for many more plant conservation successes.

Invertebrates

California has an estimated thirty thousand insect species, the focus of this section, and approximately four thousand species of noninsect invertebrates, nearly 30% of all invertebrate species in the United States and Canada combined (Powell and Hogue 1980, Ballmer 1995, Carlton 2007). Over 95% of all described animal species and over 80% of all species on Earth are invertebrates, 85% to 90% of those invertebrates are insects, and many more are yet to be discovered (Price 1997, Cardoso et al. 2011) (Figure 11.3). Beetles alone make up 25% of all global biodiversity and comprise ten times more species than all vertebrates combined (Cardoso et al. 2011). California's diverse ecosystems, from snow-capped mountains to arid deserts to kelp forests, each harbor a unique set of invertebrates. California contains thirty-two listed threatened and endangered invertebrate species, which make up more than half of the federally listed insects in the United States (Connor et al. 2002). Ten California invertebrate species are known to be globally extinct, but knowledge gaps almost certainly make this an underestimate.

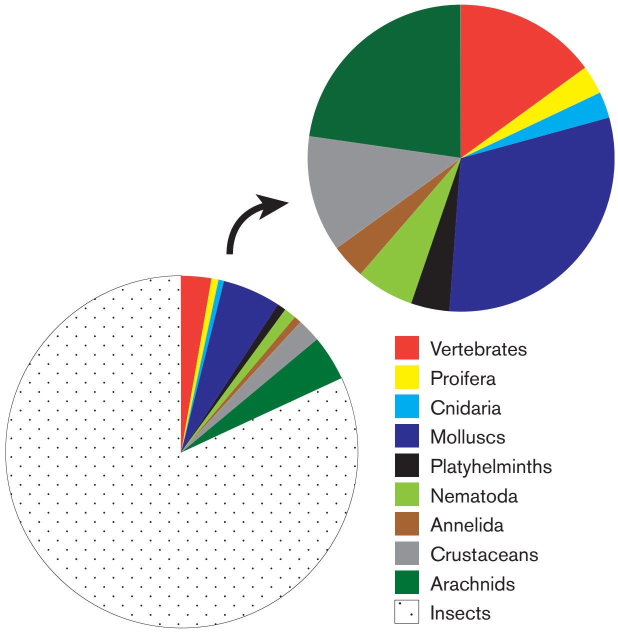

FIGURE 11.3 Invertebrates make up 95% of all animals globally, and insects are 85–90% of all invertebrates.

Evolutionary Diversification

Invertebrates are found in every ecological niche imaginable in California: on land, in freshwater, in the sea, and in between. At each location different invertebrates play roles of scavengers, predators, herbivores, detritivores, and parasites. While some are generalists and opportunists, other species are strict specialists that have evolved to consume one particular host or prey item. Invertebrate diversity stems from the variety of invertebrate forms and functions as well as habitat specializations within ecosystems, allowing them to exploit all available microhabitats. For example, nearly 50% of insects are herbivores, and a single plant can host a variety of species that feed on roots, stems, trunks, flowers, phloem, fruits, and leaves—both externally and internally—such as leaf miners, gall-makers, and root borers (Ballmer 1995).

This fine division of niches and correspondingly high diversity are possible because of several features of invertebrates. Most invertebrates are size-limited for physiological reasons; for instance, insect growth is limited by their tracheal method of gas exchange (Gullan and Cranston 2010). In addition, invertebrates have both complex sensory systems and faster generation times than vertebrates, allowing them to quickly adapt to heterogeneous habitats (Gullan and Cranston 2010). Finally, because of their high levels of diversity and niche specialization, invertebrates exhibit intricate relationships with other species that act to further diversify species through coevolution. For example, an adaptive radiation occurred in one of the largest insect superfamilies, the Scarabaeoidea (scarab beetles), following the radiation of angiosperm plants fifty million years ago. This radiation resulted in one of the largest phytophagous (plant-eating) Scarab subfamilies, the Melolonthinae (June beetles), comprised of ten thousand species (Price 1997).

California's high invertebrate diversity relative to the rest of the U.S. is linked to the climatic and topographic heterogeneity of the state. The combination of California's long dry

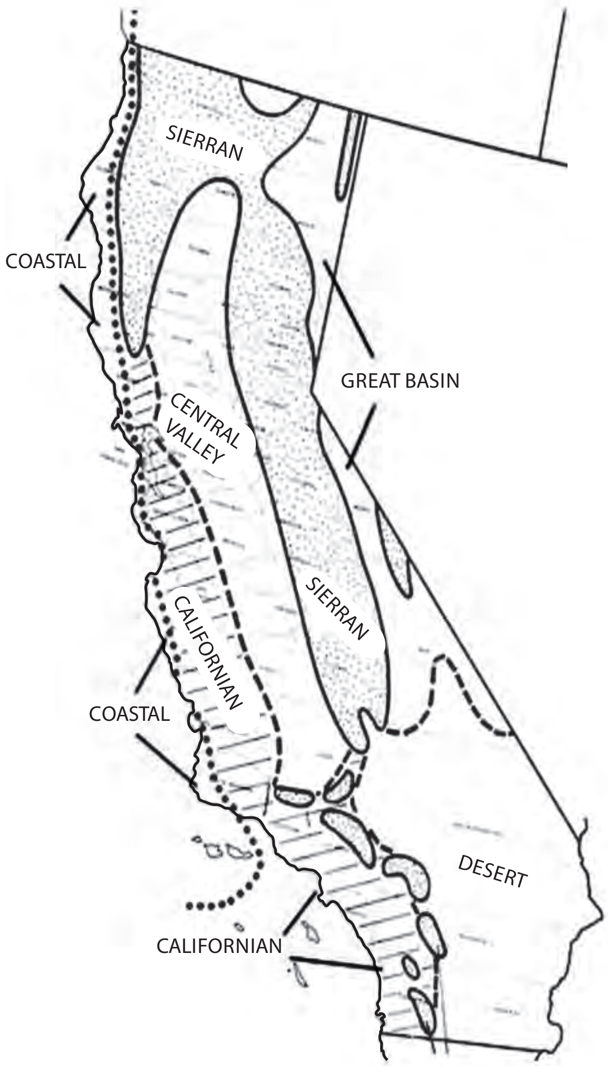

FIGURE 11.4 The six invertebrate faunal zones in California. Source: Powell and Hogue 1980.

season and varying topography creates a strong selective force on plants and animals, including invertebrates. California's climate has fluctuated from subtropical to glacial over geological time (Ballmer 1995), and as the climate fluctuated, invertebrates repeatedly either adapted, survived in refugia, or became extinct, resulting in local adaptations and in the great beta-diversity seen today throughout California.

As a result of California's long dry season from May to October, most invertebrate activity occurs in the wet winter and spring during the annual period of plant productivity (Powell and Hogue 1980). This pattern deviates from most states, where the majority of invertebrate activity occurs during the warm, humid summers. However, to grasp the entirety of California's invertebrate diversity, all seasons and locations must be examined. For example, insect activity in the Sierras peaks in the foothills in May, at intermediate elevations in June, and at the highest elevations in July and August (Powell and Hogue 1980). For insects, Powell and Hogue (1980) delineated six major faunal divisions in California: Great Basin, Sierran, Desert, Central Valley, Coastal, and Californian (Figure 11.4). The last of these contains the highest number of endemic species. These six major areas can also be used to describe overall invertebrate diversity. For each of these major invertebrate faunal divisions in the state, we highlight selected invertebrate diversity, species interactions, and conservation issues. We also describe geographic concentrations and distinct assemblages of invertebrate diversity for each, and introduce key controllers of these patterns.

Biogeography

The Great Basin high desert reaches into California at the eastern and northeastern edge of the state and is composed mainly of sagebrush scrub. Although the Great Basin is species-rich, it contains almost no endemic California insects (Powell and Hogue 1980). However, the California Great Basin is home to Mono Lake, a unique and productive ecosystem supported by halophile invertebrates (see Chapter 32, "Lakes"). Mono Lake is extremely alkaline because of high evaporation and no ocean outflow. Thus Mono Lake is tolerable only to a few species of algae and algal feeders, including the endemic brine shrimp (*Artemia monica*) and alkali flies (*Ephydra hians*). The brine shrimp and alkali flies thrive in Mono Lake due to lack of aquatic predators and competition, and the two species form the basis of the food chain for millions of migratory birds each year. Unfortunately, both upstream water diversion and climate change threatened this unique ecosystem (Ficklin et al. 2013). Water diversion and increased evaporation due to rises in temperatures raises the salinity of Mono Lake to levels lethal to even the endemic brine shrimp (Dana and Lenz 1986) and alkali fly (Herbst et al. 1988), in turn threatening the birds that depend on them (Rubega and Inouye 1994). The lake was also home to the now-extinct Mono Lake diving beetle (*Hygrotus artus*).

The standing and running waters of the Sierra Nevada support a rich diversity of dragon and damselflies (Odonates), stoneflies (Plecoptera), mayflies (Ephemeroptera), and caddisflies (Trichoptera). The alpine meadows of the Sierras are also home to numerous butterfly species. However, in the conifer forests of the Sierra Nevada, fire is a primary controller of arthropod biodiversity. In particular, fire and fire management greatly impacts leaf litter arthropods, which are responsible for forest health via nutrient cycling in Sierra mixed-conifer forests (Apigian et al. 2006). Studies investigating the changes in litter-dwelling arthropods after fire found that while the abundance of arthropods was negatively affected, species richness and diversity increased—by thirty-two species in one case—as a result of increased postfire habitat heterogeneity (Apigian et al. 2006, Ferrenberg et al. 2006). Species that increased after fire included bark and other wood-boring beetles, saproxylic (feeding on dead or decaying wood) insects, phytophagous (plant-eating) insects, and parasitic arthropods (ticks and parasitic insects). Thus frequent, low-intensity fires, common in the Sierras prior to European settlement, likely acted to sustain Sierra invertebrate diversity (Apigian et al. 2006, Ferrenberg et al. 2006). The role of large, high-intensity fires, such as the 2013 Rim Fire in the Yosemite National Park vicinity, could be less beneficial to insect diversity, as this type of fire has been facilitated by fire suppression and climate change (see Chapter 3, "Fire as an Ecosystem Process").

California's Mojave and Colorado Deserts are thriving with invertebrate life and host a prime example of the effects of coevolutionary forces on invertebrate diversity: yucca moths and their hosts. Yucca moths include several species of the

Lepidopteran family Prodoxidae that are obligate pollinators and herbivores of Yucca plants (*Yucca* spp.). Yucca moths have evolved specialized mouthparts that allow them to insert pollen directly into Yucca flowers and their own eggs directly onto the plant's ovary (Pellmyr et al. 1996). When the Yucca moth larvae hatch, they eat only some of the developing Yucca seeds, leaving the rest to propagate their host plant and continue the cycle. This has led to the radiation of at least twenty species of Yucca moths and an equal number of Yucca species (Pellmyr 2003).

California deserts are also well known for their charismatic species of Arachnids that have adapted to long, hot desert days by burrowing in the cool ground. For example, the Coachella Valley is home to the Giant Red velvet mites (*Dinothrombium pandorae*), which at 1 centimeter are orders of magnitude larger than average mites. Giant mites burrow in the desert sand to emerge only after rains that bring their target prey, swarming termites (Tevis and Newell 1962). The California deserts are also home to numerous species of scorpions, tarantulas, and the ever-strange Solifugae, or wind scorpion. California is home to sixteen hundred species of native bees, about half the number of native bees in all of the United States and Canada (Frankie et al. 2009). The exotic European honey bee (*Apis mellifera*) is by far the largest pollinator in in the U.S., with estimated value of $15 billion annually, most of which is generated in California and especially in its Central Valley; for example, California almond pollination by European honey bees alone is estimated to be worth $2 billion annually (Ratnieks and Carreck 2010). However, if the European honey bee continues to decline due to colony collapse disorder, the native bees that they outcompete are expected to take over some pollination services (Goulson 2003). Native bee pollination will only be successful with restoration and protection of natural areas in and surrounding agricultural fields, as native bees require these areas for nesting sites and floral resources (Kremen et al. 2004). For example, Kremen et al. (2002) found that native bees could provide full pollination services for watermelon when provided natural habitat.

California coastal terrestrial systems are teeming with invertebrate life, from the banana slugs under the fog-draped coastal redwoods (*Sequoia sempervirens*) to the migrating Monarch butterflies (*Danaus plexippus*) in coastal woodlands. The San Francisco Bay Area, which compromises nine counties surrounding the San Francisco and San Pablo Bays, has a topographic, climatic, edaphic (soil type), and geologic heterogeneity unparalleled in any other urban area. This diversity of habitats has led to the discovery of nearly four thousand insect species per county, including 142 butterfly species, with a high degree of endemism (Connor et al. 2002). This extraordinary habitat heterogeneity and corresponding great insect diversity has, in the context of over a century of rapid urbanization, spelled disaster for many species and has led to many species threatened with extinction (Connor et al. 2002). The urbanization of the Bay Area resulted in the first recorded extinction of an insect in the United States, the Satyr butterfly (*Cercyonis sthenele sthenele*), during the nineteenth century. As urbanization increased, sand dunes that once dominated the San Francisco Bay were destroyed and two more butterflies, the Xerces blue (*Glaucopsyche xerces*) and the Pheres blue (*Icaricia icariodes pheres*), went extinct. The remaining dune habitat at Antioch Dunes was once home to the extinct Antioch Dunes shieldback katydid (*Neduba extincta*) and is now home to another critically endangered butterfly, the Lange's metalmark (*Apodemia mormo langei*).

Conservation Context

Invertebrates perform myriad ecosystem functions, from decomposition and soil aeration to pollination and seed dispersal, that are essential in the provisioning of regulatory, supportive, and cultural ecosystem services worth billions of dollars (McIntyre 2000, Losey and Vaughan 2006, Cardoso et al. 2011). As research continues to examine human dependence on ecosystem services and the vital roles of invertebrate diversity in performing those services, invertebrate conservation can no longer be ignored (Cardoso et al. 2011, Cardinale et al. 2012). At present, thirty-two California invertebrates are on the state threatened and endangered species list due to land conversion, invasive species, and overexploitation (CDFW 2013). Of the thirty-two invertebrates listed by the state of California (CDFW 2013), three (9%) are gastropods, eight (25%) are crustaceans, and twenty-one (66%) are insects. The listed insects include fourteen butterflies, one moth, four beetles, one fly, and one grasshopper; the crustaceans include seven shrimp (five fairy shrimp) and one crayfish; and the gastropods include two species of snails and the white abalone. Invertebrate habitats are often fine-grained such that local scale, within-region characteristics are central to population persistence (e.g., Thomas et al. 2001, Fleishman et al. 2002, Collinge et al. 2003, Poyry et al. 2009, Beyer and Schultz 2010). Conservation of threatened invertebrates is greatly facilitated by understanding their habitat requirements so suitable habitat can be protected or restored (New 2007).

The endangered Ohlone tiger beetle (*Cicindela ohlone*) (Figure 11.5) is a prime example of the threats to and status of endangered insects in California. The Ohlone tiger beetle is endemic to the coastal prairies of Santa Cruz County, where it is found in five remnant patches. Adult tiger beetles are visual predators on small arthropods and require bare ground to both forage and oviposit. Larvae are sit-and-wait predators that generally require bare ground to capture prey from the mouths of their burrows in the soil (Pearson and Vogler 2001). The California coastal prairie evolved with disturbances that created conditions for bare ground, such as natural and anthropogenic fire by Native Americans, grazing and soil disturbance by native ungulates and burrowing animals, and periodic drought (Anderson 2007, Wigand et al. 2007). After European settlement, grazing regimes changed, time between fires increased, and annual exotic plants replaced perennial bunch grasses, decreasing bare ground (Hayes and Holl 2003, D'Antonio et al. 2007). Today, the remaining Ohlone tiger beetle populations depend on habitat protection and creation via grazing and vegetation removal (Cornelisse et al. 2013) and on managed mountain biking and hiking trails (Cornelisse and Duane 2013) to maintain bare ground habitat. Some Ohlone tiger beetle habitat is managed because landowners hold Incidental Take Permits under the federal Endangered Species Act (ESA) that subject them to Habitat Conservation Plans, in which they agreed to maintain habitat as mitigation for destruction elsewhere.

California is home to the rare butterflies that sparked the original Habitat Conservation Plan provision in the ESA: the Mission blue (*Icaricia icariodes missionensis*), Callippe silverspot (*Speyeria callippe callippe*), Edith's Bay checkerspot (*Euphydryas editha bayensis*), and San Bruno elfin (*Callophrys mossii bayensis*) (Beatley 1994). Today, California is home to numerous Habitat Conservation Plans for threatened invertebrates the provide habitat protections and management. Hab-

FIGURE 11.5 Ohlone tiger beetle (*Cicindela ohlone*). Photo: John Hafernik.

itat protection is key to both conservation of native pollinators and to natural enemies that provide biological control of herbivorous arthropods (Pickett and Bugg 1998). Conservation biological control that includes habitat protection and management is a key component of sustainable agroecosystems and maintenance of invertebrate biodiversity in California. For example, natural areas including hedgerows, roadside vegetation, and riparian corridors can provide nesting sites and overwintering sites for beneficial arthropods, such as parasitic wasps and predacious beetles, which can then control outbreaks of herbivores in agricultural fields (Ballmer 1995, Pickett and Bugg 1998).

Although in this chapter we focus on terrestrial biodiversity, habitat protections for rare species, including invertebrates, are not limited to the land. One of the most critically endangered invertebrate species is found in the ocean off the southern California coast: the white abalone (*Haliotis sorenseni*). The white abalone was the first marine invertebrate listed under the federal Endangered Species Act after years of overexploitation. The white abalone reproduces by broadcast spawning, and despite the federal ban on white abalone fishing in 1996, historical exploitation reduced adult densities to below those required to effectively reproduce (Hobday et al. 2001). Conservation efforts have been under way since 2001 and now include the White Abalone Restoration Consortium of scientists, fisherman, NGOs, and agencies that have developed a four-step restoration plan that includes surveying current populations, collecting brood stock, captive breeding, and establishing refugia of self-sustaining brood stocks in the wild—all in hopes to bring back the white abalone from the brink of extinction (NMFS 2008) (see Chapter 35, "Marine Fisheries").

California's expanding human population will cause further habitat loss (see Chapter 5, "Population and Land Use"). With climate change further altering species' physical and ecological habitats, protecting invertebrate species and their ecosystem functions will require comprehensive science, adaptive management, and a committed public. The Ohlone tiger beetle and white abalone are examples of how California contains the scientific and regulatory capacity and the political will needed to protect even the most critically endangered invertebrates.

Reptiles and Amphibians

As of October 2013, California harbors 171 species of reptiles and amphibians of which forty-seven (27%) are endemic: twenty-eight species of frogs of which three are endemic to the state, forty-two salamander species of which twenty-nine are endemic, forty-eight lizard species of which twelve are endemic, forty-four snake species of which only two are endemic, and nine turtle species (marine, freshwater, or terrestrial) of which only one is endemic. These calculations are date-stamped because four new species of legless lizards were added in September 2013. In addition, not all of the widespread reptile and amphibian species have undergone thorough diversity assessments with modern molecular methods, so their recognized diversity could increase, even in the well-studied herpetofaunal hotspot of the California Biogeographic Province. Here we discuss the biogeographic origins of this herpetofauna, factors influencing endemism, and their current conservation status and future prospects in the face of urbanization, climate warming, and other threats.

Evolutionary Diversification

California's extraordinary amphibian and reptile diversity is concentrated in the south (Figure 11.6), largely at the meeting points of the Sonoran and Mojave Deserts. This diversity is the by-product of the barrier formed by the Transverse Ranges, which have bisected southern Californian herpetofauna into those with northern affinities and those with southern affinities, though other breakpoints can be found to the north in the Sierras (Calsbeek et al. 2003). The origins of California's herpetological diversity can be traced directly to very old geological processes that gave rise to the entire state and, for some taxa, to even older global tectonic processes. Because the biogeography of salamander diversity is by far

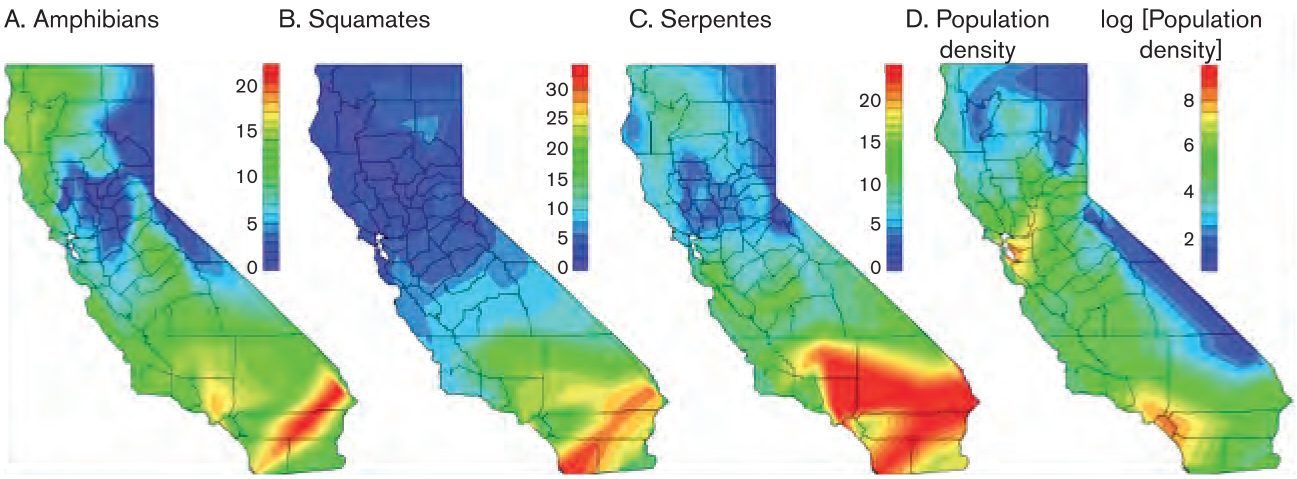

FIGURE 11.6 Plots of Amphibian, Squamates, and Serpentes species diversity and of human population density, estimated by county. Biodiversity for each group is based on museum records in Herpnet.org, which were summed by species and by county and then plotted (using the *Akima* package in [R]) by the average county location of those that were georeferenced in the Herpnet records. County population records are from the most recent census.

the best understood, we begin with the history of processes important in their speciation.

Biogeography

During the Eocene, California was underwater, with the first of the accreted TERRANES having slammed into the coast during the mid-Mesozoic and created the northern Siskiyou Mountain Range (Ernst et al. 2008). Thereafter, during the Oligocene and Miocene, more terranes accreted onto California's evolving coastline further to the south (McWilliams and Howell 1982), giving rise to the present-day Coast Range. During much of the mid-Miocene the Coast Ranges sat offshore like islands, with an inland sea in the place of the modern-day Central Valley. These offshore islands gave rise to considerable biodiversity in modern P ETHODONT D salamander lineages, as the lineages became isolated and evolved into distinct species.

During this Cenozoic Era of island biogeography, many radiations of endemic species in the family Plenthodontidae originated in situ in California, with at least seventeen California endemics in the genus *Batrachoseps*. Thus, more than half of all of California's endemic herpetofauna are in this single family of salamander. Thereafter, the Central Valley was uplifted as dry land. A major geographic break in herpetological diversity is present at the Pajaro River (Jockusch and Wake 2002, Kuchta et al. 2009), the ancient outlet of a marine embayment in the Central Valley two million years ago. Eventually this marine embayment drained, but an enormous freshwater lake still drained out of the Central Valley from this same outlet until it was rerouted to the current drainage of the Sacramento River in more geologically recent times (six hundred thousand years ago). The spectacular number of California salamanders, 70% of which are endemic, is in large part due to these plethodontid speciations in the context of these geologic events. A lack of aquatic larval stages (their eggs develop directly on land into crawl-away juveniles) also contributes to their endemism: they have often become restricted to isolated locations due to both plate tectonic activity and mountain building along the western margin of the North American plate (Jockusch and Wake 2002). Many endemic *Batrachoseps* salamanders are found as relicts at desert oases and seeps in and around the Saline and Death Valleys and other Desert Ranges, separated from other evolving lineages by a drying climate since the Pleistocene.

Other plethodontid groups have a more complex global biogeographic history. All plethodontid salamanders originated in the Jurassic in the Appalachians and then moved west to California and also to Asia, where the genus *Hydromantes* originated. Ancestors of *Hydromantes* then subsequently spread back to North America and over to Europe (Vieites et al. 2007). This reinvasion of *Hydromantes* from Asia to North America occurred over the Eocene Bering Strait land bridge, during the warmest time in the last sixty-five million years, when the Arctic supported luxuriant temperate forests. Three species of *Hydromantes* are endemic to California and restricted to the high elevations of the Sierra Nevada Range.

Another radiation of speciose (sensu the definition "beautifully lovely" [Hart 2008] as well as its more recent usage as species-rich) salamanders in the genus *Ensatina* comprises, in our view, a single "R NG SPE ES complex" of related subspecies that spread from the north and radiated in a bewildering array of color and pattern PO YMORPH SM recognized as serving antipredator functions. These *Ensatina* mimic other, harmful species as a means of defense against predators. The species that various members of the *Ensatina* complex mimic include members of the family Salamandridae and western newts (*Taricha* sp.). Both the *Ensatina* and *Taricha* speciated and diversified along parallel biogeographic routes and timeframes (Kuchta and Tan 2006), indicative of the coevolutionary processes expected for a model (the species mimicked) and its mimic (Sinervo and Calsbeek 2006). Other researchers might separate the *Ensatina* complex into as many as eight biological species. If we were to count these, the number of California endemic salamanders would increase to thirty-six out of forty-eight (75%) of plethodontid species.

Many frogs are more recent (Cenozoic) in their invasion of California, but the tailed frog (*Ascaphus truei*) is in the most basal frog family, Ascaphidae. Its nearest extant relative (*Leiopelma* sp.) is in New Zealand, implying an even more ancient invasion of North America than the *Hydromantes* salamanders, or in another alternative biogeographic scenario, range extinction across Gondwana and Laurasia as they split some two hundred million years ago. The split between California's tailed frog (*Ascaphus truei*) and its New Zealand relative *Leiopelma* is dated at 180 mya based on this biogeographic event (Waters and Craw 2006), but upwards of 260 mya (Permian) based on a molecular clock (San Mauro et al. 2005).

The California state reptile, the endemic desert tortoise (*Gopherus agassizii*) also derives from an Eocene invasion across the Bering land bridge from Asia to North America, as evidenced by a clear trail of fossil remains (Eberle and Greenwood 2012). Despite their great antiquity in North America, ancestors of the modern desert tortoise only reached California in the Pleistocene (Morafka and Berry 2002). The Californian legless lizards (Annielidae) invaded North America from Asia during this same Eocene warming period (Macey et al. 1999). The single species in the genus *Anniella* was recently divided into five species (Parham and Papenfuss 2009). Their species status is too recent to have been formerly evaluated for protected status, but it is quite likely that one or more of these species should be considered for federal and state listing.

The Anguidae include California's alligator lizards in the genus *Elgaria*, of which one (*E. panimantina*) is a California endemic restricted to the mountains around Death Valley. They are closely related to the Annielidae and have basal members in Morocco and a large diversification in North America. Other nonendemic reptiles in California derive from South America, such as the whiptail lizards (Teiidae). Other families like the Xantusidae that harbor many California endemic lizard species were derived from Mexico and Caribbean ancestors (Noonan et al. 2013). The Helodermatidae, with only two species in the family, are restricted to North America and include the only venomous lizard in the United States, the Gila monster (*Heloderma suspectum*). In California, Gila monsters are now restricted to the Providence Mountains, and although only slightly more widespread in the past, they are now thought to be nearly extirpated from several other isolated historical locations in the state (Lovich and Beaman 2007). Others groups of purely North American origin include the diverse Phyrnosomatidae, consisting of widespread species in the genera *Uta*, *Sceloporus*, *Urosaurus, Petrosaurus*; the species-poor Crotophytidae (including collared and leopard lizards); and the horned and sand lizards in the genera *Phrynosoma* (now in three new genera *Tapaja*, *Anota*, and *Doliosaurus*) (Leaché and McGuire 2006) and *Callisaurus* (Pyron et al. 2013), respectively. Other families of lizards found in California, such as the Iguanidae (with three California species), are global in their biogeographic distributions.

The Serpentes (snakes) are originally derived from Asian radiations. California harbors both ancient and globally distributed Boid snakes like the rubber and rosy boas, as well as members in the cosmopolitan family Colubridae, which includes most of California's snakes. Sea snakes (*Pleamis platurus*) are occasionally found swimming off the shores of San Diego. Rattlesnakes (Viperidae) are entirely of New World origin. California also harbors ancient basal members of the Serpentes including those in Leptotyphlopidae such as the western blind snake (*Rena humilis*). This short review cannot do justice to all the diversity of Serpentes, which is tremendous in southern California and penetrates deeply up into the more northern San Joaquin Desert. North of the limit of the San Joaquin Desert ecosystem (Germano et al. 2011), snake diversity falls off rapidly (see Figure 11.6).

Conservation Context

To date, no California herpetofauna have gone extinct. However, twenty species are federally listed as threatened or endangered or proposed for listing, including three salamanders, six frogs and toads, five turtles and tortoises, two lizards, and three snakes. The isolated San Joaquin Desert (Germano et al. 2011), distinct from California's other two desert ecosystems, harbors the Californian endemic blunt-nosed leopard lizard (*Gambelia sila*), one of the two terrestrial reptiles listed as federally endangered. The other is the San Francisco garter snake (*Thamnophis sirtalis tetrataenia*), restricted to the San Francisco peninsula north of Rancho Del Oso. The Alameda whipsnake (*Masticophis lateralis euryxanthus*) is on the federal and state threatened species list because its range is largely restricted to the rapidly developing Bay Area counties. The giant garter snake of the San Joaquin Valley (*Thamnophis gigas*) is likewise listed as threatened because of urban and agricultural development of wetlands, critical habitat for this endemic.

More California amphibian species are endemic than reptiles; this has likely contributed to the large number of amphibians currently listed or proposed as federally threatened or endangered. Besides greater levels of endemism, the greater vulnerability of amphibians reflects a combination of classic anthropogenic development pressure and the more recent, emerging threats of anthropogenic climate change and the linked, rapid spread of the fungal chytrid disease (Rohr and Raffel 2010). These two causes are driving rapid extinctions worldwide, including many extinctions of local populations in the state of California (Vrendenburg et al. 2007).

Diverse factors underlie the listed status of other California salamanders. Introduction of the invasive barred tiger salamander (*Ambystoma mavortium*) from the U.S. central plains (Johnson et al. 2011) is driving the endemic California tiger salamander (*A. californiense*) to the brink of extinction through hybridization. The invader is thought to have rapidly spread from bait shops south of Hollister, California, across the Salinas Valley (Fitzpatrick and Shaffer 2007) and across the Coast Range to "infect" Central Valley populations of California tiger salamander. Genetic assimilation of these endemic genotypes into a synthesized hybrid species may be unstoppable, as the hybrids appear to have higher fitness than the pure species (Fitzpatrick and Shaffer 2007). The other Californian endemic salamander in the family Ambistomatidae is the federally endangered Santa Cruz long-toed salamander (*A. macrodactylum croceum*). Most of its habitat has been lost to coastal development (see Figure 11.6), but its number of breeding sites has increased from two to seven thanks to a Habitat Conservation Plan involving successful collaboration between conservation organizations, local land owners, and federal, state, and county agencies. The desert slender salamander (*Batrachoseps major aridus*) is a classic microendemic only known from two localities in the Santa Rosa Mountains (Hidden Palm Canyon and Guadalupe Canyon), making it the amphibian with the most restricted distribution in North America. Several other salamanders in the same family are listed as state threatened largely because of their microendemic status, including two other slender salamanders (*B. stebbinsi* restricted to the Tehachapis and *B. simatus* restricted to Kern Canyon), web-toed salamanders (*Hydromantes brunus* restricted to two drainages in the Sierra Range and the eponymous *H. shastae*), and woodland salamander species (*Plethodon stormi* and *P. asupak*).

Of all the herpetofauna, frogs are undergoing the most severe extinction crisis. In California, frogs at several locations have been extirpated by an introduced disease, the fungal chytrid (*Batrachochytrium dendrobatidis*); introduced vertebrates, including a number of fish species and the bull frog (*Lithobates catesbeianus*); pesticide and herbicide impacts (Hayes et al. 2002); and habitat degradation. Notable among extirpations in the frog genus *Rana* are most historical sites of mountain yellow-legged frog (*R. muscosa*) in the Sierra Nevada Range and their near extirpation from almost all historical locations in the Transverse Ranges. Fungal chytrid has been strongly implicated in local extinctions of mountain yellow-legged and Sierra Nevada yellow-legged (*R. sierra*) frogs (Vredenburg et al. 2007, 2010), although introduced trout have also played a major role given that trout removal has stabilized population declines (Vredenburg 2004). The California red-legged frog (*Rana draytonii*) is all but extinct in the Sierra foothills, now restricted to only six known breeding populations there (Barry and Fellers 2013). It is extinct from all but two locations in the Transverse Ranges of California (south of Santa Barbara and on the Santa Rosa plateau) (Federal Register 2008). One of its last strongholds in California appears to be Central Coast Range, where it is still common but still faces impacts from invasive species—males preferentially mate with female bullfrogs that are larger than females of their own species (D'Amore et al. 2009). The cause of extirpation of the closely related Cascades frog (*Rana cascadae*) from over 50% of its California range is even more enigmatic. Nevertheless, climate change is a likely cause given that it went extinct from over 99% of its Mount Lassen sites, near the southern end of its Pacific Northwest distribution, during a long-term drought (Fellers and Drost 1993).

The challenge of protecting California's herpetofauna is complicated by the striking correlation of amphibian, lizard, and snake biodiversity with the human footprint of development (population density, see Figure 11.6) and further exacerbated by the impacts climate change (Rohr and Raffel 2010). The potential impact of urban sprawl has an enormous reach beyond the urban landscape, given its hunger for energy. Wind and solar power installations have recently begun to proliferate across California desert ecosystems, with potentially huge impacts on reptiles (Lovich and Ennen 2013) from the footprint of energy installations, increased incidence of fire, and urban heat island effects (Millstein and Menon 2011). Particularly vulnerable species are the endangered Blunt-nosed leopard lizard, whose two best remaining refuges, Carrizo Plain and Panoche Valley, are slated for adjacent solar development; and the threatened desert tortoise, which faces a similar threat from climate change and planned solar development in the core parts of its Mojave Range.

Around the world, contemporary extinctions of local reptile populations are linked to rising temperatures (Sinervo et al. 2010). Even small changes of 0.5C° in maximum daily air temperatures have started to drive local extinctions in those taxa near the edges of their physiological high-temperature range limits. In the past four decades the Mojave and Sonoran Deserts have warmed considerably, and precipitation has decreased in both fall-winter and spring-summer periods. This overall drying trend may have been a significant driver of extinction for one population of the threatened Coachella Valley fringe-toed lizard (Barrows et al. 2010) and could drive other species toward extinction. Despite the challenges, there are remarkable herpetofauna conservation successes. Two excellent examples are recovery of the endangered green sea turtle (*Chelonia mydas*) through effective regulations that eliminated overharvestings in Mexico and Hawaii and the threatened island night lizard (*Xantusia riversiana*), which was protected by eradicating invasive cats (*Felis catus*) and herbivores from most of the Channel Islands (USFWS 2013a). These and other successes demonstrate the ability of California's endangered species to rapidly recover from overexploitation or invasive species following effective regulation, enforcement, or restoration, as long as suitable habitat is still available.

Birds

California has the most species-rich avifauna in the United States and the second highest levels of bird endemism besides Hawaii (see Figure 11.2). California boasts over three hundred breeding species, from boreal great gray owls (*Strix nebulosa*) in the high Sierra Nevada to desert species such as Le Conte's thrasher (*Toxostoma lecontei*). California contains globally important bird areas and spectacular migrations such as through the Central Valley wetlands, Monterey Bay Marine Sanctuary, and Salton Sea. Perhaps because of its high bird diversity and levels of endemism, California has a rich legacy of field ornithology and a highly active community of birdwatchers, making it one of the most studied avifaunas in North America.

William Dawson's three-volume tome, *The Birds of California* (1923), was the first thorough inventory of the Californian avifauna. Joseph Grinnell greatly expanded our knowledge of California birds and their finer-scale distributions during his tenure as the founding director of the Museum of Vertebrate Zoology at UC–Berkeley (1908–1939). He published the first comprehensive checklist of California birds (1902) and started the landmark text "The Distribution of the Birds of California" (Grinnell and Miller 1944). His biodiversity transects are still being used to examine how birds in the Sierra Nevada have tracked their climate niches over the past hundred years (Tingley et al. 2009). Beginning in the 1960s, a growing bird-watching community of field ornithologists such as Guy McCaskie and Rich Stallcup greatly improved our knowledge about species ranges, patterns of vagrancy, and rare species in California. The California Rare Bird Committee (CRBC), established in 1970, continues to maintain the California state list of birds (CRBC 2013) and has made significant contributions to the knowledge of California birds through the journal *Western Birds* and the publication of *Rare Birds of California* (Hamilton et al. 2007).

Evolutionary Diversification

Fossil evidence suggests that bird diversity suffered a major extinction event at the Cretaceous-Tertiary boundary, now associated with the Chicxulub crater impact approximately 65 mya. Major bird orders then likely radiated rapidly in the early Tertiary, but controversy exists as phylogenetic approaches estimate the radiation of passerine birds as far back as the mid-Cretaceous (120–90 mya) (Cracraft 2001, Feduccia 2003). The geographic and physiographic diversity of California have surely aided in the evolution of birds in the state, and over a hundred species have been found in the fossil record from more than one hundred thousand specimens excavated across a swath of California habitats (Miller and DeMay 1942). Fossils of extinct Mesozoic toothed birds such as *Alexornis*, a genus of primitive Enantiornithines, and *Ichthyornis*, a genus of fish-eating seabird similar to modern-day Charadriiformes, have been found in California's Great Central Valley (Hilton 2003). A single bone of a Neognath has also been unearthed, but this tells us very little about how this subclass diversified into the ten thousand species that are known globally today. For other taxonomic groups it is well established that much of California's genetic diversity arises from the region's geographic complexity, whereby most phylogeographic patterns are due to population genetic breaks between the Sierra Nevada, Coast, and Transverse Mountain Ranges (Calsbeek et al. 2003). However, the origin and diversification of California bird populations is less clear given their highly mobile and migratory habits (Calsbeek et al. 2003).

A total of 653 species have been documented in California (CRBC 2013), more than any other state. For example, Texas has 639 species, Florida 514 species, and New York 480 species. Of those 653 species documented in California, 464 are "regularly occurring" (CRBC nonreview species) and 313 likely breed within the state (USGS Patuxent Wildlife Research Center 2013). Ten non-native species have established breeding populations in the state, of which 7 are widespread and likely affect native species. The California native avifauna represents 72 of the world's 231 families of birds from 19 of the 27 orders (CRBC 2013, Clements 2013).

California boasts more endemic species and subspecies than any other state except Hawaii. BirdLife International recognizes California as one of the largest Endemic Bird Areas including southwest Oregon and northwestern Baja from the coastline up to 2,000 meters and mirroring the boundaries of the California Floristic Province (Birdlife International 2013). Many endemic and range-limited taxa in California fall into three broad categories: Channel Island endemics, Maritime Chaparral and Scrub specialists, and Oak Woodland specialists. California harbors three species-level endemics: the California condor (*Gymnogyps californianus*) (once extirpated from their wider range and eventually the wild but now being reintroduced around central California and outside the state), the island scrub-jay (*Aphelocoma insularis*), and the yellow-billed magpie (*Pica nuttalli*). An additional sixty-one subspecies are endemic to California, many of which are from the Channel Islands. Nine species and forty-five subspecies are near-endemic (>80% of their range in California) (Shuford and Gardali 2008).

The California condor is perhaps the best-known endemic species, after being once far more widespread across the western United States but restricted to California by 1937 (Wilbur and Kiff 1980), and their conservation is discussed later on. Condors are large scavengers that likely suffered with the collapse of North American megafauna. They have the largest wingspan of any North American bird (2.8 meters) and are one of the heaviest at about 8.5 kilograms (Snyder and Schmitt 2002). The island scrub-jay is a Channel Islands endemic within the scrub jay complex that also includes the range-restricted Florida scrub jay (*A. coerulescens*). Island scrub jays have been separated from mainland populations for at least one hundred thousand years (Delaney and Wayne 2005) and have a heavier bill and bolder plumage than coastal Western scrub jays (*A. c. californica*). They number fewer than three thousand individuals and are found only on Santa Cruz Island, where they use a large variety of habitats from oak woodlands to Bishop Pine forest (*Pinus muricata*). Fossil evidence shows that scrub jays were once present on neighboring Santa Rosa Island and may have disappeared as late as the nineteenth century (Collins 2009). The yellow-billed magpie is a particularly range-limited, but locally abundant, endemic species in California that inhabits open oak woodlands, riparian zones, and even suburban areas of the interior valleys and coast. They are highly social, nesting in loose colonies and roosting in large flocks. They are generally smaller and longer-winged than black-billed magpies, which are found in a nonoverlapping northeast area of the state. Recently yellow-billed magpie populations declined by as much as 49% within two years coinciding with the arrival of the avian disease West Nile virus (Crosbie et al. 2008).

Biogeography

Because of California's large latitudinal gradient, it contains the transition from bird species that generally inhabit the Pacific Northwest south to species of the arid Southwest (Olson et al. 2001). We break down the state into the same ecoregions used by Shuford and Gardali (2008) adapted from the Jepson geographic subdivisions of California (Hickman 1993). Here we briefly describe each region and its notable species, and notable Important Bird Areas (IBAs) as designated by California Audubon (Cooper 2004). The biogeography of California's birds reflect the state's great mosaic of habitat types. Bird communities are more species rich as one moves from north to south, and from inland to the coast, with the highest species diversity in the southwest part of the state.

NORTHWESTERN CALIFORNIA, CASCADE RANGE, AND SIERRA NEVADA

The northwest California coastal region holds the largest and least impacted rivers in the state (e.g., Klamath River) along with relatively pristine wetlands and coastal dunes, all of which contribute to bird diversity (Cooper 2004). Lakes, ponds, and other standing water provides important habitat for many wildlife in northwestern California (PRBO Conservation Science 2011). Bird taxa generally restricted to this region include Aleutian cackling goose (*Branta hutchinsii leucopareia*), ruffed grouse (*Bonasa umbellus*), barred owl (*Strix varia*), gray jay (*Perisoreus canadensis*), black-capped chickadee (*Poecile atricapillus*), and breeding individuals of the American restart (*Setophaga uticilla*). One of the most significant Important Bird Areas in this region is the Del Norte Coast IBA, which includes Castle Rock, the most structurally diverse island off the California coast and home to the largest common murre (*Uria aalge*) colony in the California Current, eleven nesting seabird species, and over 121,000 birds including roost sites for the Aleutian cackling goose and brown pelican (*Pelecanus occidentalis*). This IBA contains the entire global population of Aleutian cackling goose, which stages in the area during the spring and fall; the entire California breeding population of the Oregon vesper sparrow (*Pooecetes gramineus affinins*); and the majority of the California population of the fork-tailed storm-petrel (*Oceanodroma furcata*).

To the east, the Cascade Range is the southernmost portion of a volcanic mountain range that stretches north through Oregon and Washington, ending in British Columbia, Canada. This area is notable for its large populations of breeding willow flycatchers (*Empidonax traillii*), possibly representing the state's nesting population of the *brewsteri* (Sierra-Cascade) race. The IBAs in the region, such as the Lake Almanor Area and Big Valley/Ash Creek, support over five thousand waterfowl including over 10% of the California population of the greater sandhill crane (*Grus canadensis tabida*) and between eight and twelve sensitive species (Cooper 2004; National Audubon Society 2013b).

The Sierra Nevada range supports a diverse range of bird species due to its extreme altitudinal gradients and montane forests. It houses species found nowhere else in California, such as the great gray owl (*Strix nebulosa*) and gray-crowned rosy-finch (*Leucosticte tephrocotis*), pine grosbeak (*Pinicola enucleator*), and breeding American pipits (*Anthus rubescens*). Important bird areas include the northern and southern Sierra Meadow IBAs, which are home to California spotted owl (*Strix occidentalis occidentalis*) and a total of nine sensitive species including the endangered willow flycatcher. The northern IBA has six distinct meadow systems and distinct bird communities that depend on willow thicket habitat (e.g. Lincoln's sparrow [*Melospiza lincolnii*], Wilson's warbler [*Wilsonia pusilla*], willow flycatcher) or that concentrate at the meadow-forest interface (e.g., pine grosbeak and multiple species of owls, woodpeckers, flycatchers, and sapsuckers). The southern IBA also contains the extremely high-altitude peaks of the region and is home to great gray owls and almost the entire global populations of Mount Pinos blue grouse (*Dendragapus fuliginosus howardi*), an endemic subspecies (Cooper 2004, Bunn et al. 2007).

SACRAMENTO AND SAN JOAQUIN VALLEYS

The Sacramento Valley subregion is the cooler and wetter end of the Central Valley and contains the salt marshes and rice fields between Red Bluff and Suisun Slough, bisecting the delta area of the Sacramento and San Joaquin Rivers where it meets with the southerly San Joaquin subregion (Jepson Flora Project 2013). While 95% of the Central Valley's historic wetlands, riparian areas, and grasslands have been destroyed or modified, the area still supports important migratory waterfowl and raptor habitat. The Sacramento National Wildlife Refuge complex is comprised of five refuges and three wildlife management areas, which makes up 70,000 acres of wetland, upland, and riparian habitats that are intensively managed for wintering and breeding waterbirds (Cooper 2004, USFWS 2013b). Some agricultural lands are also managed to mimic grasslands and wetlands to attract migratory shorebirds. Arguably, the most significant bird habitat in the region is in the Cosumnes River Preserve, adjoining the only major river that drains from the western Sierra Nevada and maintains more or less natural flow regimes that allow flooding of lowland areas in spring (Cooper 2004). The preserve provides habitat to over fifty thousand migratory waterfowl and thirteen sensitive bird species, including long-billed curlew (*Numenius americanus*) and thousands of greater and lesser sandhill cranes (*G.c. tabida* and *G.c. canadensis*, respectively) (Pogson and Lindstedt 1991, Cooper 2004, Cosumnes River Preserve 2014).

The southern portion of the Great Central Valley, the San Joaquin subregion, is larger and drier than its northern counterpart with desert elements in the far south. Despite pervasive agricultural development, remnants of grasslands, vernal pools, and alkali sinks (e.g., the Carrizo Plain) as well as a few marshes and riparian woodlands along major rivers remain intact and sustain critical stopover habitat for migratory birds (Jepson Flora Project 2013). The extensive Sacramento–San Joaquin Delta, once a vast tule marsh, contains only small islets of native riparian and tidal marsh habitats and is a critical IBA for migratory shorebirds and waterfowl including long-billed curlews, sandhill cranes, rarer species such as the short-eared owl (*Asio flammeus*) and black rail (*Laterallus jamaicensis*), and breeding colonies of double-crested cormorant (*Phalacrocorax auritus*) along restored marshland habitats (Cooper 2004).

CENTRAL WESTERN AND SOUTHWESTERN CALIFORNIA

The central portion of California's north-south running Coast Range has relatively diverse habitats and avifauna due to its extensive riparian habitat, coastal marshes and estuaries (although 90% of the San Francisco Bay Area's wetlands have been developed), chaparral, oak savanna and coniferous woodlands, including enclaves of redwood forests, deep canyons, rugged headlands, sandy beaches, and pastureland. This region is home to familiar California species such as the wrentit (*Chamaea fasciata*), endemic and locally abundant yellow-billed magpie, greater roadrunner (*Geococcyx californianus*), California thrasher (*Toxostoma redivivum*), sage sparrow (*Artemisiospiza belli*), and California towhee (*Melozone crissalis*), among many others. The most famous bird species in the region is the California condor, which can be found in low numbers in the wild throughout the Big Sur Area (also a recognized global IBA) and in parts of the Los Padres National Forest. This region contains a variety of important bird areas. South San Francisco Bay contains extensive waterbird and shorebird habitats in its tidal marshes, creeks, and leveed evaporation ponds and is home to the endangered California Ridgeway's rail (*rallus obsoletus obsoletus*) and California least tern (*Sterna antillarum browni*), the endemic saltmarsh common yellowthroat (*Geothlypis trichas sinuosa*), and the endangered western snowy plover (*Charadrius nivosus nivosus*). Vandenberg Air Force Base is the farthest-south site on the mainland for many breeding marine birds, also supporting California least terns and over 10% of the coastal-breeding population of the western snowy plover.

Southwestern California, the most species-rich of California's ecoregions, overlaps the southern range edges of many northern species and the northern range edges of more southern coastal specialties such as California gnatcatcher (*Polioptila californica*). The Tijuana River Reserve IBA contains the California least tern, the light-footed Ridgeway's rail (*Rallus obsoletus levipes*); the population-size second only to Upper Newport Bay), and least Bell's vireo (*Vireo bellii pusillus*). Another IBA, the San Jacinto Valley, hosts nearly all of southern California's raptor species and is one of the few remaining areas in southern California that still supports winter flocks of shorebirds such as the long-billed curlew and white-faced ibis (*Plegadis chihi*). The mountain plover (*Charadrius montanus*) and sandhill crane once wintered here but appear locally extirpated (Cooper 2004, National Audubon Society 2013b).

No discussion of the avian biogeography of California can be complete without the Channel Islands. Together these eight islands host seventeen endemic subspecies and one endemic species, the island scrub jay (Johnson 1972). Most of these taxa are characterized by darker/drabber plumage, longer and/or heavier legs, bills and/or toes than their continental counterparts. At least some of the taxa appear to be Pleistocene relicts that have since changed in their island setting, such as the horned lark (*Eremophila alpestris insularis*) (Johnson 1972). The Channel Islands also harbor at least fourteen species of breeding seabirds. IBAs on and around these islands contain the entire U.S. breeding population of Scripps' murrelet (*Synthliboramphus scrippsi*), over 10% of the global population of black storm petrel (*Oceanodroma melania*), Cassin's auklets and California's breeding brown pelicans, and nearly half the global population of ashy storm-petrels (Cooper 2004, National Audubon Society 2013b).

CALIFORNIA DESERTS

The Mojave Desert contains the lowest and hottest areas in North America (e.g., Death Valley). The region also contains striking granitic mountains, such as the Cima Dome and Granite Mountains, with underground water seeps that feed springs and provide food and refuge for many bird species (e.g., Butterbredt Spring). Along the eastern border of this region is East Mojave Peaks, an Important Bird Area that contains over 10% of the California populations of gilded flicker (*Colaptes chrysoides*), gray vireo (*Vireo vicinior*), and Bendire's thrasher (*Toxostoma bendire*). Also within this IBA are large populations of other desert birds found in the Joshua Tree woodlands and pinyon chaparral along steep-sloped canyons. Hepatic tanager (*Piranga flava*) and Mexican whip-poor-will (*Caprimulgus arizonae*) are known to occur in California only on top of the mountain peaks in this desert.

The Sonoran Desert region occupies the southeastern corner of the state and includes the Colorado Desert. The area is arid but contains woodland habitat located along the flight path of migrant songbirds moving between California and Mexico. The Colorado Desert Microphyll Woodland IBA is one of the few important migratory habitats in this area and the only area in California with elf owls (*Micrathene whitneyi*) and northern cardinals (*Cardinalis cardinalis*). The Anza-Borrego Riparian IBA (the largest state park in the U.S.) contains least Bell's vireo (*Vireo bellii pusillus*), important populations of vermilion flycatcher (*Pyrocephalus rubinus*), and summer tanager (*Piranga rubra*). The Salton Sea, formed in 1905 after a break in a canal from the Colorado River, might be the most important body of water for birds in the interior of California. This IBA is home to the Yuma Ridgeway's rail (*R. obsoletus yumanensis*) and other birds found nowhere else in the western U.S., such as wood stork (*Mycteria Americana*), yellow-footed gull (*Larus livens*), breeding laughing gulls (*Leucophaeus atricilla*), stilt sandpiper (*Calidris himantopus*), black terns (*Chlidonias niger*), and the rare *Gelochelidon nilotica vanrossemi* race of gull-billed tern (Cooper 2004, National Audubon Society 2013b).

The Great Basin in California includes the Modoc Plateau in the northeast corner of the state and Mono Lake south to the Owen's River Valley along the central-eastern border. The Modoc Plateau IBA supports a total of fourteen sensitive species (e.g., redhead [*Aythya americana*], purple martin [*Progne subis*], and yellow-headed blackbird [*Xanthocephalus xanthocephalus*]). It also supports the highest diversity of breeding waterfowl in the state due to its location on the Pacific flyway and its dozens of reservoirs and artificial wetlands. Mono Lake supports millions of migratory birds each year and provides important habitat for western snowy plover (over 10% of California's interior breeding population), California gull (*Larus californicus*), Western and least sandpipers (*Calidris mauri* and *C. minutilla*), and American avocet (*Recurvirostra americana*).

MARINE REGIONS

The nutrient-rich waters of the California Current, which flow from Alaska, support abundant and diverse marine plants and animals, including 163 bird species (Bunn et al. 2007). The northern coastal section of California's northern marine region is arguably the most productive nearshore area due to its steep, deep-water canyons and nutrient-rich waters. This area contains important bird areas and "hot zones" such as the Cordell Bank, Bodega Canyon, and Monterey Canyon, supporting large seabird colonies on the Farallon Islands and Año Nuevo Island (Sydeman et al. 2013). The waters of this northern region move away from the coast at Point Conception, where the California coastline turns abruptly east and the cool water moving south is diverted offshore. In Monterey Bay incredible numbers of visiting seabird species have been documented; for example, a global record of eight shearwater species have three times been observed in single day (Shearwater 2013). From Point Conception south, in the Southern Bight Marine Region, exist many of the same northern marine species with the addition of more tropical species such as red-billed tropicbird (*Phaethon aethereus*), brown booby (*Sula leucogaster*), Scripps murrelet, black-vented shearwater, and Leach's storm-petrels (*Oceanodroma leucorhoa*).

Conservation Context

Many species of birds are vulnerable to extinction in California because they are range-restricted, are habitat specialists, or have relatively small population sizes. In addition to preserving rare species, California has a global responsibility to provide safe harbor for more abundant taxa that chiefly reside within the state boundaries, and to provide safe passage and quality stopover habitat for migrating birds in the Western Flyway and in the California Current. No California native bird species have gone globally extinct in the past hundred years. However, California has nine federally endangered and six threatened bird species or subspecies, and coastal California has been identified as one of two hotspots of endangered bird diversity in the continental U.S. (Godown and Peterson 2000). Shuford and Gardali (2008) conducted an exhaustive quantitative review of 238 bird taxa and found that 74 species and subspecies warrant official status as "California Bird Species of Special Concern." Habitat loss and fragmentation are the most pervasive threats to threatened California birds, affecting 97% of the Species of Special Concern, followed by non-native species (43%), pollution (24%), overexploitation (13%), and disease (5%). Wetlands harbored twenty-seven listed species, followed by thirteen in scrub habitats and twelve in grasslands; at the other end, only one species of concern was found in mixed evergreen forests.

The southwest California ecoregion contains the greatest number of listed species at thirty-seven, including six Channel Island endemic taxa. Central-western California contains thirty listed taxa, with other regions containing between eighteen and twenty-one listed species (Shuford and Gardali 2008). Despite high levels of endangerment, only two species have been extirpated from the state in modern times: the California condor (now reintroduced) and the sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) (formerly in the northeast corner of the state). Conservation efforts have helped recover several declining species including the marbled murrelet (Peery et al. 2004, Peery and Henry 2010) and brown pelican (Anderson et al. 1975). The California gnatcatcher (*Polioptila californica*), whose northernmost subspecies (*P. c. californica)* in southern California was listed as threatened in 1993 (USFWS 2009), has been conserved relatively recently with the protection of 60,000 hectares through the State of California Natural Communities Conservation Program (NCCP). The Scripp's murrelet, a small crevice-nesting seabird, has benefited from the removal of most invasive mammals from its known current or suspected historical island nesting sites in the U.S. and Mexico (McChesney and Tershy 1998, Whitworth et al. 2013, Aguirre-Munoz et al. 2008). Bans on fishing and other extractive uses have been made within important areas of the Channel Islands National Marine Sanctuary; light pollution in important nearshore murrelet staging areas has been reduced; and the bird has received additional legal protections of Mexican breeding islands by the Mexican Natural Protected Areas Commission (CONANP 2014).

The ongoing recovery of the formerly extirpated California condor is perhaps the most well-known reversal of a declining bird in California. The condor was widespread before the late Pleistocene megafaunal extinctions (Emslie 1987) but by the 1950s was restricted to a small portion of southern California (Koford 1953). The condor was a charter species of the Endangered Species Act in 1972 and the subject of the nation's first endangered species recovery plan in 1975. Early conservation efforts were unsuccessful, and by 1982 only twenty-two condors remained in the wild. In 1986 the decision was made to capture the last three wild individuals for the captive breeding program. By the late 1990s the program produced twenty chicks per year (Walters et al. 2010). The captive breeding program then developed successful approaches to behaviorally condition birds for the wild, including puppet and parent rearing (Meretsky et al. 2000) and power line aversion training (Mee and Snyder 2007). Captive condor breeding programs now return birds to release sites in southern California (since 1992), Arizona (1996), Big Sur (1997), Baja California, Mexico (2002), and Pinnacles National Park (2003). Reintroduced birds first fledged a wild-born chick in California in 2004 (Walters et al. 2010). Lead poisoning, a major proximate cause of the historical population decline, continues to be the major obstacle to recovery (Cade 2007, Finkelstein and Doak 2012). However, in 2013, California became the first state to ban all lead ammunition. This is expected to greatly aid condor recovery and to protect other species of wildlife as well as human health (Bellinger et al. 2013).

The future management of California's bird biodiversity will confront two accelerating challenges: growing habitat loss and an increasingly volatile climate. The highest projected rates of human population growth are in the coastal southwest region, home to the highest number of threatened birds in the state (Shuford and Gardali 2008, CDF 2013). Growing human populations affect birds directly by destroying habitat or corridors that connect isolated foraging or nesting areas, and indirectly by altering the numbers of native and introduced species, often resulting in higher numbers of predators, nest parasites, and non-native competitors. Although the details about how California's climate will change are uncertain, abundant, connected bird populations will surely be better able to cope with climate change. Thus improved and expanded conservation efforts are the best protection for California's birds. Not all species have similar threats; Jongsomidt et al. (2012) used species distribution models to measure potential impacts from housing development and climate change and found oak woodland species suffering 80% of their losses from development, whereas birds associated with coniferous forests see the greatest losses due to climate. Across the board, 32% of species range reductions were attributed to housing development. Attempts at modeling future bird distributions under climate change scenarios suggests shifting ranges and novel communities of birds, highlighting uncertainty about how birds may respond (Stralberg 2009). Fortunately, one does not have to look far in California to see avian conservation success stories involving broad partnerships between industry, stakeholders, and scientists. Hopefully the future will remain bright for California's birds.

Mammals

Since the end of the age of the dinosaurs about sixty-six million years ago, mammals have diversified and thrived as one of the most successful animal lineages on Earth. Mammals are found in every California landscape; more than other vertebrate lineages (e.g., birds and fish), mammals have diverse modes of locomotion that allow them to flourish in air, sea, and land. They play essential roles in all California ecosystems, acting as seed hoarders and dispersers (e.g., kangaroo rats [*Dipodomys* sp.] and tree squirrels [*Sciurus* sp.]), grazers (e.g., deer [*Odocoileus* sp.]), pollinators (e.g., bats [Chiroptera]), ecosystem engineers (e.g., beavers [*Castor canadensis*]), insectivores (e.g., shrews [Soricidae]), and large predators (e.g., killer whales [*Orcinus orca*] and mountain lions [*Puma concolor*]). Consequently, their distributions are often closely tied to biotic community composition and environmental changes (see Blois et al. 2010), and their conservation is a crucial component of maintaining ecological dynamics.

California has the highest mammal diversity in the United States (NatureServe 2002). Depending on the definition of species, it has approximately 227 mammal species (including 38 marine species, about 163 native terrestrial species, and around 26 introduced terrestrial species; CDFW 2008), ranging from the diminutive Preble's shrew (*Sorex preblei*, 2.1–4.1 grams) to the largest known animal, the blue whale (*Balaenoptera musculus*, 170,000 kilograms). California's native wildlife hail from seven mammalian orders: Artiodactyla (even-toed ungulates such as deer and sheep), Carnivora (carnivores), Cetacea (dolphins and whales), Chiroptera (bats), Lagomorpha (rabbits, hares, and pika), Rodentia (rodents), and Sorimorpha (e.g., shrews and moles). Two additional mammalian orders were introduced to California: Perissodactyla (horse and donkey) by Spanish explorers and the marsupial Didelphimorpha (Virginia opossum) during the Great Depression in the early twentieth century (Lidicker 1991). About half of the terrestrial mammals in California are rodents.

Biogeography

Like plants and other animals, mammal diversity varies among California's ecoregions. The highest native mammal species richness is in the northern portion of the state (ecoregions 1 and 3 in Figure 11.7; Figure 11.8); "rare" species with limited distributions, small populations, and threatened status are most common in the southern portion of the state and the San Francisco Bay Area (mostly ecoregion 5 in Figure 11.7; CDFW 2003). This pattern reflects the fact that southern California and San Francisco Bay Area landscapes are more fragmented than those in northern California, leaving little suitable habitat for the mammal species that are now rare or restricted in the former regions. It may also suggest

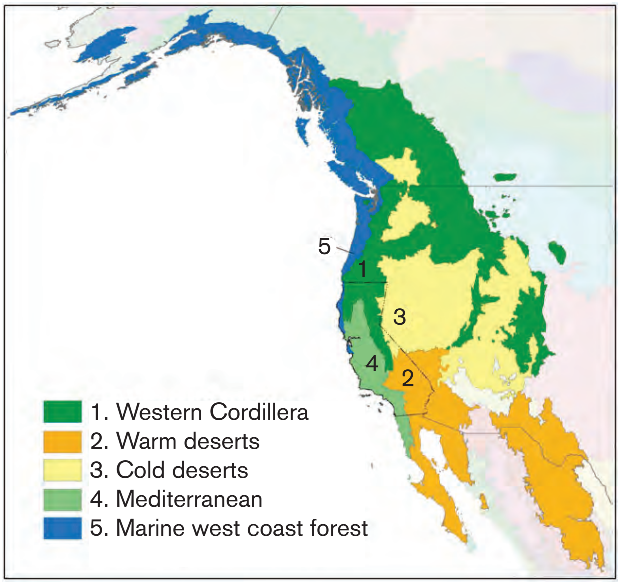

FIGURE 11.7 In this ecoregion map based on definitions of the Commission for Environmental Cooperation's Ecoregion Level II, five ecoregions overlap with California. They are (1) the Western Cordillera mountain chain, (2) warm deserts, (3) cold deserts, (4) Mediterranean region, and (5) marine west coast forest.

that northern California served as a refugium over a longer period of time than did southern California. Areas with rapid and recent intraspecies diversification occur along the California coast and southern portion of Sierra Nevada (Davis et al. 2008), which may indicate recent fragmentation of species geographic ranges, recent colonization, or both. When looking at the full range of native mammal species present in California, most of the diversity comes from northern forests, the Great Basin, and the northern coasts.

When examining California mammal species ranges, including portions that are outside of the state (see Figure 11.8a), rodents and lagomorphs show high diversity in the Great Basin and Sierra Nevada. Since rodents are the most numerous mammalian order, comprising about half of the mammal species in California, their distributions play an important role in the overall diversity pattern. Bats are the second most speciose mammalian order in California. As the only flying mammal, they have large species and individual ranges compared to other mammals of their size. The center of diversity for bats in California is the southeastern part of the state, near Mexico. Most shrews and moles are found along the Pacific Northwest coast, where rainfall is plentiful (see Figure 11.8b).

Twenty-five mammal species have more than 75% of their ranges in California (Davis et al. 2008). Among them, seventeen species (about 9%) are unique to the state; hence California has the highest mammal endemism among all the states (Table 11.2; CDFW 2003, Stein et al. 2000). With the exception of the island fox (*Urocyon littoralis*) in the Channel Islands, all of these endemics are small mammals: fifteen species of rodents and one species of shrew. These endemic species share small body size and/or small species range. In addition, California has endemic subspecies such as the Tule elk (*Cervus canadensis nannodes*), the smallest elk subspecies in North America. Many endemic mammal species are found within the unique Mediterranean landscape in the southwestern portion of the state or in other geographically complex and isolated regions (Figure 11.9). While it is not surprising that the Mediterranean environment fosters diversity unique to California, isolation and recent diversification might also contribute to this pattern. For example, approximately four thousand to eight thousand years ago dry climatic conditions allowed desert species from east of the Sierra Nevada, including several species of kangaroo rats, to expand into the San Joaquin Valley, where they became isolated when moist conditions returned.

Conservation Context

California had a diverse megafauna, animals with body mass greater than 45 kilograms (100 pounds) such as saber tooth cats (Felidae) and pygmy mammoths (*Mammuthus* sp.), until about thirteen thousand years ago (Johnson et al. 2011). Concurrent with climate change and human arrival in the Americas, many megafauna disappeared from North America (see Chapter 9, "Paleovertebrate Communities"). More recently, breeding colonies of northern fur seals (*Callorhinus ursinus*) became extinct along the coast of California eight hundred to two hundred years ago, partly due to overexploitation and disturbance. Following restrictions to commercial sealing in 1911, breeding fur seals returned to California, but the populations that recolonized from the Pribilof Island lacked the unique behavior of weaning pups at an older age that characterized California's former fur seal population (Newsome et al. 2007).

Today, nineteen species and eighteen subspecies of mammals in California are listed as endangered or threatened by either the state or federal government (California Nature Resources Agency 2013). Unlike the list of endemic species that consists predominantly of small mammals, the threatened and endangered list includes many medium- to large-sized species such as the Sierra Nevada red fox (*Vulpes vulpes necator*), two subspecies of bighorn sheep (*Ovis canadensis californiana* and *O. c. cremnobates*), and seven species of whales. Fortunately, no California mammal species are globally extinct. However, four mammal species have been extirpated (driven locally extinct) from California in the past century: the bison (*Bison bison*), gray wolf (*Canis lupus*), jaguar (*Panthera onca*), and grizzly bear (*Ursus arctos*)—the official state animal featured on the California flag.

Many furred animals were hunted to near extinction by the early twentieth century. Before the gold rush, harvesting pelts of sea otters (*Enhydra lutris*), martins (*Martes americana*), and fishers (*M. pennant*) was a major incentive for many people to explore California. In just eighty-two years between 1786 and 1868, two hundred thousand sea otters along California's coast were killed (Grinnell et al. 1937), reducing the populations to one thousand to two thousand individuals occupying a fraction of their range before the fur trade (Riedman and Estes 1990). Improved regulation of hunting and trapping, including outright bans on hunting of sea otters (such as a 1911 International Protection Treaty), halted declines and allowed most species to rebound as long as suitable habitat was available. The absence of sea otters resulted in an overabundance of sea urchins, which overgrazed the kelp forests that are habitats for many marine species. Recovery of sea otters, aided by reintroductions, helped restore kelp forests. We know less about the ecosystem impacts of reducing populations of other mustelids, wolverines, fishers, river otters, and badgers, but they were likely significant.

Anthropogenic landscape modifications (e.g., agricul-

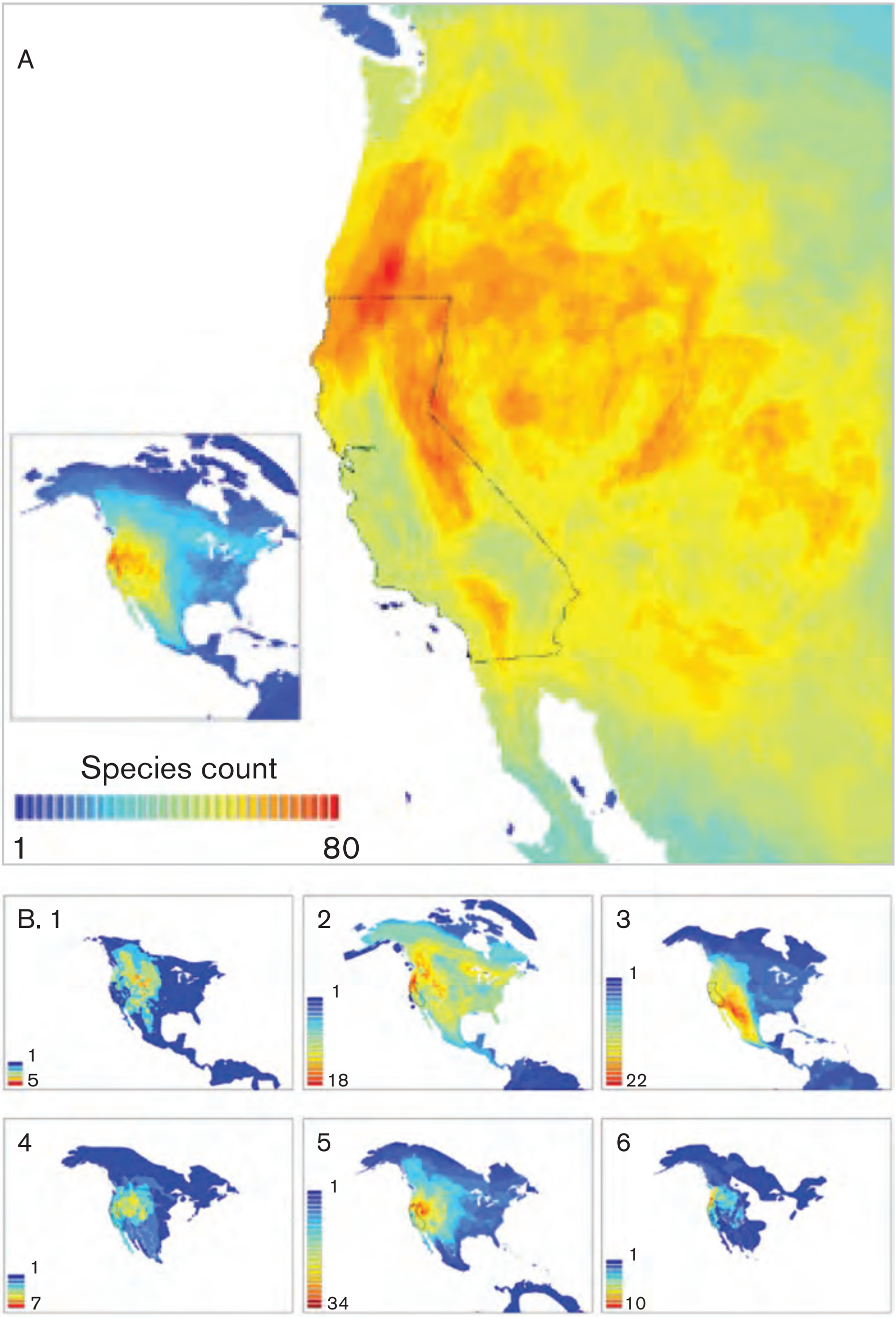

FIGURE 11.8 Diversity hotspots of terrestrial mammalian wildlife present in California, excluding species introduced to California after 1900. These maps are constructed by overlapping full species ranges (IUCN 2013) for (A) overall diversity and (B) diversity by order. From left to right, the mammalian orders are: (1) Artiodactyla, (2) Carnivore, (3) Chiroptera, (4) Lagomorpha, (5) Rodentia, and (6) Soricimorpha. Source: C. Li and E. Hadly, unpublished data.

ture and urbanization) also continue to reduce natural habitats. For example, about 43% of California was converted to agriculture land throughout the twentieth century (Kuminoff et al. 2001). The salt marsh harvest mouse (*Reithrodontomys raviventris*) is threatened by development of San Francisco Bay marshland as well as by pollution and declines in native plants. Humans have also introduced twenty-six species of terrestrial mammals, some of which are invasive and affect native mammals through predation (especially red fox, cats, and rats), overgrazing (especially sheep, goats, pigs, cattle), disease transmission, and competition for food and water. Humans have also introduced approximately a thousand nonnative plant species (including about 140 aggressive invasive species such as giant reed [*Arundo donax*] and yellow starthistle [*Centaurea solititialis*]) that alter habitat available for native mammals) (CDFW 2003). Moreover, temperature increases and unusual rainfall patterns associated with global climate change are affecting California mammals. For instance, in the span of a hundred years at least twenty-eight species of small mammals in Yosemite National Park have moved to higher elevations as temperatures have increased (Moritz et al. 2008).

Mammals with different body sizes and life history strategies face different challenges. Small mammals with small species ranges are easily impacted by local changes. For example, many kangaroo rats (e.g., *Dipodomys nitratoides nitratoides* and *D. nitratoides exilis*) in the Central Valley are threatened by habitat destruction. Compared to small mammals, large mammals typically require larger individual home ranges; increasing urbanization fragments reduces available habitat to them. Larger mammals also tend to have longer gestation periods, fewer offspring per litter, more time required to reach

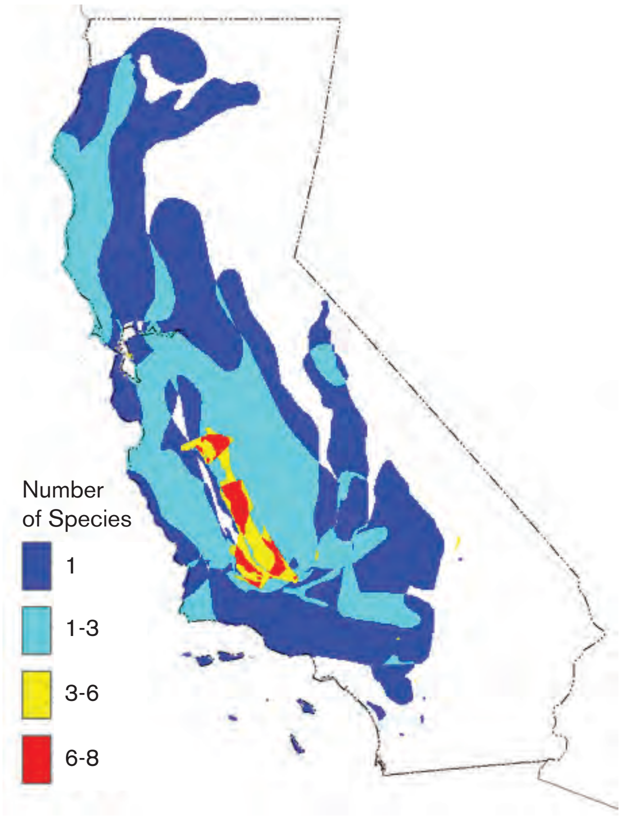

FIGURE 11.9 Diversity hotspots of mammal species endemic to California. Source: Li and Hadly unpublished data.

TABLE 11.2
Mammals endemic to California

Order	Family	Scientific name	Common name
Carnivora	Canidae	*Urocyon littoralis*	Island gray fox
Rodentia	Cricetidae	*Arborimus pomo*	California red tree vole
		Reithrodontomys raviventris	Salt-marsh harvest mouse
	Heteromyidae	*Dipodomys agilis*	Pacific kangaroo rat
		Dipodomys heermanni	Heermann's kangaroo rat
		Dipodomys ingens	Giant kangaroo rat
		Dipodomys nitratoides	Fresno kangaroo rat
		Dipodomys stephensi	Stephen's kangaroo rat
		Dipodomys venustus	Narrow-faced kangaroo rat
		Perognathus alticolus	White-eared pocket mouse
		Perognathus inornatus	San Joaquin pocket mouse
	Sciuridae	*Ammospermophilus nelsoni*	San Joaquin antelope squirrel
		Spermophilus mohavensis	Mohave ground squirrel
		Tamias alpinus	Alpine chipmunk
		Tamias ochrogenys	Yellow-cheeked chipmunk
		Tamias sonomae	Sonoma chipmunk
Soricomorpha	Soricidae	*Sorex lyelli*	Mount Lyell Shrew

SOURCE: IUCN 2013.

sexual maturity, and longer generation times. Therefore they typically recover more slowly than small mammals when populations are reduced. Whales, as the largest of all animals, are particularly at risk due to their low reproductive rate. Specialist species with particular habitat requirements are especially vulnerable to certain global environmental changes. For example, as temperature increases, suitable habitats for montane mammal species such as American pika (*Ochotona princeps*) become smaller, and these cold-adapted montane specialists can only move so high before they have nowhere to go.

State and federal hunting and fishing regulations combined with enforcement efforts have helped to protect California mammals from overharvesting, and further protections have come from state and federal laws on pollution, development, and agriculture (e.g., California Endangered Species Act, California Environmental Quality Act, and California Department of Fish and Wildlife). Today, approximately 200,000 km^2 of California (46% of the state) is protected, though much of this is desert and high mountain habitat lacking lowland species (CDPA 2013). The increasing number of protected areas has facilitated successful reintroductions of threatened mammal species in California such as the Perdido Key beach mouse (*Peromyscus polionotus trissyllepsis*) (Holler et al. 1989) and Stephen's kangaroo rat (*Dipodomys stephensi*) (Shier and Swaisgood 2012). About 90% of the mammal species present in California have at least part of their range outside the state. While conservation at state level is imperative to the survival of many species, especially because California has the highest mammal diversity (NatureServe 2002) and human population in the United States (U.S. Census Bureau 2013), many conservation challenges need to be addressed at regional, national, and international levels. Effective collaborations between California and other states are necessary for the protection and recovery of most large mammals, including the sea otter and elk. Still others, such as the gray whale and jaguar, require collaboration with Mexico, Canada, or both countries.

Summary

By almost all measures, California is the most biodiverse state in the U.S. and one of the most biodiverse regions of the world outside the tropics. California's high levels of endemism and species richness are related to its physical diversity, its Mediterranean climate, and perhaps its unique evolutionary history. Over 30% of California's species are threatened with extinction. However, fewer than 0.3% of California's native species have been driven to global extinction in the past two hundred years (see Table 11.1). This is remarkable considering the sheer scale and magnitude of California's agricultural development, suburban sprawl, water diversion, resource extraction, and pollution combined with the intentional and unintentional introduction of over fifteen hundred species and a history of overhunting and overfishing. Somehow, to paraphrase Aldo Leopold, we have managed to save almost all the pieces and, remarkably, now have a second chance to move into the future with thriving populations of nearly the full complement of California's flora and fauna. California is a wealthy state with a long history of environmental leadership and one of the world's most innovative societies. More than any high-biodiversity region in the world, California has the economic, cultural, and intellectual resources needed to have both thriving human communities and thriving ecosystems with their full diversity of species.

Although imperfect and heavily concentrated in desert and high mountain areas, the state's systems of protected areas cover 46% of its land area, offering the raw material for habitat in which species can persist and recover. With increasingly effective environmental regulation of wildlife harvest and pollution and the creation of new protected areas and smarter development, overharvest, pollution, and even habitat loss could become less significant drivers of new declines and extinctions. If this happens, then the most acute remaining challenges will be the damaging impacts of invasive species within natural and protected areas and the inability of protected areas to meet the needs of all their current species as California's climate changes. In California the days of government agencies casually introducing new species are long gone, and smarter policies govern invasive species prevention and management. Climate change will stress existing reserves and wildlife populations but may also provide new conservation opportunities. Just as California has been a national and global leader in a range of other social and economic areas, California can be a global leader in biodiversity conservation.

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Glossary

HERPETOFAUNA A collective term referring to all reptiles and amphibians that comprise the ectothermic (cold-blooded) tetrapods (four-limbed animals).

PLETHODONTID Referring to lungless salamanders, which make up the family Plethodontidae.

POLYMORPHISM The occurrence of more than one distinct type or "morph" in a single, interbreeding population.

RELICT In biology, a naturally restricted population whose distribution was much broader in an earlier period, typically on geological time scales.

RING SPECIES A series of populations geographically arranged in a ring, such that neighboring populations along the ring can interbreed but more distant populations cannot; and such that the "end" populations (where the ring historically closed) cannot interbreed even though they occur near each other. The *Ensatina* ring complex, which some argue is actually a series of distinct species, occurs in the ring of mountains surrounding the Central Valley.

TERRANES Mini-continents floating on oceanic crustal plates.

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