ONE

Introduction

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It is no small task to understand the characteristics of the various ecosystems that occupy California, since there are more different types here than anywhere else in the United States. This is the joy and marvel of living in a state where in a short distance, you can be in a completely different landscape from the one you live in. It could be the coast, a beautiful lake, a magnificent river, dramatic deserts, or the rich and diverse forests that occupy the state—or, for that matter, all of those landscapes depending on the direction you pick. As pioneering California biologist and university president David Starr Jordan (1898) wrote, "There is from end to end of California scarcely a common mile."

The task that we lay out in this book is to bring together the necessary knowledge to understand the nature of California's diverse landscapes and their biotic and social character so we can not only appreciate their uniqueness but also position ourselves to ensure that they are being utilized sustainably, at present and into the future. We take the position that these diverse systems are not totally isolated from one another but rather are linked and interacting to varying degrees. Thus we take on the challenge of assembling information on all of California's systems, managed and natural, terrestrial and aquatic. We look not only at the status and dynamics of these systems at present but also at how these systems came to be and how they are likely to look in the future. We understand that although California is somewhat of an ecological island, isolated by mountains and climate from much of the continent that it bounds, it is not unconnected from the rest of the nation and world. The lessons we gather from a comprehensive look at this singularly diverse and complex state can, we hope, inspire integrative and dynamic thinking about ecological systems elsewhere.

The Need for This Book

More great books about the NATURAL world and our connections to it have been written about California than probably anywhere else. So far, however, these books have not included a comprehensive, process-oriented ecology of the entire state. California contains more distinct ecosystem types by far than any other U.S. state. California has also had a long, complex, and unique history as a dynamic social-ecological system. It is both the most biodiverse and the most demographically diverse state in the nation. It hurtles towards a complex, unique, and uncertain future. In this book we strive to focus on process in every sense—on the cross-scale processes that define the boundaries and character of each of California's

ecosystems; the interacting social and ecological dynamics that have shaped the ecosystems we see today and continue to shape them going forward; the articulations between systems defined ecologically and systems defined by human enterprise, from fisheries to agriculture to cities; and the prospects for stewardship now and in the coming century. The result is a book with twice as many chapters as we first planned, and even so with gaps.

Why did we feel we needed this book? First, although many courses are taught about California's ecology in the state's institutions of higher learning, there has been no comprehensive text available to cover the diverse ecosystems of the state from terrestrial to aquatic to marine; their distribution, structure, and composition and functional attributes; and least of all the range of natural and managed systems. We both have been teaching university courses about California's ecology for a long time without an accompanying text. One of us (Hal) taught *Ecosystems of California* at Stanford for some forty years using materials culled from a great variety of sources. Especially in a state renowned globally for its university system, it ought to be easier for people to teach and learn about California's tremendous diversity of ecological systems. Beyond the classroom, a comprehensive overview of the state of knowledge about California's many ecosystems could serve as a valuable reference for researchers, decision makers, and stewards. Among other things, each of the chapters in this book addresses knowledge gaps that highlight opportunities and needs for new scholarship; history that provides context for what we see today; and past, current, and future threats and losses that highlight opportunities and needs for policy and management action. The volume is intended as a source book for teaching and for conservation, policy, planning, and decision-making in California.

Second, we wanted to capture the complexity and dynamism of a more comprehensive set of systems in California than other works have. The field of ecology has evolved over the past several decades to embrace perpetual dynamism, historical contingency, cross-scale interactions, and emergent features. This approach has replaced a more static view and a focus on structure, inviting more attention to function and processes. Much of this contemporary perspective on ecology has been explored but not synthesized in California, and it deserved to be brought together in one place. Finally, an up-to-date treatment of the history, ecology, management, and future of each of California's ecosystems could undergird targeted research, informed management and stewardship, and inspired decision-making and citizenship. It could make plain what we know—and what we need to know. It could also provide a view of the state's ecology as integrated with and dependent on, rather than artificially separated from, the state's economy, culture, and human communities. Because we care about the diversity and ecology of California, we want to explore and articulate how contingent its past has been and its future will be on our collective choices and decisions.

Photo on previous page: California brown pelicans (*Pelecanus occidentalis californicus*) and early winter swell, Scotts Creek, California. Listed as endangered in 1970 due to severe DDT exposure throughout the U.S., brown pelicans recovered gradually after DDT was banned in the early 1970s and were officially delisted in 1999. Their recovery reminds us that California's ecosystems today reflect a history of conservation successes as well as human impacts. Photo: Ed Dickie (eddickie.com).

The Early Development of Ecology in California: A Different Path Taken

What we know best and least about California's ecosystems is colored by the unique development of ecology as a science in this state. California is an island ecologically, and it was also an island in the way our knowledge of natural systems developed through time. This yielded both innovations originating in the state and gaps peculiar to California. Michael Smith (1987) noted, for example, that early Californian scientists were influenced by their "observation of California's physical environment [that] profoundly affected their thinking—both about science and about their new home. The peculiarities of their social environment influenced the ways in which they sought support for science and eventually prompted their efforts to arbitrate between the land and its occupants. These forces, compounded by geographic separation from other scientists, contributed to a professional role for earth and life scientists that differed in significant ways from that of their Eastern counterparts" as did the "rich intermingling of environmental influences [that] checkerboards California with dissimilar ecosystems . . . [that] compress into dramatic adjacency in California" in contrast to the gradual nature of ecosystem change (through space) in other parts of the country.

California did not achieve statehood until 1850, three-quarters of a century after the establishment of the United States. In 1853 a small group of citizens in San Francisco founded the California Academy of Sciences to provide a home for the state's growing natural history collections. The San Francisco Bay Area became the initial hot spot for the early buildup of local scientific capacity at the academy as well as at the emerging universities. In 1868 the University of California was founded, and early faculty including Joseph LeConte, E. L. Greene, Willis Lynn Jepson, and Joseph Grinnell combed the state to catalog its geological, plant, and animal diversity. They rapidly accumulated deep knowledge about both the state's biogeography and the ecological and behavioral traits of the specimens that they collected. The scientific basis for the optimal use of California's natural resources by society was fostered from the outset because the new University of California was designated from its beginnings as a land grant university. A College of Agriculture was established in 1875, and in 1913 a forestry division was added.

In much of the U.S. and beyond, scientists involved directly in studying natural systems often avoided those with a human presence. In California, environmental science and protection of natural systems coevolved more closely, reducing the lines dividing ecology from conservation. In the early twentieth century, leading ecologists in the state became alarmed at the extensive overexploitation of its natural wealth and took direct actions to ensure its protection. They became directly involved in conservation efforts and helped ignite a national conservation movement through their roles in founding the Sierra Club and the Sempervirens Club. Then as now, California had the opportunity for leadership in bridging scientific knowledge to sound conservation and resource management policies and actions.

Emergent Patterns

The chapters in this book were written by a diverse cadre of experts on California's ecosystems. Each team of authors, of

FIGURE 1.1 Wildfire sunrise in Lassen Volcanic National Park. Photo: Ed Dickie (eddickie.com).

course, brought its own set of perspectives to the chapter in question and chose to a large degree how best to structure the chapter to reflect its subject. This inevitably produced differences in the emphases of each chapter on particular ecological scales, taxonomic groups, trophic levels, and so on. Nevertheless, we strived for strong coverage in every chapter across ecological scales (from organismal adaptations to species interactions to feedbacks and interactions between community and ecosystem scales), time periods (from historical to future), and applications (from basic ecology to conservation, management, and policy implications). As a result, variation among chapters reflects genuine differences in knowledge, state, and stressors of each system, among other things. For example, it became clear in the process of developing the chapter on alpine ecosystems (29) that very little research has been done on the ecosystem ecology of California's alpine; this is reflected in the chapter's coverage of that topic.

By the same token, consistency among chapters reveals some genuine, emergent patterns that we did not necessarily expect at the outset. A strong pattern emerging across many ecosystems from chapters here deals with the historic moment we inhabit in California's conservation trajectory. Chapter after chapter describes the recovery of species and systems from a nadir of environmental quality that occurred roughly forty to fifty years ago. To a surprising extent, some trends have been successfully reversed, such as declining air quality in California's cities (see, e.g., Chapters 7 and 39) and declining species from island endemic plants to peregrine falcons to sea otters in the face of stressors from DDT to overharvesting and invasive species (see, e.g., Chapters 11 and 34). Older legacies, like the widespread damage caused by overgrazing and gold mining in the nineteenth century, have both continued to fade with time and been actively addressed by restoration and remediation efforts (see, e.g., Chapters 5, 19, and 33) and changes for the better in management of such forces as fire and grazing (see, e.g., Chapters 3, 23, and 37) (Figure 1.1). These successes are tempered by at least two other trends: the ongoing loss of habitat to continued urban and exurban development (see, e.g., Chapters 5, 22, 25, and 31) and the emergence of climate change as a growing, ubiquitous force influencing California's ecosystems (see, e.g., Chapters 14, 17, 26, 27, and 29, among many others).

California's ecosystems can be profound integrators of the complexity around interacting environmental changes at various temporal and spatial scales; for example, the acid neutralizing capacity of Emerald Lake in the Sierras declined steadily from about 1920 to 1970 before beginning to climb from the late twentieth century to the present, possibly reflecting first the effects of rising fossil fuel burning and acid deposition, then the effects of advancing snowmelt under increasing temperatures (Chapter 32). Examples from throughout the volume make clear the prevalence of interactions of this nature across ecosystems. Across the state, matter and energy move downstream, such as the movement of sediment, nutrients, and other compounds from forest to river to estuary to intertidal and kelp forest ecosystems (Chapters 17–19, 28, and 33); and upstream, such as in the fires that burn from the montane forest up into the subalpine forest (Chapters 3 and 28), the nutrients moved by anadromous fishes from the ocean to freshwaters and nearby terrestrial settings (Chapters 33 and 35), and the air masses that carry moisture, pollutants, and even propagules from the coast to the mountains (e.g., Chap-

ters 2, 7, and 27). Source and sink relationships abound; entire heterotrophic ecosystems in California, subsidized by flows of energy and matter from other ecosystems, range from its estuaries (Chapter 19) to its cities (Chapter 39). Offshore, upwelling associated with the California current generates tremendous marine diversity and productivity that move among the porous boundaries of intertidal, rocky reef, estuarine, open ocean, and sandy beach ecosystems (Chapters 16–20) in forms ranging from carcasses to suspended particulate organic matter.

A third, emergent pattern from across systems concerns north-south distinctions in dynamics, threats, and in some cases perspectives on ecology that arise from differences in what studies have emphasized as well as in the underlying systems themselves. These contrasts and gradients across the latitudinal range of the state are most clear for ecosystem types that span a large part of the state. For example, the dynamics and dominance of invasive plant species vary markedly from south to north in coastal sage scrub (Chapter 22) and grasslands (Chapter 23). The historical and present roles of fire vary from south to north in chaparral ecosystems (Chapter 24); treeline elevation shifts (Chapters 28 and 29); and dominant species turnover in systems ranging from desert scrub (Chapter 30) to montane (Chapter 27) and kelp forests (Chapter 17). Finally, although statewide development patterns have altered coastal, low-elevation ecosystems more and interior, high-elevation ecosystems less (e.g., highly altered and fragmented coastal sage scrub, intermediate desert [low, interior], and relatively unfragmented subalpine and alpine), the condition of particular ecosystems tends to vary more, and in complex ways, along north-south lines than from west to east. For example, coast redwood forests (Chapter 26) experienced historically high rates of clearing throughout the coast but are now more affected by fire, climate change, and disease to the south than in the state's north. Grasslands (Chapter 23) are more fragmented, converted, and invaded in the south than in the north within the coastal and interior valley grassland types.

Structure of the Book

We designed this book to be used in a variety of ways to reflect a diversity of needs. We provide this brief overview as a road map to the book and a guide for selecting sections and chapters for reference, teaching, and study. Throughout the volume, chapters include recommended further readings and chapter-specific glossaries of technical terms not described in the text. We also chose to keep the references with each chapter to facilitate use of individual chapters for reference and teaching.

The first part of the book following this introduction examines overarching drivers of patterns and processes on the California landscape ("Drivers," Chapters 2–7). Although we initially conceived of them as more or less abiotic drivers, in reality they occupy a range from strongly abiotic (e.g., oceanography, climate) to largely influenced by biotic forces (e.g., fire, soils) and all incorporate, again to varying degrees, the effects of human activities. In particular, the chapters on atmospheric chemistry (7) and population and land use (5) explicitly focus on human drivers, and the chapter on fire as an ecosystem process (3) deals extensively with human effects on fire regimes. The chapter on population and land use is a hybrid between a historical and a driver chapter; it is the abridged story of how human population and land use dynamics and in the postcolonial era have shaped the lay of the land today. We felt that if we placed it in the history part of the book ("History," Chapters 8–10), we would erroneously convey that land use and human habitation are less-than-critical drivers of ecosystem patterns and processes in California.

The next three chapters focus on history: the paleohistory of vegetation and animals, respectively, and an ecological history of indigenous Californians and their roles in shaping the California we see today. The chapter on paleovegetation (8) necessarily tackles the stage for vegetation history in the region and covers the geomorphological, climate, and ecosystem history of California. The chapter on vertebrate prehistory (9) focuses on mammals as the best-understood group in the paleorecord and traces their history in the region from sixty million years ago. The chapter on indigenous California (10) illustrates the degree to which scholarly debate and changing political contexts can influence, over time, conceptions of how people related to and shaped their environment in the past, and how that history has influenced today's ecosystems.

The next five chapters ("Biota," Chapters 11–15) describe overarching biotic patterns, threats, and concepts as a foundation for the rest of the book. The chapter on biodiversity (11) provides an overview of the state's biological diversity and its spatial distribution, threats, and success stories across five focal taxonomic groups (plants, birds, mammals, invertebrates, and herptiles [amphibians and reptiles]); subsequent chapters give an overview of the state's major patterns of terrestrial vegetation (12) and of the special, widespread issues of biological invasions (13) and climate change impacts (14) in relation to the state's ecology. The final chapter in this section (15) describes emerging understanding and framing of the relationships among biological diversity, ecosystem functioning, ecosystem services, and natural capital, which recur in nearly every subsequent chapter.

The next part of the book describes the state's ecosystems ("Ecosystems," Chapters 16–33). This section proceeds roughly from the offshore Pacific Ocean towards land, then inland and upward in elevation, and finally down the eastern mountain slopes to the desert. Chapters 31–33 double back and tackle the major freshwater systems (wetlands, lakes, rivers) distributed across the state's terrestrial ecosystems. Each chapter in this part describes the process-based ecology of an ecosystem: its distribution and the factors that shape it; key constituent species, species interactions and processes such as disturbance regimes; ecosystem dynamics, including trophic interactions and the cycling of elements; and ecological history, including the influences of people. Each chapter also describes the services to society associated with that ecosystem; the threats and challenges it faces; and likely future trends, challenges, and opportunities for its management.

In this section we had to make some tough decisions about how to lump and split, and where to accept uneven coverage that reflected space constraints as well as knowledge gaps. For example, we decided not to split estuarine subtidal and salt marsh systems into separate chapters but to include both within a single chapter on estuaries (19), or to split deserts (30) into the various desert types that characterize eastern California but to combine them in one large chapter. Enough is known about each subsystem for a book, but this book had to fit between one set of covers. The chapters vary in length and balance among components, reflecting author choices as well as varying availability of knowledge about particular

systems. For example, the chapter on alpine ecosystems (29) focuses especially on geomorphological processes and biotic communities, with less emphasis on ecosystem dynamics, simply because less is known about them specifically in California's alpine.

The next part of the book describes managed ecosystems ("Managed Systems," Chapters 34–39), defined variously by the societal endeavors that created them and proceeding roughly from less to more strongly human-altered managed systems. California's islands (Chapter 34) are a microcosm of many of California's coastal systems but are distinct both ecologically, as islands, and in terms of their management for diverse purposes ranging from military to conservation to recreation. California's marine fisheries (Chapter 35) are defined by the organisms they harvest, while forestry (Chapter 36) is an activity defined by the ecosystems that can support it, and range (Chapter 37) is what livestock do when they are let out to forage. The chapter on agriculture (38) emphasizes the history and economy of an activity that defines much of the state's landscape and water use and supplies much of the country. The chapter on urban ecosystems (39) enters relatively new terrain, applying ecological concepts to the city as an ecosystem and examining how it supports biodiversity and ecosystem services in unique ways.

The final two chapters in the book return to stewardship ("Policy and Stewardship," Chapters 40 and 41). The chapter on regulation for resource conservation (40) traces efforts to regulate land use and stewardship over California's history. The chapter on stewardship, conservation, and restoration in the context of environmental change (41) pulls together themes and cases from across the book to examine effective paths to sustain California's ecological legacy into the future.

We live in exciting times; California is in a state of accelerating change, but so is our knowledge about its ecological dynamics and their articulation with conservation and management efforts. In keeping with the spirit of pervasive dynamism that kindled this effort, we have already begun to think about the next edition of this volume; we would be grateful for your feedback. Finally, we hope this book will build understanding and guide stewardship of California's incredible diversity, with appreciation for the layers of historical and dynamic forces reflected in the landscapes of this great state.

Recommended Reading

A diversity of great books tackle California's ecology from many angles. They include the literary—from John Muir's *The Mountains of California* (1875) to John McPhee's "Los Angeles against the Mountains" (1989) and *Assembling California* (1993) to the anthology of Jack London's California works, *Golden State* (Haslam 1999). They include the taxonomic—from Jim Hickman's great *Jepson Manual* of the state's vascular plants (1993), now in its second edition (Baldwin et al. 2012), to *Inland Fishes of California* (Moyle 2002). They include a great many natural histories, including Allan Schoenherr's *A Natural History of California* (1995) as well as scores of guides to particular systems, regions, groups of organisms, weather, glaciers, ethnobotany, and geology. They include conservation surveys—the *Atlas of the Biodiversity of California* (Parisi 2003) summarizes tremendous information and knowledge in maps; while *Life on the Edge: A Guide to California's Endangered Natural Resources* centers on wildlife, threats, and their management (Thelander and Crabtree 1994).

We cannot fail to mention the works of historical ecology, like Laura Cunningham's *A State of Change* (2010) and the comprehensive *California Grizzly* (Storer and Tevis 1996); the comprehensive *Manual of California Vegetation* (Sawyer et al. 2009) and *Terrestrial Vegetation of California* (Barbour et al. 2007); and the many whole volumes exploring the comprehensive ecology of individual ecosystems (like *California Grasslands*, Stromberg et al. 2007), processes (like *Fire in California's Ecosystems*, Sugihara et al. 2006), and threats (like biological invasions in *California's Fading Wildflowers*, Minnich 2008). Many books—from Ray Dasmann's rousing *Destruction of California* (1965) to the cautious optimism of volumes like *In Our Own Hands* (Jensen et al. 1993)—lay plain the conservation challenges that we face in California and impel us to act.

Finally, a number of valuable California ecosystem resources exist online. The California Naturalist Program (http://calnat.ucanr.edu/) provides naturalist certification and training to members of the public interested in stewardship. It is one of many excellent efforts to build citizen science and service in the state. Considerable data and educational resources reside on the websites of the California Academy of Sciences, Berkeley's Jepson Herbarium and Museum of Vertebrate Zoology, the California Invasive Plant Council, the California Native Plant Society, and many state agency sites.

We have surely forgotten to mention volumes and efforts that we cherish, but their sheer numbers make it hard to call them all up at once.

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