Adapting California's Ecosystems to a Changing Climate

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Significant efforts are underway to translate improved understanding of how climate change is altering ecosystems into practical actions for sustaining ecosystem functions and benefits. We explore this transition in California, where adaptation and mitigation are advancing relatively rapidly, through four case studies that span large spatial domains and encompass diverse ecological systems, institutions, ownerships, and policies. The case studies demonstrate the context specificity of societal efforts to adapt ecosystems to climate change and involve applications of diverse scientific tools (e.g., scenario analyses, downscaled climate projections, ecological and connectivity models) tailored to specific planning and management situations (alternative energy siting, wetland management, rangeland management, open space planning). They illustrate how existing institutional and policy frameworks provide numerous opportunities to advance adaptation related to ecosystems and suggest that progress is likely to be greatest when scientific knowledge is integrated into collective planning and when supportive policies and financing enable action.

Keywords: adaptation, adaptive capacity, ecosystem service, global change, Mediterranean climate.

Climate change will transform the Earth's ecosystems over the twenty-first century (Diffenbaugh and Field 2013, Grimm et al. 2013). The speed and pervasiveness of these changes pose significant challenges for ecosystem management and conservation, because they require managing systems that are moving relatively rapidly along uncertain trajectories of change. Nevertheless, substantial efforts are underway to understand and meet these challenges, and a marked shift is occurring from building conceptual knowledge about climate change impacts to taking practical action to secure future ecosystem benefits. In this article, we examine this ongoing transition, drawing on recent experience in the state of California.

Adapting ecosystems to climate change

Well-functioning ecosystems are crucial for societal well-being and the source of tremendous economic wealth (e.g., MA 2003). They provide numerous benefits (often called *ecosystem services*), such as water storage and delivery, flood protection, nutrient cycling, carbon storage, shoreline protection, timber and agricultural production, recreational opportunities, and habitats for wild species. Goals related to sustaining or enhancing the delivery of these and other benefits are firmly embedded in federal, state, and local public policies and the missions of diverse private sector organizations. The rapidly changing climate is placing the benefits that society derives from ecosystems at risk, in that it alters the underlying ecosystem structures, functions, and processes that generate these benefits (IPCC 2014). In addition, natural and managed ecosystems are key to many emerging strategies for adapting public infrastructure to climate change, such as relying on wetlands for shoreline protection (e.g., ecosystem-based adaptation, nature-based solutions, green infrastructure; IPCC 2014). Designing climate adaptation strategies to secure well-functioning ecosystems, consequently, has become an urgent priority.

In this article, we focus on societal efforts to adapt ecosystems to climate change by implementing strategies that support the functioning of and optimize the delivery of diverse benefits from current and future ecosystems, even as those ecosystems undergo significant climate-driven changes (box 1). In many places, this will require finding ways to optimize benefits from ecosystems that are in transition or have transformed to alternative states—shifts likely to alter the portfolio of benefits derived from a given ecosystem (Hobbs et al. 2013). It will also require maximizing the adaptive capacity of ecosystems—that is, the ability of an ecosystem (made up of living organisms, the abiotic environment, and associated interactions) to adjust to climate change in ways that sustain ecological functions and benefits or that enable desired ecosystem transitions.

Biological diversity arguably provides the raw material for this adaptive capacity, which can be enhanced or reduced by management choices (MA 2005, Chapin et al. 2009). Genetic

BioScience 65: 247–262. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. This work is written by US Government employees and is in the public domain in the US.
doi:10.1093/biosci/biu233 Advance Access publication 11 February 2015

Box 1. Key terms.

In this article, we use definitions provided by the Intergovernmental Panel on Climate Change (IPCC) as applied to ecosystems (IPCC 2014).

Adaptation. "The process of adjustment to actual or expected climate and its effects. In human systems, adaptation seeks to moderate harm or exploit beneficial opportunities. In natural systems, human intervention may facilitate adjustment to expected climate and its effects" (IPCC 2014, glossary p. 1). The IPCC definition includes *incremental* actions to maintain the essence and integrity of a system or process at a given scale and *transformational* actions to change the fundamental attributes of a system.

Adaptive capacity—"The ability of systems, institutions, humans, and other organisms to adjust to potential damage, to take advantage of opportunities, or to respond to consequences" (IPCC 2014, Glossary p. 2).

and population diversity can enhance species persistence by enabling evolutionary adaptation or range shifts as conditions change. In turn, population, species, and community diversity can support ecosystem state transitions, shifts in an ecosystem's geographic boundaries (e.g., inland migration by coastal wetlands), and continued delivery of benefits by ecosystems in transition (Isbell et al. 2011). Biodiversity conservation is therefore both a benefit provided by certain ecosystems and a crucial strategy for ensuring the long-term delivery of societal benefits from many ecosystems under climate change.

Setting goals and managing ecosystems in transition will be among the most significant technical challenges ahead. Such choices will necessarily be context dependent and bounded by the anticipated trajectory of change; the feasibility of influencing the direction or rate of change; and the desired benefits from current, transitional, and future ecosystems (Chapin et al. 2009). Adapting ecosystems to climate change may, in some cases, involve preventing undesired changes (e.g., the disappearance of coastal habitats). In others, it may require slowing rates of change to facilitate more-gradual transitions, such as by preventing intense wildfires (Moritz et al. 2013) or unprecedented flooding, which rapidly degrade adaptive capacity. Sometimes, however, the best approach may be to enable and shape ecosystem shifts. Enabling strategies will range from passive (e.g., protecting habitat to support species range shifts) to active (e.g., facilitating rapid ecosystem state transitions after major disturbances through restoration choices or managed relocation).

Applied efforts to adapt ecosystems to climate change must surmount scientific and practical impediments. Uncertainties will persist in projections of climate change's ecological effects (Lawler et al. 2010) and in identifying causal links among ecosystem structures, functions, and processes and many ecosystem benefits (Daily and Matson 2008). Also, diverse interests, jurisdictions, and sectors will often need to adopt shared goals and to act cooperatively, despite differing priorities. Setting these goals can be complex, involving trade-offs between short- and long-term goals or differences in the perceived benefits provided by alternative ecosystem states that vary with observational scale. Importantly, opportunities for adapting ecosystems often occur amid other human activities and resource uses and, therefore, require balancing goals for long-term ecosystem condition with other societal needs and directing limited funding and political will toward the ecosystem goals.

Despite such challenges, considerable progress has been made over the past decade in identifying practical and tractable steps to improve the status and condition of ecosystems as climate changes (Harris et al. 2006, Millar et al. 2007, Chapin et al. 2009, Heller and Zavaleta 2009, Lawler 2009, Hobbs et al. 2013, CBI 2014), and common principles have begun to emerge (Peterson et al. 2011, NFWPCAP 2012, Stein et al. 2013). Conditions on the ground will significantly affect where and how these principles are applied in practice.

The California context

California provides a particularly good place for understanding and rapidly piloting approaches for addressing climate-driven ecosystem changes. The needs arising in California are common to many other places, and the levels of scientific knowledge and capacity are high (CNRA 2009, Franco et al. 2011). The state is aggressively undertaking reductions in greenhouse gas emissions, carbon mitigation, and renewable energy options, and California has had a statewide climate adaptation strategy since 2009 (CNRA 2009).

Much is already known about how California's climate is changing (CNRA 2009, Franco et al. 2011). Temperatures are increasing, precipitation patterns are shifting, the sea level is rising, and stream flows are becoming more variable (CNRA 2009). Projections show that these changes will persist or intensify over the next century (Franco et al. 2011). Less precipitation will fall as snow, and the snowpack will melt earlier in the spring, altering seasonal water flows. The summer and fall dry season will become longer, and rising temperatures will reduce soil moisture (Flint et al. 2013). The frequency and magnitude of extreme events—heat waves, droughts, intense wildfires, coastal storm surges, and inland flooding—are expected to deviate further from historical norms.

The ranges of many animals and plants in California have already shifted in response to changing temperatures and water availability (e.g., Moritz et al. 2008, Rapacciuolo et al. 2014). Looking ahead, existing ecological systems will, in most places, change substantially as species respond individualistically to climate-driven change and as biophysical processes that structure ecosystems become less hospitable to current plant and animal assemblages. As society adapts to new climate

Box 2. Operating principles for adapting California ecosystems to climate change.

(See RLF 2012 for rationale and details.)

Create a landscape that will optimize the adaptive capacity, benefits, and options for desired transitions of California's ecosystems

- Strategically augment protected areas and protected area networks to capture a greater diversity of ecological settings and to include climate gradients, complex topography, and native species refugia. *Ecological settings* are relatively stable physical attributes of the environment that, in combination, give rise to the ecological and evolutionary processes that generate and support biological diversity. Such attributes can be directly observed (e.g., enduring landscape features like topography and soils) or inferred (e.g. from vegetation and climate patterns).
- Link today's habitats with suitable habitats of the future to enable ecosystem transitions and range shifts of species that have diverse dispersal capabilities. Strategically augment current connectivity areas with enduring landscape features (support range shifts under any future climate), climate gradients (allow species to track changing climates), riverine features (persistent conduits for animal movement), physically heterogeneous areas (provide refugia during rapid climate change), and appropriately managed working lands.

Plan for a future of greater water scarcity and altered seasonal flows in conserving and managing aquatic ecosystems

- Maintain and restore priority watersheds that have high conservation value and where feasibility of maintaining well-functioning aquatic ecosystems in the future is also high. Choose water management actions that meet societal needs (e.g., water delivery, flood control) while sustaining watershed functions and adaptive capacity.
- Maintain ecologically viable remnants of California's river and stream ecosystems by providing flows and cold-water habitats for high value native species like salmonids (e.g., adjust dam operations or protect cold-water springs and headwaters).

Sustain coastal ecosystems as sea level rises

- Anticipate risks to coastal wetlands, dunes, bluffs, beaches, and estuaries from flooding and accelerated erosion. Sustain ecosystem functions (e.g., enable inland retreat, adjust sediment flows, breach levees to transition from fresh- to saltwater marshes).

Optimize cobenefits for people and ecosystems of societal strategies for adaptation and mitigation

- Rely on intact ecosystems, where possible, to reduce climate related threats to people and infrastructure. Anticipate and reduce harm to ecosystems from built solutions for adapting human communities and infrastructure and for mitigating climate change.

Manage ecosystems in ways that anticipate increased frequencies of extreme events (e.g., coastal surges, droughts, intense fires, high heat days, invasive species and disease outbreaks)

- Where appropriate, manage ecosystems to sustain functions and benefits, to prevent undesired changes, or to slow, direct, or facilitate transformations (e.g., prevent catastrophic fires, enhance floodplain capacity to store and gradually release floodwaters).

Manage for the future

- Integrate future projected conditions into management decisions by recalibrating existing mandates and policies, anticipating dynamic species ranges and novel ecosystems, and developing new decision tools for controversial choices (e.g., when to facilitate ecosystem transitions).

Make decisions now and act adaptively

- Use burgeoning information resources that match the scale of resource management decisions (e.g., downscaled climate projections, projected ecosystem effects and sea-level rise) coupled with flexible decisionmaking processes to address uncertainties (e.g., adaptive management, scenario planning, robust decisionmaking, bet hedging).

regimes, shifting infrastructure and resource uses may further alter the state's ecosystems and the associated societal benefits.

In 2012, a California philanthropy, the Resources Legacy Fund, invited several of us (EAC, DDA, PB, FWD, LEF, JJL, MAM, and PBM) to synthesize the best available scientific knowledge into concise principles for advancing efforts to adapt California's ecosystems to climate change. The resulting operating principles (box 2) are intended to support current and future ecosystem functions, benefits, adaptive capacity, and transitions (RLF 2012). They are consistent with emerging national approaches (e.g., NFWPCAP 2012, Stein et al. 2013) but are tailored to California conditions, which include high topographic and environmental heterogeneity, biodiversity, and endemism; seasonal water flows and water scarcity; fire-dependent ecosystems; and extensive coastlines. The principles are focused primarily on ecological systems, rather than on individual species, and are intended to support diverse and dynamic species assemblages. They also address the potential for extreme events to cause ecosystem state shifts and require articulating expectations for a different future, despite the uncertainties.

In the four California case studies that follow, we explore real-world applications of the principles. Because societal efforts to adapt ecosystems to climate change are just now starting, they are all in the initial phases. The case studies span large spatial domains and encompass various ecological systems and uses and diverse institutions, ownerships, and policies (figure 1).

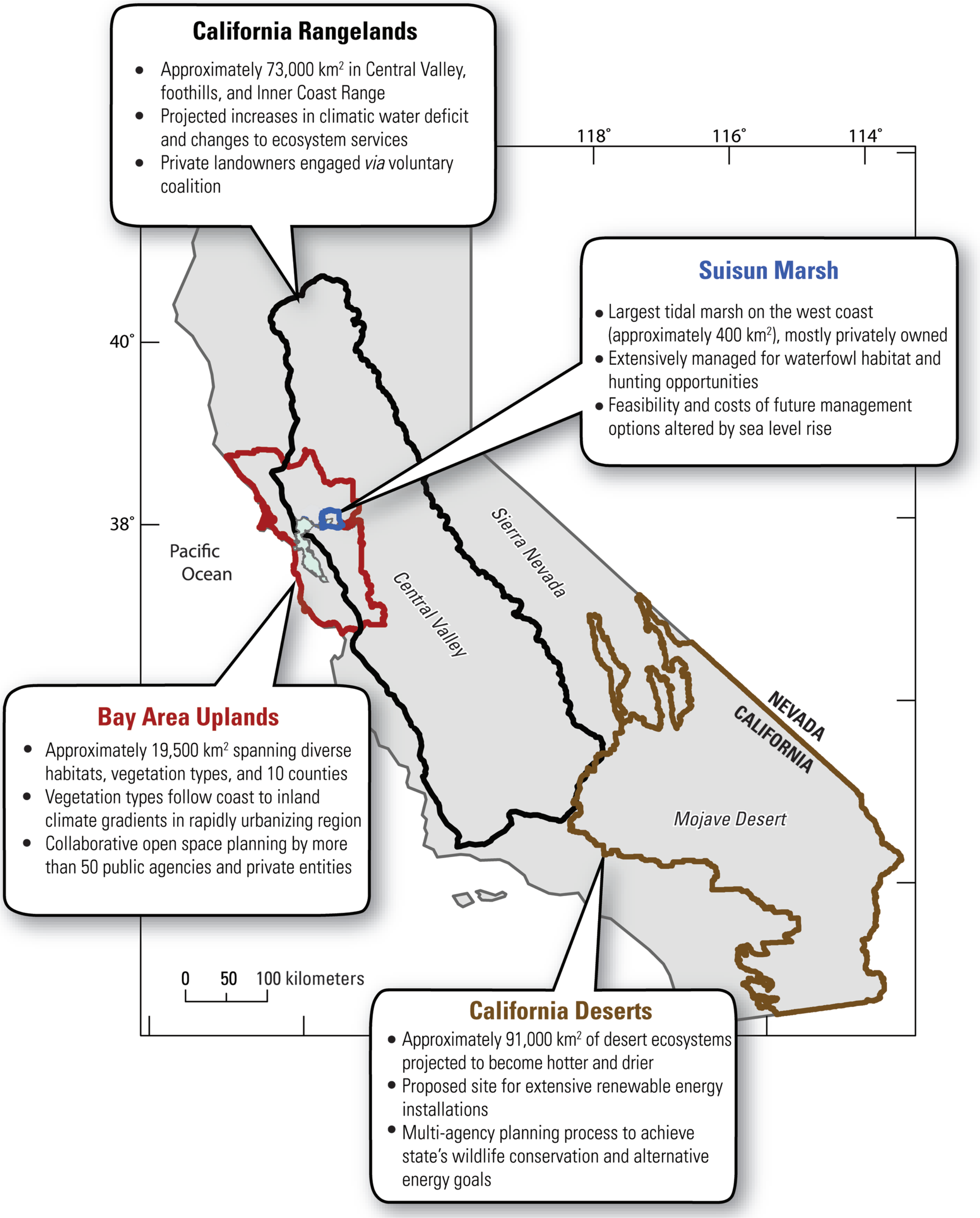

Figure 1. The California case studies. The four case studies span large spatial domains and encompass various ecological systems and uses and also diverse institutions, ownerships, and policies.

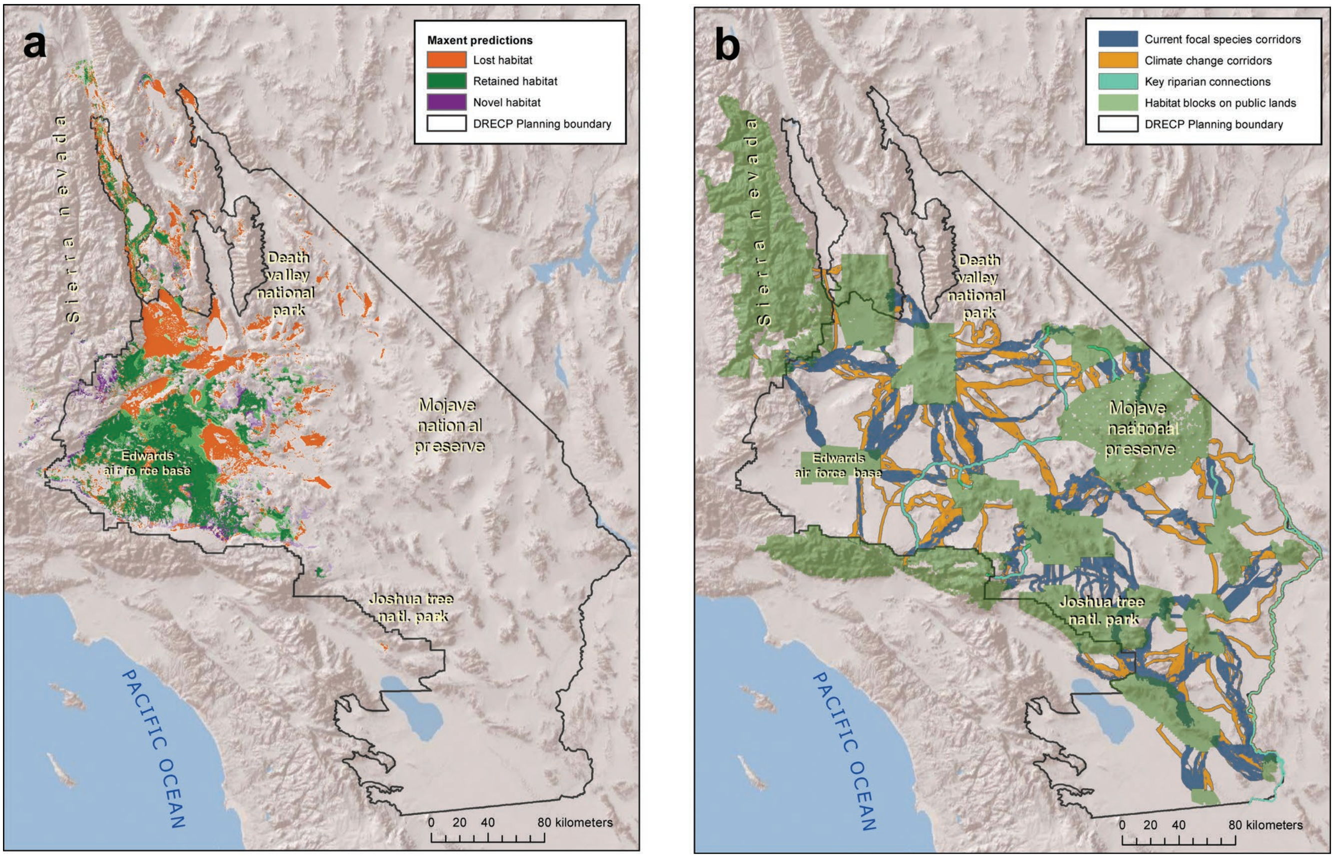

*Figure 2. How decisions about the siting of infrastructure for alternative energy development in California's southeastern deserts can consider the ecological effects of changing climate. The geographic distribution of suitable habitats will shift for many species. Mid-century projections for the threatened Mojave ground squirrel (***Xerospermophilus mohavensis***), based on the current association of the species with climate and soils, is shown in panel (a). The orange, green, and purple areas are projected lost, stable, and novel habitats, respectively, based on climate means for the period 2040–2069. The different shading levels indicate the level of agreement in projected species distribution based on three different climate models and business-as-usual emission scenarios, with the darkest shades indicating consensus among the three models. Conserving corridors that link today's habitats with suitable habitats of the future will be necessary to support species range shifts. The linkage design for the Desert Renewable Energy Conservation Plan region prepared for the US Bureau of Land Management and The Wildlands Conservancy shown in panel (b) combines current corridors for 44 focal species (including mammals, birds, lizards, snakes, insects, and plants) with corridors designed to support species movements under climate change. The latter are intended to support movement under any future climate and time, including but not limited to the scenario shown in panel (a). These climate corridors are based on land facets—enduring features of the landscape defined by topographic and soil properties such as landform, elevation, slope, insolation, soil wetness index, soil texture, and soil nutrients (Beier 2012; see the supplemental material for additional detail). Figure by Kristeen Penrod, adapted from (a) Davis and colleagues (2015) and (b) Penrod and colleagues (2012).*

Case study 1: Adaptation meets utility-scale development of renewable energy in California deserts

California's approximately 91,000 square kilometers (km^2) of southeastern deserts, encompassing parts of the Mojave and Sonoran Deserts, constitute the state's largest and most intact natural landscape; about a third is designated as wilderness. The most significant human impacts over the past 10,000 years have been a handful of linear infrastructure projects, including highways, canals, railroads, and power transmission lines, and substantial areas affected by military activity. These deserts, already the hottest and driest region of the United States, have warmed significantly since the 1970s (Redmond 2009) and are projected to become hotter and drier in the twenty-first century (Karl et al. 2009). The geographic distribution of suitable habitat for many species may shift significantly and rapidly (figure 2a; Davis et al. 2015).

In 2008, California Executive Order S-14-08 mandated that 33% of the state's electricity must come from renewable sources by 2020, spurring proposals for approximately 36,000 km^2 of industrial solar and wind energy projects in the region. The 4000–8000 km^2 of energy projects that are eventually likely to be built could have substantial ecological impacts. Large installations—and the associated roads, transmission lines, and human workforce—could significantly fragment the landscape, thereby limiting opportunities for species range shifts; degrading desert habitats; and undermining the ecosystem's conservation benefits, adaptive capacity, and transitions under climate change. Numerous *endangered* species could be affected, such as the desert tortoise (*Gopherus agassizii)*, the desert bighorn sheep (*Ovis canadensis nelsoni*), and the Mohave ground squirrel (*Xerospermophilus mohavensis*).

To reduce such collateral ecological impacts and achieve California's dual policy goals of wildlife conservation and renewable energy development, a collaborative effort was initiated in 2008 to create the Desert Renewable Energy Conservation Plan (DRECP) by the California Energy Commission, the California Department of Fish and Wildlife (CDFW), the US Bureau of Land Management (USBLM), and the US Fish and Wildlife Service (USFWS). If approved, the DRECP will serve as a general conservation plan, covering approximately 22,300 km^2 of nonfederal lands to streamline the development of habitat conservation plans under the US Endangered Species Act; a USBLM land-use-planning amendment covering approximately 40,000 km^2 of federal lands; and a natural community conservation plan under the California Natural Community Conservation Plan Act for reconciling economic development and conservation across the entire planning region.

Although measures to benefit covered species (i.e., those listed or likely to be listed as *threatened* or *endangered* under federal or state law) are the DRECP's primary focus, it is also intended to support the region's biodiversity and ecosystems as they shift under climate change. The USBLM took a promising step in this direction in 2010, when it commissioned a regional plan designed to support connectivity under current and future climatic conditions (figure 2b; Penrod et al. 2012). The plan builds on the region's existing large protected areas and includes 22 broad, multistranded linkages. Each linkage includes high climate diversity, supports large populations (and, therefore, large evolutionary potential and demographic resilience) of most species, and has a low edge-to-area ratio (reducing exposure to noise, light, pollutants, and other threats originating in developed areas).

The linkages combine corridors for focal species under today's climatic conditions with corridors designed to support connectivity and viable metapopulations of most species as the climate changes (figure 2b; Penrod et al. 2012). The latter are defined by enduring features of the landscape (Beier and Brost 2010). This approach avoids the significant uncertainties that would arise in modeling suitable climate space for every focal species over the next 50 to 100 years (Davis et al. 2015) and in joining all those corridors into a coherent design. The combined network links today's habitats with what should be suitable habitats in the future, thereby providing live-in and move-through habitat as species' ranges shift. This blended approach is a bet-hedging strategy for a changing climate, because it identifies linkages that should work under a wide range of future climates.

If adopted, this linkage design would be the most geographically extensive attempt thus far to use the conservation of corridors as a climate adaptation strategy. Therefore, the DRECP has the potential to robustly support the adaptation of desert ecosystems over a large area while promoting alternative energy. Key public agencies—including the seven affected counties that are to use the DRECP to amend their land-use plans—have the appropriate legal authority to shape factors that influence ecosystem conditions and adaptive capacity.

The DRECP recently released a draft report and environmental impact statement to comply with the National Environmental Policy Act and the California Environmental Quality Act and opened a public comment period (CEC 2014). The draft identifies a preferred alternative that prioritizes large habitat blocks and linkage areas for 37 covered species and 31 natural communities, as well as approximately 8,200 km^2 for solar, wind, and geothermal development (to produce approximately 20 gigawatts of renewable energy). The plan and a preferred alternative are likely to be modified in response to public comment, and their implementation will take years and will involve decisions by many different entities.

Simple procedures are available that the DRECP and the plan implementers could use to quantitatively estimate the loss of connectivity associated with each energy-siting alternative under consideration (Rudnick et al. 2012). Combining these results with estimates of the amount of energy produced or transmitted under each alternative would describe a trade-off curve that could inform the choice among alternatives and identify compromises which meet energy needs while conserving a well-connected landscape that supports species range shifts and ecosystem transitions. Complementary analyses, using other tools (e.g., Mojaveset; Davis et al. 2015), could estimate how siting alternatives alter the conservation value of the landscape through the loss of habitat to energy development.

The DRECP is likely to result in the rapid implementation of long-lived and expensive energy infrastructure over a significant proportion of California's desert ecosystems. Surprises are inevitable, even if the DRECP relies on the best available data and models. Monitoring in an adaptive management framework can help address uncertainty, but the rapid infrastructure development makes it unlikely that monitoring will produce strong inferences in time to mitigate unanticipated effects of the installations built within the next decade. This argues for a precautionary strategy that builds a significant margin for error into the connectivity plans and projections of climate change effects.

Case study 2: A choice among alternative futures for Suisun Marsh

Suisun Marsh is the largest tidal marsh on the West Coast, covering approximately 400 km^2 in the middle of the San

Francisco Estuary, and is affected by the Sacramento–San Joaquin Delta upstream and the San Francisco Bay downstream to the west (Moyle et al. 2014). Past sea-level rise created the marsh approximately 6000 years ago, and human activities have always influenced marsh conditions. Climate change is now further altering the salinity and hydrology of Suisun Marsh, along with the rest of the estuary, and these changes are accelerating. Sea-level rise is increasing saline inputs from the bay, whereas freshwater flows from upstream are declining in volume and becoming warmer and more variable. Projections show increasingly long droughts interspersed with large floods (Moyle et al. 2014).

The management of Suisun Marsh in recent decades has been directed at retaining conditions suitable for waterfowl hunting. Brackish-water tidal channels flow past diked nontidal marsh that is managed by the region's 158 private duck clubs or by the CDFW. A complex system of dikes, pumps, drains, and massive tidal gates (through which Sacramento River waters enter the Marsh) reduce the penetration of salty water into these interior marshes. Because soils subside when the duck club ponds are drained annually, many areas are now below sea level.

The surrounding urban communities value Suisun Marsh as open space and for nonhunting recreation, and some undiked portions are part of the National Estuarine Research Reserve System. This heavily managed marsh supports a high diversity of plants, invertebrates, fish, birds, and mammals (Moyle et al. 2014). Both native and nonnative species are abundant, making Suisun Marsh an excellent example of a *novel ecosystem*, one in which an unprecedented combination of species interacts in a highly altered environment (Moyle 2013, Moyle et al. 2014).

Various government planning and legislative actions since the 1970s have sought to protect these benefits and uses by limiting development, maintaining waterfowl habitat, and mitigating potential salinity changes caused by public water projects (USBR et al. 2011). Most recently, the US Bureau of Reclamation, the USFWS, the CDFW, and other agencies developed a 30-year plan for managing and restoring Suisun Marsh (USBR et al. 2011). This plan details an approach for restoring approximately 20–28 km^2 of tidal wetlands and enhance approximately 162–202 km^2 of managed wetlands to benefit waterfowl, wildlife, and migratory and *endangered* species while protecting water supplies. However, climate change will eventually make even these goals difficult to achieve, because dike improvements to protect the managed wetlands are unlikely to hold off sea-level rise after the 30-year planning horizon, resulting in breached dikes, marsh inundation, and large open-water areas (USBR et al. 2011, Moyle et al. 2014).

This expectation of eventual failure raises important questions about whether alternative goals might be more successful and cost efficient in light of ongoing climate change. Moyle and colleagues (2014) developed four descriptive scenarios of widely divergent management strategies to help stakeholders, managers, and public agencies consider this question and visualize possible alternative options (figure 3).

The fortress marsh scenario envisions a huge Dutch-style dike, built to protect approximately 75% of the marsh, leaving the rest inundated. The protected marsh would be managed as it is today, and subsidence would continue. The dike would be enormously expensive but might be justified to protect cities.

The flooded marsh scenario continues the *status quo*, with no special efforts to protect the marsh from sea-level rise, large floods, or earthquakes. The existing dikes would fail after 30–40 years, giving way to large areas of open water and shallow baylands, with relatively small areas remaining vegetated, in part because the subsided lands would be too deep for marsh plant growth. The construction of large dikes would protect the fringing urban areas.

The reconciliation marsh scenario involves managing much of the marsh as tidal marsh to mitigate habitat losses for threatened native species elsewhere in the estuary (resulting from a proposed new water diversion) and to protect urban areas from flooding and erosion due to sea-level rise. Dike enhancement and management measures to reduce subsidence would sustain significant areas as waterfowl habitat, although less than today. Connectivity improvements would expand fish habitats and allow marsh expansion and tule elk (*Cervus elephas nannodes)* grazing into nonurban uplands.

The ecomarsh scenario has as its primary goal maximizing habitat diversity for native biota. Corridors would connect the marshlands with outside habitats, such as Jepson Prairie (a University of California natural reserve northeast of current marshlands). The marsh would help protect urban areas and would sequester carbon, because marsh plant growth would keep pace with sea-level rise. Its managers would treat the entire marsh as an interconnected, but novel, ecosystem and would manage with change rather than resisting it.

Which scenario comes closest to the future of Suisun Marsh will depend on whether and how diverse interests—including duck clubs, cities, and federal and state resource management agencies—can agree on what they want and can realistically achieve as conditions and options change. No forum involving all stakeholders yet exists to develop a long-term vision. However, delays in decisionmaking will reduce the management options, because the conversion of diked marsh into tidal marsh (rather than open water) will become increasingly difficult as the sea level rises, soils subside, and other large-scale changes occur in the rest of the estuary. The heritage of fragmented private ownership and management for waterfowl hunting may make it challenging to adjust management goals to address climate change. At the same time, there is growing interest in converting diked marshlands to tidal marsh as mitigation for the negative effects of public water projects elsewhere in the estuary. The potential for carbon sequestration and protection of urban areas from sea-level rise and erosion could provide additional incentives for considering alternative management pathways, such as those presented in the reconciliation or ecomarsh alternatives (figure 3).

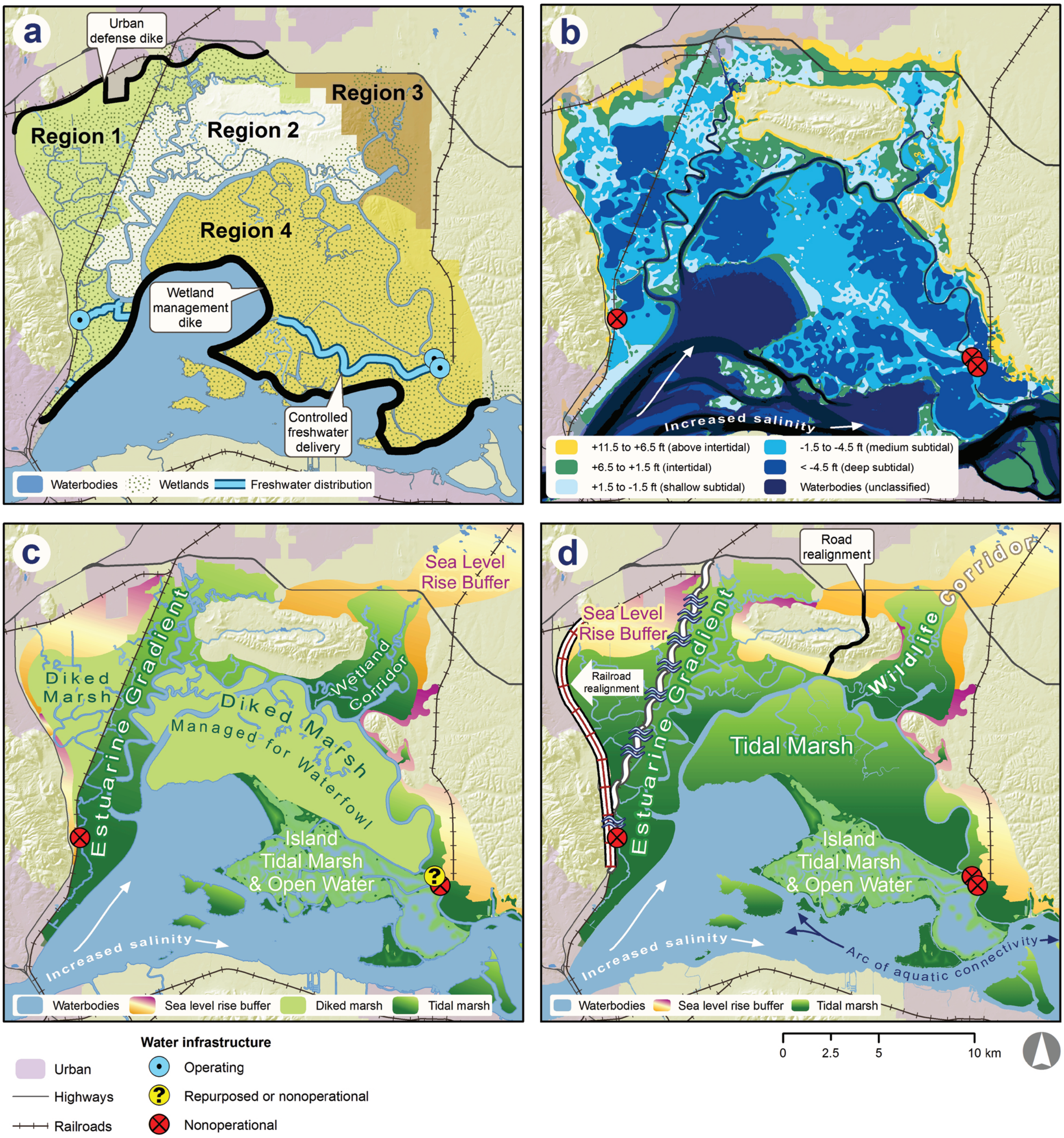

Figure 3. Four alternative future scenarios for Suisun Marsh. These descriptive scenarios provide a graphic illustration of how choices made by stakeholders and managers today could yield very different futures for the marsh. (a) The fortress marsh, based on the marsh's most recent management plan, is well-fortified by a large levee to protect historical conditions, with small percentages of the area allocated to restoration of tidal marshes in each of four management regions (8%–16% per region; USBR et al. 2011). (b) The watery flooded marsh envisions a future in which levees fail and inundated marshes convert to open water. The estimated depth in the figure was calculated by combining current elevation with projected sea-level rise (Moyle et al. 2014). Scenarios (c) and (d) are conceptualizations of two options for restoring tidal marshes. (c) The reconciliation marsh consists of tidal marshes with significant areas dedicated to waterfowl habitats. (d) The ecomarsh is designed to optimize native biodiversity, retain natural values, and create a system that can adjust to future climate change and sea-level rise with fewer interventions. The area labeled "Island Tidal Marsh and Open Water" in panels (c) and (d) would be inundated as in panel (b). Abbreviation: km, kilometers. Figure by Amber Manfree, adapted from Moyle and colleagues (2014).

Case study 3: Optimizing the delivery of ecosystem services by California rangelands

The region composed of California's Central Valley, surrounding foothills, and Inner Coast Range includes approximately 73,000 km^2 of rangelands, most of which are privately owned and managed for livestock production. Many rangelands are in the state's fastest-growing counties, where land uses are rapidly converting from grazing lands and open spaces to urban, suburban, and exurban development. Climate change will further alter rangeland habitats, such as grasslands and oak woodlands, through shifts in water availability (the combination of recharge and runoff) and species' distributions and abundances. In this quickly changing landscape, appropriately managed ranchlands can provide wildlife and vegetation corridors for enabling species range shifts and sustaining biodiversity. They also deliver important ecosystem services beyond livestock production, including carbon sequestration and water flows for drinking and irrigation (e.g., Shaw et al. 2011; Havstad et al. 2007). Interest is growing in maintaining such working landscapes to simultaneously support the persistence of agriculture and conserve wildlife habitat in areas of intense development pressure (Brunson and Huntsinger 2008).

Developing and implementing strategies to adapt rangeland ecosystems in ways that facilitate connectivity and the provision of ecosystem services at large spatial scales will require compatible and collective actions across the region's mosaic of small private and public ownerships. The California Rangeland Conservation Coalition provides a potential forum for advancing this objective. Since 2005, more than 120 ranching and private landowners, nonprofit organizations, public agencies, and others have joined the coalition to "conserve and enhance the ecological values and economic viability of California's working rangelands" by developing shared goals, information resources, and input to policy proposals (CRCC 2010). Scientists working with the coalition are developing integrated scenarios to assist their members in understanding the combined effects of land-use change and climate change on water resources, carbon stocks, and habitat—an important first step before initiating the consideration of climate adaptation strategies.

The scenarios require translating model projections into spatial scales and formats that are relevant and usable for diverse stakeholders. In practice, this involves integrating outputs from several land-use change, biogeochemical, and hydrological models under six different future scenarios. The six scenarios are based on three carbon emission scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) compared across two climate models (hot and dry, warm and wet). The IPCC scenarios were augmented through stakeholder consultation with additional assumptions about land conservation to reflect the California rangeland context, and all projections and models were downscaled to a spatial resolution of 270 meters to allow finer-scale evaluations that reflect local soils and geology. (For detailed methodology, see the supplemental material.)

So far, the analyses of the integrated scenarios at a regional scale have been used to visualize the following:

First, projections have been developed for changes through 2040, for each watershed in the region, in priority wildlife habitat, climatic water deficit (a measure of summer drought intensity), recharge–runoff ratio, and grassland soil carbon sequestration capacity. Climatic water deficit, for example, increases under all scenarios by as much as 30%, and many locations become more arid. Most models show longer droughts and larger precipitation events. Suitable climatic conditions for blue oak (*Quercus douglasii*) shift up in elevation as a result of these water stress patterns, to be replaced by grassland habitat on the valley floor.

A second set of projections examine changes in each watershed for a combined average of three ecosystem services—soil carbon sequestration, wildlife habitat, and water availability (figure 4). Results show certain watersheds experience greater loss of ecosystem services than others by 2040, even under the more optimistic scenarios, including those surrounding the San Francisco Bay and near Redding and Sacramento. This holds for the warm and wet projections (not illustrated) as well as the hot and dry ones in figure 4.

A third set of projections examine water-wildlife hotspots within the region, where declines in water availability and a loss of priority habitat coincide. Most habitat loss occurs in grasslands. Only one hotspot appears by 2040, Suisun Marsh in the A1B scenario (figure 4). By 2100, additional hotspots occurs even under more optimistic (B1) scenarios, including the Lower Butte, Paso Robles, and Estrella watersheds.

The results have been assembled on a Web page maintained by the California Climate Commons (CCC 2014), and workshops are being organized with the Resource Conservation Districts to ensure that the science is accessible and useful for coalition members and other rangeland stakeholders. This scientific framework could eventually be used to help direct land-use patterns (e.g., urbanization or land conservation) in ways that protect deep soils needed for groundwater recharge and sustained stream flows or that optimize the future delivery of other ecosystem services. Other regional applications might include integrated regional water management planning supported by state bond funding (CDWR 2012) or the development of systems to pay private landowners for ecosystem services, such as carbon sequestration.

Building a better understanding among members of the coalition about how climate change will affect California's rangeland ecosystems and services is still in the early stages. Many private landowners remain skeptical about climate change and distrust government agencies and conservation organizations, setting a high bar for their participation in collective efforts to adapt ecosystems. At the same time, private landowners and local managers are likely to be the first observers of ecological shifts related to climate change (e.g., altered hydrology, fire regimes, or phenology). Spurring their engagement may require economic or other incentives, as well as a better explanation of how climate change is affecting them personally and the likely costs and benefits should they undertake various adaptation or mitigation actions.

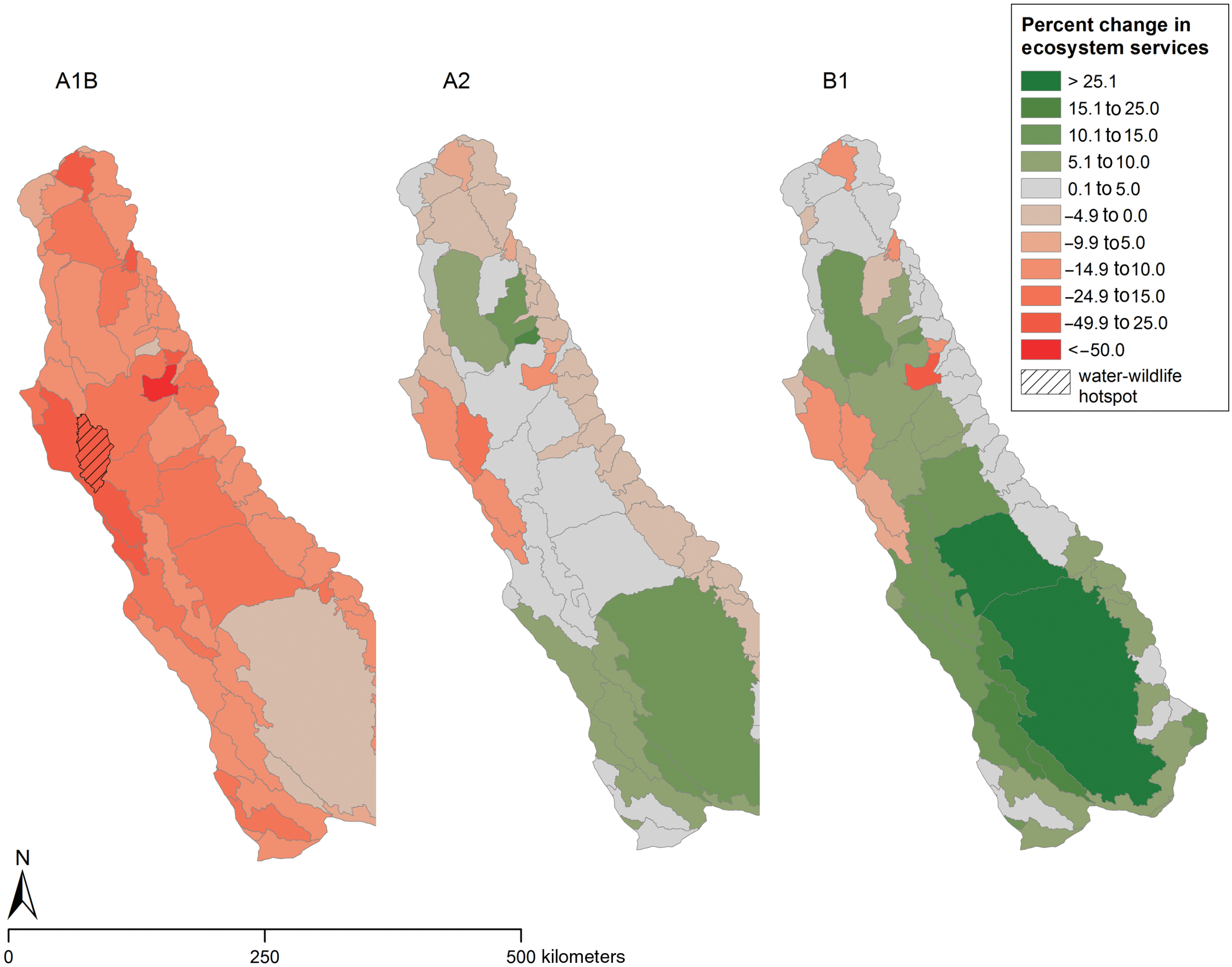

Figure 4. Projections of the average percentage change in three ecosystem services from 2010 to 2040 for watersheds across approximately 73,000 km² of California rangelands. The maps display the average change for soil organic carbon sequestration (the top 20 centimeters), crucial wildlife habitat, and water availability (recharge plus runoff) for three augmented scenarios based on the International Panel on Climate Change Special Report on Emissions Scenarios under a hot, dry climate future. Under the A1B scenario (i.e., mitigated emissions, moderate public investment in conservation near population centers, low development density, expansion of high value perennial crops into rangelands), ecosystem service losses are extensive, driven primarily by diminished water availability, and one hotspot of declining water and wildlife habitat appears. Under the A2 scenario (i.e., business-as-usual emissions, low public investment in conservation, low development density, intensive agricultural development), diminished water availability in the Sierra foothills and reduced capacity for soil carbon sequestration in urban areas drive ecosystem service losses. Under the B1 scenario (i.e., highly mitigated emissions, significant public investment in conservation of high biodiversity lands, high development density, moderate agricultural development), ecosystem service losses result from urbanization around large population centers, such as the Bay Area, where grassland conversion reduces soil carbon sequestration capacity. Gains in ecosystem services also occur under the B1 scenario throughout the Central Valley because of increases in water availability through 2040. Note, however, that projections through 2100 show water availability decreases during the latter half of the century. (See the supplemental material for additional information about the methods.)

Case study 4: Adapting ecosystems through open space conservation in the Bay Area uplands

The San Francisco Bay Area spans 100 municipalities, ten counties, and an area of approximately 19,500 km^2. The landscape is a complex patchwork of urban, suburban, rural, and agricultural lands interspersed with an extensive network of protected open space. Upland habitats support coastal redwood forests, deciduous and evergreen oak woodlands, fire-prone shrublands, and widespread grasslands (now dominated by alien grasses; figure 5a). This

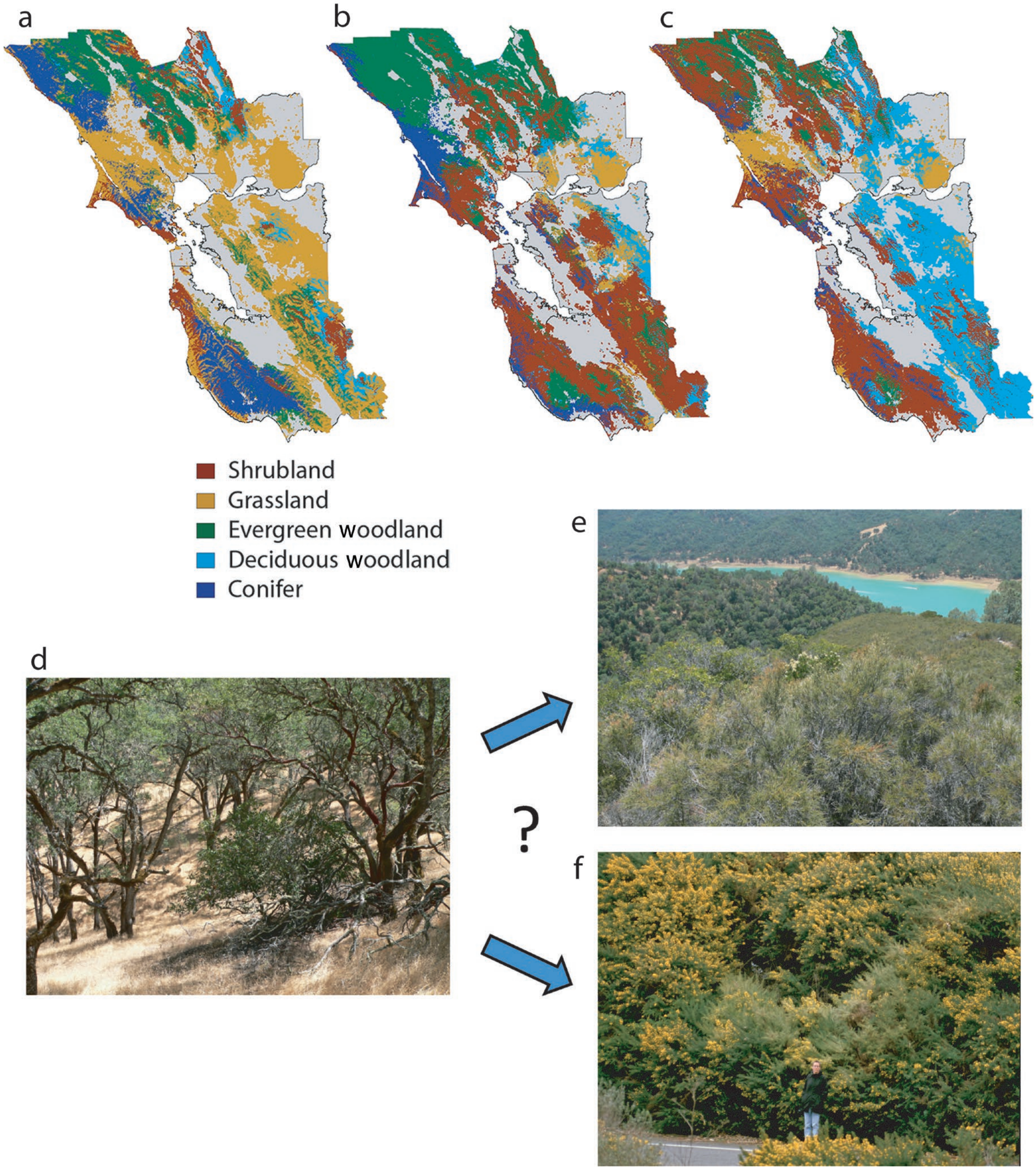

*Figure 5. The trajectory of vegetation transitions in the Bay Area uplands will be affected by the interaction of climate change with local factors such as extreme events, site characteristics, and management choices. The maps show the distribution of major vegetation types in the San Francisco Bay Area (a) under historical baseline climates (1951–1980), (b) in response to 4°C of warming with reduced rainfall, and (c) in response to 4°C of warming with increased rainfall. (See Cornwell et al. 2012 for methods.) The future distributions in panels (b) and (c) reflect projected equilibrium responses to climate change; such large-scale vegetation shifts may take hundreds of years or more to unfold. Many factors in addition to climate change will determine whether or how fast these distribution shifts occur. For example, (d) an oak woodland today that experiences significant drought or intense fire might transition to (e) native chaparral or to invasive shrubs, such as (f) this French broom (*Genista monspessulana*), depending on the proximity of seed sources, management practices, and other site factors.* G. monspessulana *is a harmful nonnative plant that has invaded Mediterranean-climate regions around the world; it forms monocultures that suppress native plants, and its foliage and seeds are unpalatable and potentially toxic to grazing animals. Both panels (e) and (f) are shrublands, but the first is better aligned with regional goals to conserve native vegetation. Note that the definitions of the geographic area covered by the San Francisco Bay Area vary. This case study is based on the boundaries defined by the Bay Area Open Space Council (BAOSC 2011). Photographs: (d, e)* D.D. Ackerly; *(f)*Barry Rice, www. sarracenia.com.

vegetation range reflects diverse environments created by rugged topography and varied soil types interacting with strong coast-to-inland climate gradients. Coastal climates are characterized by cool summer fog and low seasonal temperature variation, whereas hot summers and much greater seasonal variation prevail inland.

Since 1990, the Bay Area Open Space Council (BAOSC)—which draws members from more than 50 public and private entities that manage open space—has promoted an "interconnected system of healthy communities with parks, trails, agricultural lands, and natural areas" across the San Francisco Bay area (BAOSC 2015). The BAOSC developed a strategic land conservation plan in 2011 that identifies shared regional priorities for future open space acquisition and management (BAOSC 2011). The plan sets goals for increasing protected areas, currently 25% of the region, to 50% in order to support all of the region's vegetation types, provide habitat for nearly 500 targeted plants and animals (species, subspecies, and varieties), and enhance public access to open space (BAOSC 2011). However, the plan does not explicitly address the potential for climate change to reshape the region's biodiversity, ecosystems, and associated societal benefits. A multi-institutional group of researchers, the Terrestrial Biodiversity and Climate Change Collaborative, is working to fill this gap (Micheli and Ackerly 2013).

Mean annual temperatures in the region could rise by up to 6 degrees Celsius (°C) by between 2070 and 2100, profoundly shifting the climate gradients that underlie habitat distributions in the Bay Area (Micheli et al. 2012, Thrasher et al. 2013). Although the projections for future precipitation are much less certain, water balance models show that the climatic water deficit increases in almost all future scenarios, because increased evapotranspiration reduces soil moisture even when rainfall increases (Flint et al. 2013). Changes to wind-driven coastal upwelling are not yet well understood but will affect fog production and could significantly alter coastal habitats.

High-resolution maps of temperature, water deficits, and other climate variables are now available to support the modeling of how climate change may affect the region's landscapes and ecosystems (Flint et al. 2013). The projections show climates that are suitable for different vegetation types shifting across the region (Cornwell et al. 2012). Above 4°C of warming, the effects will become increasingly dramatic as drought-adapted shrublands and deciduous oak woodlands (blue oak, *Q. douglasii*) spread across much of the Bay Area (figure 5a, 5b, 5c). Past vegetation shifts of this magnitude took hundreds to thousands of years, so the twenty-first century is likely to be dominated by transient dynamics, as the rate of climate change exceeds the speed of biotic responses (Svenning and Sandel 2013). Episodic events—droughts, heat waves, pest outbreaks, and fires—may have dramatic but difficult to forecast effects on the direction and rate of vegetation change (figure 5d, 5e, 5f; e.g., Allen et al. 2010). Fire frequencies are expected to increase in the Bay Area (Krawchuk and Moritz 2011), but potential interactions between changing fire regimes, native vegetation, and invasive plants are not yet well understood.

Given these uncertainties, research currently underway is examining whether the BAOSC plan can robustly support the adaptive capacity and transitions of Bay Area ecosystems under a range of potential futures or how it might be improved. Nicole Heller and her colleagues have found that the plan, although it is based on biotic diversity, captures the region's strong climatic gradients and finer-scale heterogeneity. A complementary analysis is being used to examine how the plan's priorities might be adjusted to capture steep climate gradients to allow species to rapidly track the shifting climate (Adina M. Merenlender, University of California, Berkeley, personal communication, 1 May 2014). Rugged topography and steep climate gradients potentially enable short-distance range shifts that offset significant environmental change (Ackerly et al. 2010). These analyses address the potential importance of preserving open space that spans the region's climate and soil gradients as a strategy for adapting the ecosystems of this rapidly urbanizing region.

Even with extensive, dedicated, open space and connectivity, the ecosystems in the Bay Area are likely to remain in transitional states for the foreseeable future. This raises important questions about whether and how the management of open spaces and corridors might assist or impede vegetation transitions or even send ecosystems into alternative or undesired trajectories of change (Millar et al. 2007, Merenlender et al. 2015). When viewed through the lens of climate change, are current efforts to prevent the encroachment of grasslands by native coyote brush (*Baccharis pilularis*) and of oak woodlands by Douglas fir (*Pseudotsuga mensiezii*) a good use of limited management funds? When and how should managers facilitate vegetation transitions, such as by using genetically diverse plant material in restoration projects to optimize success in an uncertain future?

Although such management questions require further study, good potential exists that local and regional entities will be able to undertake effective actions to adapt Bay Area ecosystems because of their past successes with collaborative planning and action, and because significant scientific efforts are developing decision-relevant climate change analyses. Climate models also project less warming in coastal California than in inland regions; therefore, the Bay Area's proximity to the ocean may buy time for implementing adaptation strategies (Pierce et al. 2013). As climate change unfolds, BAOSC may need to address how changing ecosystem conditions will affect the aesthetic, health, and quality of life benefits that motivate open space preservation in this heavily populated metropolitan region.

The region's diversified governance, ownerships, and interests could facilitate or slow adaptation. Smaller entities can be more agile, but the regional coordination of many small entities can be difficult. Promising mechanisms are emerging in California that could help align actions across

Table 1. Examples of institutional and policy frameworks in California potentially supporting adaptation of ecosystems to climate change.

Conservation planning	• Conservation Plans under the California Natural Community Conservation Planning Act provide a vehicle for strategically adjusting reserves and connectivity to support species range shifts (Barbour and Kueppers 2012). (D) • State Wildlife Action Plans enable state access to federal funding to benefit wildlife and habitats. The ongoing revision to California's plan takes an ecosystem approach and seeks to better address climate change.
Transportation infrastructure and"smart growth"	• Regional transportation planning to reduce greenhouse gas emissions (i.e., *smart growth*) under the state's 2006 Global Warming Solutions Act and 2008 Sustainable Communities and Climate Protection Act potentially could integrate actions for adapting ecosystems into regional land-use and open space decisions (Barbour and Kueppers 2012). California's *cap and trade* program could make significant funding available for this purpose. (B) • Regional advanced mitigation planning provides compensatory mitigation when infrastructure improvements impact ecosystems, habitats, and species and could potentially help fund strategic augmentation of California's system of reserves and connectivity areas (Thorne et al. 2009). • Permitting of coastal infrastructure and development under the California Coastal Act of 1976 seeks, in consideration of sea-level rise, to maximize natural shoreline values, evaluate risks to ecosystem benefits, and avoid harm to ecosystem sustainability (CCC 2013).
Water management	• Wetlands restoration implemented as mitigation for state water projects (e.g., USBR et al. 2011) can be designed to support desired ecosystem functions and benefits under future climate conditions and elevated sea level. (S) • Development of integrated regional water resource management plans provides a mechanism for encouraging compatible action across ownerships and interests (CDWR 2012). The California Department of Water Resources has significant funding from state bond initiatives for this purpose, and climate change, environmental stewardship, and sustaining ecosystems are among program priorities. (R)
Local, county, and regional land-use planning	• State guidance on climate change adaptation for local municipalities, counties, and regional collaborative planning bodies encourages collective and compatible action across agencies at local to regional scales (Cal EMA and CNRA 2012). Refinements to the guidance may be needed to better address ecosystem considerations in local to regional adaptation and mitigation. Funding could remain a challenge for many counties. (R, B) • Implementation of municipal climate change adaptation plans, like that of the City of Santa Barbara, could advance local goals for adapting ecosystems (CSB 2012).
Carbon banking	• The California Air Resources Board grants credits to offset emissions for registered and verified activities. Existing protocols allow forest owners to sell offset credits based on expected carbon storage by native forests. Allowed practices include planting native trees in new locations that reflect future habitat shifts (CARB 2011). Much interest exists in developing protocols for other ecosystems. (S, R, B)
Land acquisition and management	• The California Wildlife Conservation Board supports wildlife conservation by awarding grants for land acquisition, easements, habitat restoration, and public access to public and private organizations ($62 million in 2013). The Board's Strategic Plan identifies addressing climate change impacts on biodiversity and ecosystems as a priority (CWCB 2014). • The California Coastal Conservancy's Climate Ready Program funds projects that help protect coastal resources and habitats from climate change impacts.

Note: The parenthetical initials identify institutional and policy frameworks discussed in the case studies. Abbreviations: B, Bay Area uplands; D, deserts; S, Suisun Marsh; R, rangelands.

interests. Examples include statewide guidance on county-level planning for climate change, initiatives supporting regional smart growth, and carbon sequestration protocols being developed under recent state law (table 1).

Learning from the case studies

California's ecosystems are likely to experience significant climate-related changes over the next 50–100 years. Because change will be pervasive, additional assessments of species or ecosystem vulnerabilities will be most useful if conducted in support of applied efforts to adapt ecosystems to climate change. The case studies suggest that initiating such adaptation efforts requires at least four elements operating at a scale that matches ecosystem patterns and processes (figure 6): (1) an effective venue for collaborative planning and goal setting that brings together the people and organizations that affect and that will be affected by climate-driven ecosystem change; (2) usable and relevant scientific information, such as projections of how climate change will affect ecosystems within the context of other significant ecosystem drivers (e.g., land-use change), ecological models, or site prioritizations; (3) the identification of practical steps that can be taken to sustain ecosystem functions and adaptive capacity and secure future benefits (box 2); and (4) mechanisms to encourage collective and individual action (e.g., policies, education, incentives, financing).

Numerous opportunities exist for advancing societal efforts to adapt ecosystems under existing institutional and policy frameworks in California that support one or more of the four elements, including some not initially designed for this purpose (table 1). Examples include transportation planning, water management, coastal permitting, land-use policies, and carbon banking, in addition to more obvious ones related to wildlife conservation. Taking advantage of this full range of options will broaden the set of planning tools, financing mechanisms, and sector-specific interests that can be brought into adaptation efforts focused on ecosystems—and therefore help spur collective action at large spatial scales, across ownerships, and where some of the parties most affected are uninformed or skeptical about climate change.

The California case studies highlight the importance of thoughtfully selecting the time horizon for evaluating alternatives for adapting ecosystems or for mitigating climate change, because today's choices will define future options. Decisions made now without informed consideration of

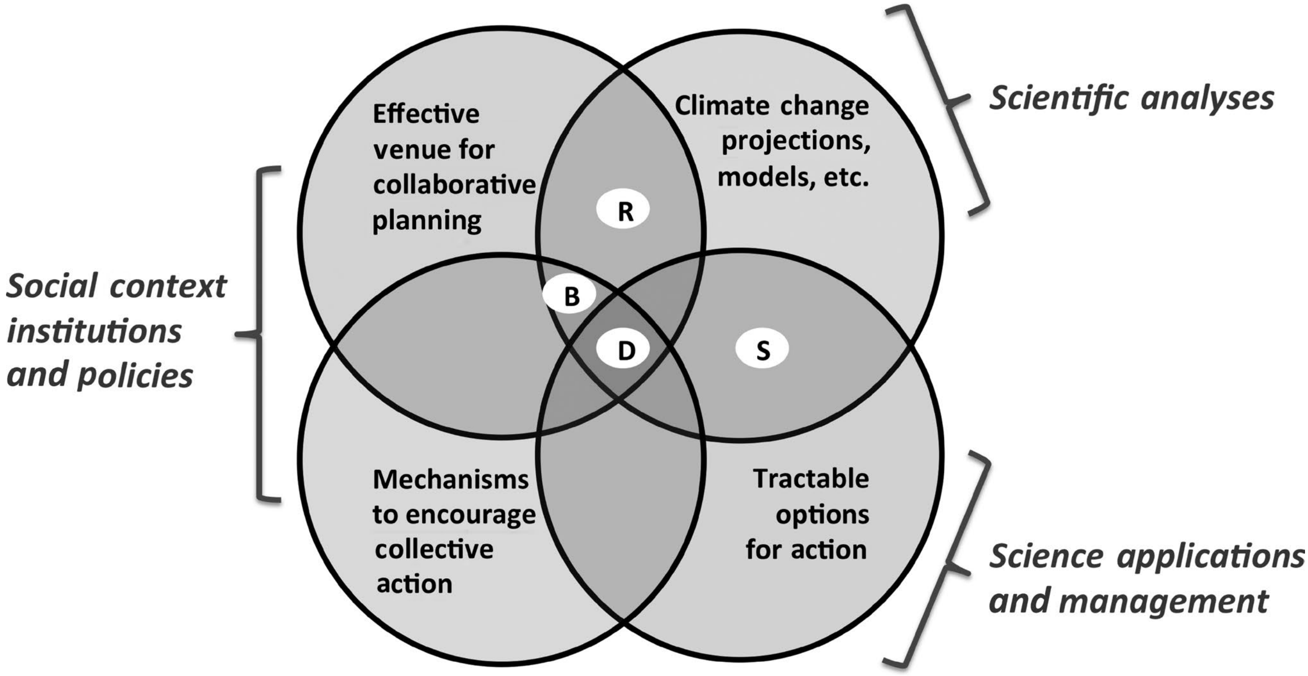

Figure 6. Enabling conditions for undertaking efforts to adapt ecosystems to climate change. Key elements include a combination of social context (e.g., effective planning venue, incentives), usable scientific knowledge (e.g., climate change projections, projected ecosystem impacts, ecological models, site prioritizations), and identified options for action (e.g., approaches in box 2). Based on the descriptions earlier in the article, the four California case studies differ in the extent to which they include these four elements (B, Bay Area uplands; D, deserts; S, Suisun Marsh; R, rangelands; the location on the diagram shows which elements are in place for each case study). In the rangelands example, action on climate adaptation will require more clearly defined options and incentives for private landowner participation. At Suisun Marsh, existing engagement processes may need to be modified or new ones developed to engage the full range of affected stakeholders into collaborative planning. The next phase for the Bay Area uplands is likely to involve identifying and potentially undertaking practical actions related to open space acquisition and management. Longer-term implementation in many cases may require sustained leadership, political will, and financing, in addition to these enabling conditions.

future change or, alternatively, delaying action on adaptation can lock in longer-term prospects for optimizing ecosystem adaptive capacity and benefits in ways that may be difficult to correct later (see the Suisun Marsh and deserts case studies). Routine assessment of such longer-term risks should be part of projects designed to secure particular ecosystem benefits today to protect infrastructure or perform other societal adaptation or mitigation functions (e.g., ecosystem-based adaptation; IPCC 2014).

The list of potential management actions to anticipate, respond to, slow, or facilitate climate-driven ecosystem change is rapidly expanding. Examples include germplasm choices for restoration, species translocations, reevaluation of invasive species risks, re-creation of historical water flows, and facilitation of ecosystem transformations (see the Suisun Marsh, rangelands, and Bay Area uplands case studies). Implementing these options may sometimes be risky, controversial, or costly. Intensified efforts are needed to develop decision-support tools and frameworks that support progress by making these choices rigorous, transparent, and credible and that consider potential long-term effects on ecosystem functions, benefits, adaptive capacity, and transitions as the climate changes (e.g., Moritz et al. 2013).

Over the past decade, federal agencies that manage large public land holdings have made significant progress integrating climate change projections into forest and protected area management planning and practices (e.g., Peterson et al. 2011). The California examples demonstrate how diverse public and private owners and interests operating at local, regional, and state levels are likewise starting to anticipate and address the impacts of climate change on ecosystems. Numerous opportunities exist to undertake efforts to adapt ecosystems within existing institutional and policy contexts. Progress will be greatest when improved scientific understanding is integrated into effective collaborative planning and when supportive policies and financing exist that enable practical action.

Acknowledgments

This article enlarges upon the findings of a working group convened in 2012 by the Resources Legacy Fund (RLF) to explore general principles for guiding efforts to adapt California's ecosystems to climate change. We are grateful to RLF for catalyzing our work in this area and for providing partial support to EAC during the preparation of this manuscript. Amber Manfree and Kristeen Penrod generously adapted figures from previous publications for our use here. We appreciate, and the paper was greatly improved by, the thoughtful comments provided by the editor and four anonymous reviewers.

Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu233/-/DC1.*

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Calendar of meetings

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April

26 **California Botanical Society**
Tiburon, CA; *http://calbotsoc.org/events*

May

3–7 **Society for Environmental Toxicology and Chemistry**
Barcelona, Spain; *www.setac.org/?page=AnnualMeetings*

23–28 **Human Anatomy and Physiology Society**
San Antonio, TX; *www.hapsweb.org/?page=Conferences_home*

17–21 **Society for Freshwater Science**
Milwaukee, WI; *www.freshwater-science.org/annual-meeting.aspx*

June

30–3 **Society for In Vitro Biology**
Tucson, AZ; *www.sivb.org/meetings/future_meetings.html*

31–3 **Society for Sedimentary Geology**
Denver, CO; *www.sepm.org/pages.aspx?pageid=21*

10–14 **Animal Behavior Society**
Anchorage, AK; *http://abs2015.org*

12–16 **American Society of Mammalogists**
Jacksonville, FL; *www.mammalsociety.org/meetings*

14–19 **Cactus and Succulent Society of America**
Claremont, CA; *http://cssainc.org/index.php/register-for-cssa-2015*

17–20 **American Society of Primatologists**
Bend, OR; *www.asp.org/meetings*

19–23 **American Arachnological Society**
Mitchell, SD; *www.americanarachnology.org/meetings/meetings.html*

22–26 **American Public Garden Association**
Minneapolis, MN; *http://2015.publicgardens.org*

25–28 **American Society of Parasitologists**
Omaha, NE; *http://amsocparasit.org/taxonomy/term/5*

23–26 **Association for Biology Laboratory Education**
Boston, MA; *www.ableweb.org/conf/conferences.htm*

July

29–2 **Society for Economic Botany**
Clanwilliam, Western Cape, South Africa; *www.econbot.org/index.php?module=content&type=user&func=view&pid=101*

30–3 **Society for Mathematical Biology**
Atlanta, GA; *www.smb.org/meetings/annual.shtml*

5–10 **International Association for Landscape Ecology, US Division**
Portland, OR; *http://usiale.org/meetings/2015-world-congress*

12–16 **Association for Tropical Biology and Conservation**
Honolulu, HI; *http://tropicalbiology.org/annual-meetings*

15–19 **American Society of Ichthyologists and Herpetologists**
Reno, NV; *www.asih.org/meetings*

19–24 **Society of Nematologists**
East Lansing, MI; *www.nematologists.org/son_annual_meeting.php*

25–29 **American Society of Plant Taxonomists**
Edmonton, Alberta, Canada; *www.aspt.net/membership/annual-meeting*

25–29 **Botanical Society of America**
Edmonton, Alberta, Canada; *http://botany.org/conferences*

25–29 **Mycological Society of America**
Edmonton, Alberta, Canada; *http://msafungi.org/meetings*

27–30 **Poultry Science Association**
Louisville, KY; *www.poultryscience.org/meetings.asp*

August

28–2 **Lepidopterists' Society**
West Lafayette, IN; *www.lepsoc.org/annual_meetings.php*

30–3 **Society for the Study of Amphibians and Reptiles**
Lawrence, KS; *http://ssarherps.org/meetings/2015-university-of-kansas-meeting*

doi:10.1093/biosci/biv042

Corrigendum

In "Adapting California's Ecosystems to a Changing Climate" (*BioScience* 65: 247–262, doi:10.1093/biosci/biu233), the caption for figure 5b and 5c incorrectly described the maps as reflecting reduced rainfall and increased rainfall, respectively. The section of the caption containing the error is reproduced below, corrected. The authors regret the error.

Figure 5. The trajectory of vegetation transitions in the Bay Area uplands will be affected by the interaction of climate change with local factors such as extreme events, site characteristics, and management choices. The maps show the distribution of major vegetation types in the San Francisco Bay Area (a) under historical baseline climates (1951–1980), (b) in response to 4°C of warming with increased rainfall, and (c) in response to 4°C of warming with reduced rainfall. (See Cornwell et al. 2012 for methods.)

doi:10.1093/biosci/biv044