Southern California Sage Scrub Habitats

Climate Change Vulnerability Assessment Synthesis

An Important Note About this Document: *This document represents an initial evaluation of vulnerability for sage scrub habitats based on expert input and existing information. Specifically, the information presented below comprises habitat expert vulnerability assessment survey results and comments, peer-review comments and revisions, and relevant references from the literature. The aim of this document is to expand understanding of habitat vulnerability to changing climate conditions, and to provide a foundation for developing appropriate adaptation responses.*


Photo by Noah Elhardt (Public Domain)

Executive Summary

Sage scrub habitats largely exhibit an open, drought-deciduous shrub canopy and an herbaceous understory comprised of annual and perennial grasses and forbs (Diffendorfer et al. 2002), although the canopy may also feature evergreen shrubs. Sage scrub habitat range and vegetation associations are determined by broad latitudinal temperature and precipitation gradients, as well as climatic gradients extending from coastal to inland locations (Rundel 2007). While climate controls larger landscape patterns and distribution of sage scrub habitats, factors such as topography, disturbance, soil type and structure, and intra-species interactions affect local distribution patterns (DeSimone and Burk 1992; Riordan and Rundel 2009). In the southern California study region, these factors contribute to three broadly recognized sage scrub associations: coastal, inland, and maritime sage scrub. The majority of this assessment focuses on coastal and inland associations because they represent the majority of sage scrub cover in the study area.

The relative vulnerability of sage scrub habitats in southern California was evaluated to be moderate[1] by habitat experts due to moderate sensitivity to climate and non-climate stressors, moderate exposure to projected future climate changes, and moderate adaptive capacity.

Sensitivity and Exposure	Climate sensitivities: Air temperature, extreme high and low temperature events, precipitation, soil moisture Disturbance regimes: Wildfire Non-climate sensitivities: Invasive & problematic species, land-use conversion/development, pollution & poisons

Sage scrub habitat distribution and composition is largely determined by precipitation and temperature. Warming temperatures and shifts in rainfall timing may affect sage scrub germination, recruitment, and overall species composition. Although sage scrub habitats are adapted to wildfire, increasing fire frequencies as a result of more human ignitions create conditions favorable for exotic annual invasion and prevent sage scrub recovery and seedbank

---

[1] Confidence: High

regeneration, driving sage scrub conversion to exotic annual grassland. Nitrogen deposition also enhances invasive species establishment. In addition, land-use conversion significantly threatens sage scrub habitat extent, continuity, and vulnerability to wildfire ignitions, invasive species introductions, and other impacts.

Adaptive Capacity	Habitat extent, integrity, and continuity: Low-moderate geographic extent, low integrity (degraded), low connectivity Resistance and recovery: Low-moderate resistance, moderate recovery potential Habitat diversity: Moderate-high overall diversity Management potential: Moderate societal value and management potential

A variety of human activities have eliminated coastal sage scrub from 70-90% of the original land area occupied by this habitat in southern California, and contributed to significant fragmentation and degradation of existing habitat. Specifically, land-use conversion, agriculture, transportation corridors, and grazing act as significant barriers to sage scrub habitat continuity and dispersal in the face of climate change. Sage scrub habitats are drought-adapted and are able to recover from disturbance, but non-climate stressors such as invasive species and nitrogen deposition undermine the natural resilience of this habitat. Sage scrub habitats exhibit moderate-high diversity, particularly between different geographic areas, and provide a variety of ecosystem services, including biodiversity, recreation, and carbon sequestration. Potential management options identified by habitat experts largely deal with restoring existing habitat and enhancing habitat integrity in the face of climate change by managing factors that exacerbate climate impacts (e.g., fire, pollution, invasive species).

Sensitivity

The overall sensitivity of sage scrub habitats to climate and non-climate stressors was evaluated to be moderate by habitat experts.[2]

Sensitivity to climate and climate-driven changes

Habitat experts evaluated sage scrub habitats to have moderate sensitivity to climate and climate-driven changes,[3] including: air temperature, precipitation, soil moisture, and extreme high and low temperature events.[4] These factors largely influence sage scrub habitat range and composition, and help distinguish coastal and inland communities (Riordan and Rundel 2009).

Air temperature

Temperature influences sage scrub distribution and community composition (DeSimone and Burk 1992; Rundel 2007; Taylor 2005). Inland sage scrub communities generally experience more extreme inter-annual temperature variation than coastal sage scrub communities (Riordan and Rundel 2009). For example, minimum winter temperatures are colder in inland

[2] Confidence: High
[3] Confidence: High
[4] Factors presented are those ranked highest by habitat experts. A full list of evaluated factors can be found at the end of this document.

locations (2°C versus 5°C for coastal communities), while maximum summer temperatures are much hotter (37°C inland versus 26°C in coastal locations; Riordan and Rundel 2009; Westman 1983). Warmer summer temperatures drive increased evapotranspiration in inland locations (O'Leary and Westman 1988), affecting species distributions (Westman 1981b) and forcing higher deciduousness amongst component species (E. Allen, pers. comm., 2015). Warmer temperatures may also affect germination and abundance of some sage scrub species. Studies in the Channel Islands documented reduced germination (Levine et al. 2011) and spring population size (Levine et al. 2008) of coastal sage scrub species following rainfall events with warmer temperatures.

Minimum winter temperature also influences species' distribution and abundance (Taylor 2005). Some species, including evergreen lemonade berry (*Rhus integrifolia*) and laurel sumac (*Malosma laurina*) are sensitive to cold temperatures, which can result in branch embolism and death; these species are restricted to mild and moist areas, typically along the coast (Boorse et al. 1998; Langan et al. 1997; Rundel 2007).

<u>Water availability (precipitation, soil moisture, relative humidity)</u>

Similar to temperature, moisture gradients define the range of sage scrub habitats and influence species composition (de Becker 1988; DeSimone and Burk 1992; Rundel 2007; Taylor 2005; Westman 1981a). Sage scrub transitions to northern coastal scrub in wetter portions of the central coast (i.e. where precipitation exceeds 450 mm/year) and to desert scrub in arid southern and inland zones (i.e. where precipitation declines below a 182 mm/year threshold; Rundel 2007). Inland and coastal sage scrub associations also experience different moisture regimes, with inland areas receiving lower amounts of precipitation (Riordan and Rundel 2009; Westman 1981a) and experiencing lower relative humidity, both of which contribute to inland sage scrub stands being more deciduous, and thus, more vulnerable to exotic invasion (Westman 1981b, 1983).

Higher annual rainfall increases overall recruitment (DeSimone and Zedler 1999, 2001) and plant growth in sage scrub habitats (Pratt and Mooney 2013), particularly amongst herbaceous annual species in the understory (DeSimone 2011; Keeley et al. 2005b). However, coastal and inland sage scrub communities in southern California are resilient to drought conditions (DeSimone and Zedler 1999, 2001; Rundel 2007; Willis et al. 2013). Drought-deciduous shrubs utilize moisture in mid- to upper-soil horizons, and feature a variety of adaptations that allow them to persist during seasonal summer dry periods and in locations with low soil moisture (Rundel 2007). Common drought adaptations include leaf abscission, stem photosynthesis, seasonal leaf dimorphism, and narrow vessels (DeSimone and Zedler 2001; Rundel 2007 and citations therein).

Although this habitat is resilient to drought, it may be sensitive to shifts in drought timing or severity. Shifts in drought onset timing can reduce seed production of completely drought-deciduous shrubs, such as common deerweed (*Acmispon glaber*, previously *Lotus scoparius*; DeSimone and Zedler 2001). Persistent dry conditions may facilitate shifts to other shrub communities. For example, field observations in eastern Riverside County have documented shifts from coastal sage scrub to desert scrub species after multiple years of minimal rainfall (5-6 inches per year; E. Allen, pers. comm., 2015). In addition, drought and precipitation variability may interact with other stressors (e.g., land use) to affect resource availability for and population stability of sage scrub-affiliated wildlife such as the Quino checkerspot butterfly (*Euphydryas editha quino*; Preston et al. 2012).

Compared to drought-deciduous shrubs, the majority of evergreen species present in sage scrub habitats have deep root systems, and maintain low water stress during summer by accessing groundwater. However, periods of increased water stress can be lethal for these species, so they are typically restricted to more mesic zones (Boorse et al. 1998; Langan et al. 1997; Rundel 2007). Within sage scrub habitats, evergreen species decline in abundance in more xeric areas, transitioning to the drought-deciduous and seasonally dimorphic shrubs that are characteristic of sage scrub habitat (de Becker 1988; Diffendorfer et al. 2002). However, in areas with more abundant moisture and inconsistent disturbance, evergreen chaparral species can outcompete sage scrub species by shading out lower-growing, drought-deciduous shrubs (Rundel 2007).

Sage scrub habitats may be more sensitive to changes in discrete climatic events (e.g., timing and temperature of first rainstorm and winter precipitation) than changes in season-long means of climatic variables (e.g., total rainfall; Levine et al. 2008, 2011). Sage scrub vegetation features some adaptations to cope with inter-annual precipitation variability. For example, component species are able to maximize productivity during winter when there is high soil moisture availability, sprouting or increasing xylem growth in response to increased water availability (Rundel 2007 and citations therein). In addition, high historical precipitation variability in southern California may be linked with higher plant plasticity amongst southern coastal sage scrub habitats (Pratt and Mooney 2013). For example, Pratt and Mooney (2013) found that under high precipitation treatments, California sagebrush (*Artemisia californica*) individuals from southern California increased growth and flower production significantly more than individuals originating from northern populations, which have historically experienced less precipitation variability. In addition, relative to invasive annual grasses, Goldstein and Suding (2014a) found that coastal sage scrub species were more competitive during periods with infrequent, but larger precipitation events.

Sensitivity to disturbance regimes

Habitat experts evaluated sage scrub habitats to have moderate sensitivity to disturbance regimes[5], including wildfire.[6] The scientific literature also suggests that biotic disturbance (e.g., rodent burrowing and herbivory) influences sage scrub habitats (DeSimone and Tang 2015; DeSimone and Zedler 1999). In general, sage scrub communities can capitalize on infrequent or small-scale disturbance. They readily colonize burned areas (Zedler et al. 1983), chaparral areas disturbed by landslides (Rundel 2007), and can recruit in small areas created by biotic

[5] Confidence: High

[6] Factors presented are those ranked highest by habitat experts. A full list of evaluated factors can be found at the end of this document.

disturbance (DeSimone and Zedler 1999). Although many sage scrub species can recover quickly post-disturbance (Diffendorfer et al. 2002; Zedler et al. 1983), significant disturbance, including altered fire regimes (Keeley et al. 2005a; Malanson and Westman 1991) and wildfire interaction with other disturbance mechanisms such as animal activities and non-climate stressors, can facilitate vegetation conversion and/or significantly alter sage scrub recruitment, composition, and distribution (Diffendorfer et al. 2002; Malanson and Westman 1991; Rundel 2007).

<u>Wildfire</u>

Fire is a natural component of sage scrub communities (Keeley 2005; Keeley et al. 2005a). Many sage scrub shrubs resprout or exhibit seedling establishment quickly post-fire, along with rapid recovery of the perennial and annual herbaceous understory (Keeley et al. 2005b; Zedler et al. 1983). Between resprouting and seed dispersal from adjacent communities, sage scrub habitats typically feature high seedling density two years post-fire, and maintain high seed and new shoot production for significant periods of time (Rundel 2007 and citations therein).

Historic fire return intervals for coastal sage scrub are fairly long, ranging from 20-120 years with a mean of 76 years (Van de Water & Safford 2011). Inland sage scrub communities likely have shorter historic fire return intervals than coastal sage scrub zones due to increased occurrence of late-summer convective thunderstorms (Rundel 2007). Since the 1950s, however, both inland and coastal sage scrub communities have experienced significantly shorter fire return intervals (<5 years) as a result of increased human ignitions (Rundel 2007; Safford & Van de Water 2014; U.S. Forest Service [USFS] 2013). Increased human ignitions are linked with transportation corridors, (Rundel 2007; USFS 2013), arson (Zedler et al. 1983), and ignitions in the wildland-urban interface as a result of expanding population centers (Syphard et al. 2007).

Highly heterogeneous burn patterns (Rundel 2007) and too-frequent fire return intervals alter species composition and abundance in sage scrub habitats (Diffendorfer et al. 2002; Keeley 2005; Malanson 1985; Zedler et al. 1983). Increasing burn frequency inhibits native shrub regeneration by killing resprouts and seedlings and preventing replenishment of soil seedbanks (Zedler et al. 1983). As a result, changes in fire frequency and burn patterns often facilitate shifts from native shrubs to annual grasses (Callaway and Davis 1993; Keeley 2005; Keeley et al. 2005b; Syphard et al. 2007; Zedler et al. 1983) and increase colonization opportunities for invasive species (Goldstein and Suding 2014b; Zedler et al. 1983), creating a positive feedback loop of shorter fire return intervals and subsequent vegetation shifts (Diffendorfer et al. 2002; Syphard et al. 2007; Talluto and Suding 2008). These effects may be particularly prevalent in inland sage scrub communities, which exhibit slower fire recovery than coastal sage scrub associations (Keeley et al. 2005b; O'Leary and Westman 1988). Inland sage scrub associations rely largely on re-establishment from seed, leading to longer recovery time compared to coastal sage scrub resprouting, which typically facilitates fire recovery in 5-7 years (Keeley et al. 2005b; O'Leary and Westman 1988). Inland sage scrub communities also exhibit higher dominance of annual species post-fire, particularly in years with higher rainfall, which is negatively correlated with shrub and sub-shrub recovery (Keeley et al. 2005b). Shifts in fire frequency and vegetative composition also have implications for animal species; after fires in the Rancho Jamul Ecological Reserve in San Diego County, small mammals associated with shrub habitat declined, while mammals associated with open, non-native grassland habitat increased (Joint Fire Science Program 2008).

A variety of factors — including fire intensity, plant species/age/size, precipitation amount and timing, nitrogen deposition, and substrate — may influence sage scrub habitat recovery post-fire. Several studies report that low-intensity fires that only burn above-ground foliage may facilitate resprouting from remnant stems (Keeley et al. 2006; Keeley and Keeley 1984; Malanson and Westman 1985). A separate study reports that high-intensity fires consuming all above-ground tissue resulted in no resprouting activity post-fire (Malanson and O'Leary 1985). Fire severity is negatively correlated with sage scrub vegetative cover and perennial herbaceous cover for several years post-fire, although higher-severity fires may stimulate dormant seedbanks of some shrubs and suffrutescent species (Keeley et al. 2005b). High-intensity fires have also been found to reduce short-term exotic annual invasion (Keeley et al. 2005a), likely by reducing exotic seed banks (Cox and Allen 2008). Post-fire recovery also varies by species, plant age, and size. Young plants are more likely to resprout after low-intensity fires (Keeley et al. 2006) while larger seedlings have been documented to experience higher burn survival (Zedler et al. 1983), and species such as brittlebush (*Encelia farinosa*), purple sage (*Salvia leucophylla*), California brittlebush (*Encelia californica*), sawtooth goldenbush (*Hazardia squarrosa*), coastal buckwheat (*Eriogonum cinereum*), lemonade berry, and laurel sumac all excel at resprouting (Kelley et al. 2006; Lloret and Zedler 1991; Malanson and O'Leary 1982). In the years following fire, intra-annual variability in precipitation as well as variations in nitrogen deposition may affect competitive interactions and relative abundance of sage scrub species versus exotic annual grasses (Cox et al. 2014; Goldstein and Suding 2014a, 2014b; Keeley et al. 2005b; Kimball et al. 2014), especially in inland sage scrub stands (Keeley et al. 2005b). Finally, substrate composition may influence vegetation composition post-fire (Callaway and Davis 1993; DeSimone and Burk 1992; Keeley et al. 2005b). For example, Callaway and Davis (1993) found that coastal sage scrub transitioned to annual grassland more rapidly on burned sites with depositional substrates.

<u>Insect and animal disturbance</u>
Vertebrate and insect activities, including burrowing, herbivory, and granivory, can mediate sage scrub recruitment and succession in a variety of ways (DeSimone and Tang 2015; DeSimone and Zedler 1999). For example, studies at Starr Ranch Sanctuary in Orange County found animal disturbance created a variety of recruitment microsites within mature grassland and sage scrub habitats, as well as within grassland-scrub ecotones (DeSimone and Zedler 1999); pocket gopher burrowing mounds allowed sage scrub colonization amongst typically thick annual grass thatch, while herbivory in ecotone and sage scrub habitats maintained gaps for new sage scrub recruitment (DeSimone and Zedler 1999). Small mammal and rabbit herbivory also mitigates annual grass invasion in the herbaceous understory of restored sage scrub stands (DeSimone and Tang 2015). However, seed predators (e.g., ants, rodents) can reduce sage scrub recruitment, although predation rates vary according to seed size and occur most frequently in shrub and ecotone locations relative to grasslands (DeSimone and Zedler 1999, 2001).

Sensitivity and current exposure to non-climate stressors

Habitat experts evaluated sage scrub habitats to have moderate-high sensitivity to non-climate stressors[7], with overall moderate-high exposure to these stressors within the study region.[8] Key non-climate stressors identified by habitat experts for sage scrub systems include: invasive and problematic species, land-use conversion, and pollution and poisons.[9] Habitat experts also identified transportation corridors and recreation as non-climate stressors affecting sage scrub habitats.[10] Habitat experts evaluated exposure to non-climate stressors to be geographically localized within the study region (Vulnerability Assessment Reviewers, pers. comm., 2015). Non-climate stressors can interact with climate change and disturbance regimes to affect the distribution, species composition, and integrity of sage scrub habitats. In addition, many of these stressors occur simultaneously, compounding impacts and exposure (Beltran et al. 2014; Cox et al. 2014; Riordan and Rundel 2014).

<u>Invasive and other problematic species</u>

Sage scrub stands can be invaded by non-native species following disturbance (Goldstein and Suding 2014b; Minnich and Dezzanni 1998), although invasion success is likely moderated by moisture availability (Goldstein and Suding 2014a), fire intensity and frequency (Keeley et al. 2005a; Rundel 2007), nitrogen deposition (Cox et al. 2014; Kimball et al. 2014), small mammal presence (DeSimone and Tang 2015), and other factors. Grazing, shorter fire return intervals, nitrogen deposition, and urban and agricultural habitat fragmentation all contribute to exotic invasion and vegetation conversion of sage scrub habitat to non-native annual grassland (Allen et al. 2000; Cox et al. 2014; Rundel 2007; Tallutto and Suding 2008). For example, portions of the interior sage scrub range have been converted to annual grassland as a result of too-frequent burning (Rundel 2007), and nitrogen deposition facilitates transition to annual grasslands under normal burning regimes (Cox et al. 2014). Conversely, herbivory by small mammals and rabbits may moderate non-native invasion success in restored sage scrub herbaceous understories (DeSimone and Tang 2015).

Exotics invade more successfully in inland locations (Keeley et al. 2005a) and after disturbance, including low-intensity fires (Goldstein and Suding 2014b). Invasive species compete for resources (e.g., soil moisture and nitrogen; Dickens and Allen 2014; Eliason and Allen 1997; Rundel 2007) and can limit sage scrub regeneration post-fire by filling interspaces (Keeley et al. 2005b) and/or limiting sage scrub propagule production, affecting biodiversity (Allen et al. 2000) and reducing resources available to sage scrub-affiliated wildlife (e.g., Quino checkerspot butterfly; Preston et al. 2012). Invasives also alter ecosystem processes by perpetuating shifting fire regimes (Diffendorfer et al. 2002; Syphard et al. 2007; Talluto and Suding 2008).

Annuals from the Mediterranean basin constitute the majority of invaders (Keeley et al. 2005a). Common invasive annual grasses include species from the genera *Bromus*, *Avena* (Goldstein

[7] Confidence: High

[8] Confidence: High

[9] Factors presented are those ranked highest by habitat experts. A full list of evaluated factors can be found at the end of this document.

[10] Not all habitat experts agreed on these non-climate stressors.

and Suding 2014b; Keeley et al. 2005a), *Vulpia*, and *Hordeum* (Allen et al. 2000). Common invasive annual forbs include *Erodium* spp., forbs of the Asteraceae family, and others (Keeley et al. 2005a). Exotic grasses typically have much larger seedbanks than native coastal sage scrub vegetation (4,000 vs. 400 seeds/m^2), increasing the likelihood of vegetation conversion following repeated disturbance (Cox and Allen 2008). For example, in portions of Riverside and Orange County, native coastal sage scrub cover declined 34-39% over a 70-year period while annual grasses increased up to 38%, largely as a result of elevated fire frequency and nitrogen deposition (Cox et al. 2014; Talluto and Suding 2008). Comparatively, in the absence of repeated disturbance, coastal sage scrub stands in Orange and San Diego Counties have low cover of non-native species (S. DeSimone, pers. comm., 2015).

<u>Land-use conversion</u>

Sage scrub habitat occurs in areas ideal for development (e.g., coastal, low-slope areas), which has contributed to historical widespread sage scrub habitat loss in southern California (Diffendorfer et al. 2002; Rundel 2007; Westman 1981a), as well as degradation of existing habitat (Beltran et al. 2014). Anthropogenic surfaces currently occupy 24.3% of available land area in southern California, and projected population growth will likely drive continued sage scrub habitat loss to human land use in the region (Riordan and Rundel 2014). For example, U.S. Geological Survey land use-land cover data project that under a A1B future emissions scenario, sage scrub habitat loss to human land use could continue in the southern California region at a rate of 117 km^2 per year through 2050, slowing to roughly 75 km^2 per year in the latter half of the century (2050-2080; Riordan and Rundel 2014). Development will likely be concentrated around existing urban centers (Riordan and Rundel 2014), and slow later in the century as undeveloped private land available for conversion diminishes (Beltran et al. 2014). However, land-use projections and associated change in shrub and other vegetative habitats are variable depending on the scenario analyzed (Sleeter et al. 2012).

Development and expanding human land use can exacerbate climate change impacts on sage scrub communities by destroying remaining habitat and limiting migration to and availability of future climate refugia (Beltran et al. 2014; Riordan and Rundel 2014; Syphard et al. 2007, 2009, 2013). Coastal sage scrub has been lost from 70-90% of the land area it occupied in in the 1970s (Westman 1981a), with losses primarily attributed to human land-use expansion (Diffendorfer et al. 2002; O'Leary 1995 cited in Syphard et al. 2007; Rundel 2007); future rates of habitat conversion to human land use could cause an additional loss of 4,575 km^2 of shrubland habitat in southern California by 2080 (Riordan and Rundel 2014). In addition to direct habitat loss, fragmentation as a result of development also limits sage scrub gene flow, migration, and dispersal, particularly for species with limited dispersal capability, potentially undermining the ability of this habitat to track changes in suitable climatic habitat (Beltran et al. 2014). Habitat fragmentation has similar effects on sage scrub-affiliated wildlife. For example, agricultural and rural development are linked with population extinctions of the Quino checkerspot butterfly in southern California during the early 20th century. Resultant and ongoing habitat fragmentation also undermines the ability of this butterfly to recover and recolonize following climate-related disturbances (Preston et al. 2012).

Development and expanding human land use can also alter system dynamics. For example, development increases the likelihood of fire ignitions, exacerbating climate-driven shifts in fire regimes (Syphard et al. 2007). Intermediate development levels translate to highest ignition risk in adjacent vegetation communities (Syphard et al. 2007), and future development, particularly development that expands the wildland-urban interface, could have significant ecological impacts (Syphard et al. 2007, 2009, 2013). In general, future population growth and urban development are likely to interact with climate drivers to create spatially variable vulnerability amongst sage scrub habitats and species (Bonebrake et al. 2014; Preston et al. 2012; Syphard et al. 2013).

Pollution and poisons

Air pollution may cause direct injury to sage scrub species and/or enhance the sensitivity of sage scrub habitats to climate-driven changes and other non-climate stressors. Nitrogen (N) deposition is the most critical form of air pollution affecting sage scrub habitats. At and above critical N deposition loads, native species in coastal sage scrub habitats decline in both diversity and cover (Allen et al. 2000; Fenn et al. 2010; Westman 1981a) and are subject to vegetation type conversion, even under "normal" fire regimes (Cox et al. 2014). Studies by Fenn et al. (2010) found that increasing soil N was negatively correlated with native shrub and forb cover, but positively correlated with exotic grass cover, higher burn frequency, and lower species richness in sage scrub canopy and understory species, as well as with reduced spore density, root colonization, and species richness of its mutualistic arbuscular mycorrhizal fungi (AMF). Talluto and Suding (2008) also found that N deposition was positively correlated with exotic grass cover in sage scrub habitats after low-intensity fire. In other studies, artificial N fertilization caused a decline in shrubs and an increase in exotic grasses (Kimball et al. 2014), reflecting observations along N deposition gradients (Cox et al. 2014; Fenn et al. 2010). N deposition may facilitate sage scrub conversion to annual grasslands, which feature higher fire frequencies that inhibit sage scrub regeneration (Allen et al. 1998; Minnich and Dezzani 1998; Padgett and Allen 1999; Talluto and Suding 2008).

Critical N loads for both coastal sage scrub and its mutualistic AMF are calculated to be between 7.8-10 kg N per hectare per year (Fenn et al. 2010) and in another study, 11 kg N per hectare per year (Cox et al. 2014). Sage scrub habitats occupy low-elevation zones close to N emission sources (e.g., highways, cities), and roughly 54% of sage scrub habitat in California exceeds critical N loads, particularly in southern California (Fenn et al. 2010). N deposition is higher in inland locations (Fenn et al. 2010; Padgett et al. 1999) as a result of onshore winds (Allen et al. 2000); ongoing studies are investigating the coastal to inland N deposition gradient and the potential interaction with invasive species vulnerability (Vulnerability Assessment Reviewers, pers. comm., 2015).

Other air pollutants may also impact sage scrub habitats. For example, ozone may reduce plant growth (Westman 1990 cited in Allen et al. 2000), affect species competition dynamics, and interact with shifting fire intensity to cause shifts in sage scrub vegetation composition (Malanson and Westman 1991). Similarly, sulfur dioxide may undermine sage scrub growth

(Preston 1988). However, both of these pollutants are less of an issue in California relative to N deposition (Allen et al. 2000; Fenn et al. 2010).

Future Climate Exposure

Habitat experts evaluated sage scrub habitats to have moderate exposure to projected future climate and climate-driven changes,[11] and key climate variables to consider include: precipitation changes, increased wildfire, increased drought, decreased soil moisture, and increased extreme high-temperature events (Table 1).[12] Habitat experts also identified increased air temperatures and increased extreme low-temperature events as important factors to consider for sage scrub habitats (Table 1).[13] For a detailed overview of how these factors are projected to change in the future, please see the Southern California Climate Overview (http://ecoadapt.org/programs/adaptation-consultations/socal). Habitat experts identified north-facing slopes and coastal areas as potential climate refugia for sage scrub species in southern California (Vulnerability Assessment Reviewers, pers. comm., 2015).

Table 1. Anticipated sage scrub responses to climate and climate-driven changes.

Climate and climate-driven changes	Anticipated sage scrub response
Air temperature and extreme heat events *+2.5 to +9°C by 2100; heat waves, particularly humid nighttime heat events, will occur more frequently, last longer, and feature higher temperatures*	• Decreased germination success for some species, driving shifts in abundance • Shifts in habitat composition and distribution
Precipitation and soil moisture *Variable annual precipitation volume and timing, with wetter winters and drier summers; increased climatic water deficit*	• High rainfall: increased recruitment and plant growth, particularly in the herbaceous understory • Shifting rainfall patterns: altered species composition, germination, recruitment, phenology, and vulnerability to invasion by annual grasses; infrequent but large rainfall events may favor coastal sage scrub over annual grasses and evergreen shrubs
Drought *Longer, more severe droughts with drought years twice as likely to occur*	• Shifts in drought onset may affect seed production of drought-deciduous shrubs • Decreased plant growth, establishment, and density • Shifts to desert scrub communities if dry conditions persist • Increased vulnerability to invasion in burned landscapes due to retarded shrub establishment and growth

[11] Confidence: High

[12] Factors presented are those ranked highest by habitat experts. A full list of evaluated factors can be found at the end of this document.

[13] Not all habitat experts agreed on these factors.

Climate and climate-driven changes	Anticipated sage scrub response
Wildfire *Increased fire size, frequency, and severity*	• Declines in native species due to seedling/resprout mortality and inhibited seedbank regeneration • Increased exotic species establishment and abundance, potentially exacerbating shifting fire regimes and leading to habitat conversion to annual grassland

Precipitation and soil moisture

Increased precipitation variability will likely affect plant stress, productivity (Fay et al. 2002; Sher et al. 2003), and overall recruitment (DeSimone and Zedler 2001). However, drought-deciduous vegetation may have a competitive advantage over annual grasses (Goldstein and Suding 2014a) and evergreen shrubs (DeSimone and Zedler 1999) under scenarios of less frequent but larger rainfall events, as well as in mesic areas that have historically supported chaparral (E. Riordan, pers. comm., 2015). For example, Goldstein and Suding (2014a) project that future precipitation shifts leading to less frequent but larger rainfall events will increase the competitive advantage of coastal sage scrub vegetation over exotic annual grasses in post-fire environments.

Drought

Although sage scrub species are generally drought-adapted (Willis et al. 2013), increasing drought frequency and/or length could affect sage scrub survival (Kimball et al. 2014) and recruitment (DeSimone and Zedler 2001). For example, a field study in Orange County showed increased exotic grass and decreased coastal sage scrub productivity under simulated drought using rainout shelters (Kimball et al. 2014). This study showed that coastal sage scrub shrub density declines with drought, as is already observed in inland sage scrub of Riverside County, which has lower precipitation and lower atmospheric humidity (Cox et al. 2014). In addition, extreme drought in burned sage scrub habitats may slow or alter succession to favor exotic annual grasslands, particularly when paired with nitrogen deposition (Kimball et al. 2014). Coastal areas appear to be the most resilient to drought and reduced soil moisture, and may act as refugia for this habitat, although they face high development pressure; in addition, more frequent fire regimes could undermine the availability and quality of coastal refugia (Vulnerability Assessment Reviewers, pers. comm., 2015).

Habitat and species distribution

Several different modeling studies project varying degrees of habitat loss and contraction for sage scrub in southern California by mid- and late-century in response to future climate change (Beltran et al. 2014; Lenihan et al. 2008; Principe et al. 2013; Riordan and Rundel 2014). Potential climatic refugia and expanding climatically suitable sage scrub habitat may exist in central California (Beltran et al. 2014; Lenihan et al. 2008; Riordan and Rundel 2014), but species' dispersal ability, habitat fragmentation as a result of human land-use expansion, and other factors (e.g., shifting fire regimes; Bonebrake et al. 2014; Syphard et al. 2013) will likely influence the ability of southern sage scrub species to migrate northward and establish new populations in response to climate change (Riordan and Rundel 2014). The southern California study area is projected to lose a considerable amount of sage scrub habitat by mid- and late-century (Lenihan et al. 2008; Riordan and Rundel 2014), as well as experience significant losses in sage scrub species richness, particularly when combined with expansions of human land use (Riordan and Rundel 2014) and shifts in fire frequency (Bonebrake et al. 2014; Lenihan et al. 2008; Syphard et al. 2007, 2013).

Species distribution modeling by Principe et al. (2013), which utilized 11 downscaled A2 emissions scenario climate projections, indicates a majority of coastal sage scrub species will experience greater than 50% reductions in suitable habitat in southern California by mid-century (2045-2065). Current foundational species, including California buckwheat (*Eriogonum fasciculatum*) and California sagebrush, are projected to fare the worst, and may lose up to 72% and 87% of current habitat in the southern portion of their range (Principe et al. 2013), although projected habitat losses are more moderate across the full species distribution (Riordan and Rundel 2014). California brittlebush (*Encelia californica*), yellow bush penstemon (*Keckiella antirrhinoides*), bush monkey flower (*Mimulus aurantiacus*), and laurel sumac are projected to maintain 40-50% of current suitable habitat, while black sage (*Salvia mellifera*), brittlebush, Menzies' goldenbush (*Isocoma menziesii*), and sawtooth goldenbush are projected to maintain 60-82% of current suitable habitat, representing the sage scrub species least likely to be affected by projected climate changes (Principe et al. 2013).

Wildlife habitat modeling for two threatened sage scrub associated species in southern California, the Quino checkerspot butterfly and the California gnatcatcher (*Polioptila californica*), predicts large reductions in potential habitat with increasing temperature and precipitation extremes. Habitat reductions were even more significant when climate models were paired with climate-based niche models of shrub vegetation types and specific shrub species on which these wildlife species depend. Both wildlife species were projected to experience suitable habitat shifts to more easterly locations than current distribution, indicating shifts to higher elevations along western mountain slopes in southern California (Preston et al. 2008).

Adaptive Capacity

The overall adaptive capacity of sage scrub habitats was evaluated to be moderate by habitat experts.[14]

Habitat extent, integrity, continuity, and permeability

Habitat experts evaluated sage scrub habitats to have a low-moderate geographic extent (i.e., habitat is quite limited in the study area),[15] low integrity (i.e., habitat is degraded),[16] and feature low continuity (i.e., habitat is isolated and/or fragmented).[17] Habitat experts identified land-use conversion, agriculture, transportation corridors, and grazing as barriers to habitat

[14] Confidence: High
[15] Confidence: High
[16] Confidence: High
[17] Confidence: High

continuity and dispersal for this ecosystem type.[18] Geologic features may also act as a landscape barrier for this habitat.[19]

Sage scrub habitats can be found throughout coastal and inland southern California, as well as in select locations along the central California coast (Rundel 2007). Coastal sage scrub communities are found from Santa Barbara to northwestern Baja California, distributed along mountainsides and foothills, while inland sage scrub communities can be found in western Riverside and San Bernardino Counties, northeastern San Diego County, and northern Los Angeles County (Rundel 2007). Sage scrub habitats are most common in foothills and valleys, but can be found up to 900 m (2,952 ft; de Becker 1988). Sage scrub habitats transition to chaparral with increasing elevation (USFS 2013) though pockets of sage scrub are distributed throughout chaparral habitat in the Coast, Transverse, and Peninsular mountain ranges (Rundel 2007). Sage scrub vegetation can thrive on a variety of soil types, including granitic, sandstone diatomaceous earth, serpentine, volcanic parent material, and clay soils in chaparral habitat (Rundel 2007 and citations therein). Maritime succulent sage shrub habitats occur only in select areas of the very southern portion of coastal southern California (e.g., Cabrillo National Monument; Rundel 2007), with their core distribution extending into northwestern Baja California (Vulnerability Assessment Reviewers, pers. comm., 2015).

Coastal sage scrub is considered one of the most threatened habitat types in western North America (Noss et al. 1995). A combination of stressors has led to the loss of 70-90% of original sage scrub habitat in southern California and contributed to significant fragmentation and degradation of existing habitat (Davis et al. 1994; Diffendorfer et al. 2002; Fenn et al. 2010; O'Leary et al. 1992 cited in Allen et al. 2000; Rundel 2007; Westman 1981a), affecting gene flow, seed dispersal (Davis et al. 1994), and the ability of sage scrub habitats to adapt to climate and non-climate stressors. In addition, sage scrub habitat loss and fragmentation has contributed to numerous endangered and threatened species listings amongst sage scrub-associated mammal, bird, reptile, and plant species (Davis et al. 1994; DeSimone 1995; Keeley and Swift 1995). However, sage scrub habitats have been the focus of increasing land-protection measures in southern California, including conservation easements and habitat conservation plans (Vulnerability Assessment Reviewers, pers. comm., 2015).

Resistance and recovery

Habitat experts evaluated sage scrub habitats to have low-moderate resistance to climate stressors and maladaptive human responses,[20] and moderate recovery potential.[21] Phenological plasticity of many sage scrub species enhances resistance to drought and precipitation variability (Pratt and Mooney 2013). Sage scrub communities also typically exhibit rapid recovery after disturbance, although recovery ability varies by species, location, and according

[18] Barriers presented are those ranked most critical by habitat experts. A full list of evaluated barriers can be found at the end of this document.

[19] Not all reviewers agreed on this landscape barrier.

[20] Confidence: High

[21] Confidence: High

to other local factors (Keeley et al. 2005b; Zedler et al. 1983). Sage scrub recruitment appears to be linked with vegetation gaps, which can be created by fire (Rundel 2007), animal disturbance (DeSimone and Zedler 1999, 2001), or other processes (e.g., landslides; Rundel 2007). Many species maintain consistent seed production and have persistent seed banks (DeSimone and Zedler 2001; Louda 1995), all of which facilitate rapid colonization of disturbed areas amongst mature sage scrub, chaparral, grasslands, and in the grassland-scrub ecotone (DeSimone and Zedler 1999, 2001; Rundel 2007). However, seed dispersal rarely exceeds 5 m, which may limit dispersal in the face of climate change (Pratt and Mooney 2013), although some species utilize wind-mediated seed dispersal (Rundel 2007) and strong Santa Ana winds may facilitate longer seed dispersal distances and persistence of sage scrub seedbanks in varying habitat types (DeSimone and Zedler 2001).

In addition, seed production varies depending on species life history. For example, facultative drought-deciduous sage scrub species, including *A. californica*, *E. fasciculatum*, and *Salvia apiana* retained high annual seed and inflorescence counts in a multi-year study with variable precipitation, while the completely drought-deciduous shrub *A. glaber* (previously *L. scoparius*) exhibited variable seed production in response to variations in drought onset (DeSimone and Zedler 2001). Genetic variation in phenological plasticity, seed production, and disturbance recovery amongst different sage scrub populations and species, as well as their potential to adapt to shifting fire and climate regimes, is likely to lead to variable resilience of sage scrub habitats to shifting climate conditions (DeSimone and Zedler 2001; Keeley et al. 2005b; Malanson and Westman 1991; Pratt and Mooney 2013).

Despite having inherent resistance and recovery potential, non-climate stressors may undermine the overall resilience of sage scrub habitats. For example, once converted to annual grassland, natural regeneration and restoration of sage scrub habitat can be difficult (Goldstein and Suding 2014b; Zink et al. 1995), although coastal sage scrub habitats have been documented to naturally colonize grassland areas (DeSimone 2011; DeSimone and Zedler 1999, 2001) and to recover from disturbance and annual grass invasion (Cox et al. 2014). Recovery is likely linked with seed availability, as recovered patches occur more frequently in areas with adjacent intact sage scrub habitat (Cox et al. 2014). Similarly, although nitrogen deposition does not influence sage scrub recovery from grass invasion, it can affect the long-term persistence of sage scrub habitats if deposition exceeds critical loads (Cox et al. 2014). In addition to non-climate stressors, topography, soil type, and local site conditions may affect sage scrub resilience and response to disturbance and climate changes (Callaway and Davis 1993; Cox et al. 2014; DeSimone and Burk 1992; DeSimone and Zedler 2001; Kimball et al. 2014; Talluto and Suding 2008).

Habitat diversity

Habitat experts evaluated sage scrub habitats to have moderate physical and topographical diversity,[22] high component species diversity,[23] and moderate-high functional group diversity.[24]

[22] Confidence: High

[23] Confidence: High

Sage scrub habitats typically feature a drought-deciduous shrub canopy and an herbaceous understory comprised of annual and perennial forbs and grasses (Diffendorfer et al. 2002). Compared to chaparral habitats, sage scrub habitat structure is shorter in height (rarely exceeding 1.5-2 m) and features less biomass (Rundel 2007). Although canopy cover may be close to 100% (Mooney 1977 cited in de Becker 1988) in coastal areas, inland sage scrub has an open canopy characterized by forb-filled interspaces (Cox et al. 2014). Even closed-canopied sage scrub features reduced woodiness relative to chaparral habitats (Rundel 2007), and enough light penetrates the canopy to allow growth and maintenance of an herbaceous understory (de Becker 1988). This canopy structure makes sage scrub susceptible to invasion, compared to denser chaparral canopies (E. Allen, pers. comm., 2015).

Sage scrub habitat species composition varies by location, contributing to high beta- and gamma-diversity across the study region (Davis et al. 1994; DeSimone and Burk 1992; Taylor 2005). Within southern California, three sage scrub associations are recognized: coastal, inland, and maritime sage scrub (Rundel 2007; see below). Within stands, species composition is relatively constant due to continual recruitment, and a diversity of shrub age and size classes is typical for stands experiencing natural or no disturbance (de Becker 1988). Within functional groups, diversity is highest amongst the native forb understory (Vulnerability Assessment Reviewers, pers. comm., 2015). Common deerweed is considered a keystone species in both coastal and inland sage scrub habitats following fire or other disturbance due to its ability to fix nitrogen (Rundel 2007). California sagebrush and California buckwheat are found across many sage scrub communities, as well as dispersed in adjacent chaparral communities (Davis et al. 1994). Sage scrub habitats also harbor many threatened and endangered plant and wildlife species which may be sensitive to climate change due to limited and declining habitat extent (e.g., see Preston et al. 2012), including 11 mammal, 26 bird, and 10 reptile species (Keeley and Swift 1995) and over 200 sensitive plant species (Skinner and Pavlik 1994 cited in Allen et al. 2000). In addition, the native forb understory is likely the most vulnerable to climate- and nitrogen deposition-driven shifts in invasive species pressure (Vulnerability Assessment Reviewers, pers. comm., 2015).

Coastal sage scrub

Coastal sage scrub habitats are composed of only a few dominant shrub species, and typically dominant species are those able to quickly colonize after disturbance, such as drought-deciduous California sagebrush, California brittlebush, and the semi-evergreen California buckwheat. Coastal sage scrub habitats can also include black sage and purple sage, evergreen shrub components including lemonade berry, laurel sumac, and toyon (*Heteromeles arbutifolia*), and a variety of other shrub, cacti, succulent, geophyte, and herbaceous perennial and annual species (Rundel 2007). Evergreen shrubs are more prevalent in sage scrub stands in mesic coastal areas, as well as in northern portions of the habitat range and at higher elevations (de Becker 1988; Rundel 2007). Coastal sage scrub diversity is typically greatest in its herbaceous understory, with lower diversity in the dominant shrubs (Westman 1981a).

[24] Confidence: High

Inland sage scrub
Inland sage scrub communities feature similar species to coastal communities, including California sagebrush, California brittlebush, California buckwheat, and black sage (Rundel 2007). However, California buckwheat is often more prevalent and dominant than California sagebrush (Davis et al. 1994). Inland sage scrub associations also commonly feature white sage (*S. apiana*) and other vegetation often found in transitional zones between Mojave scrub and chaparral such as brittlebush and cholla (*Cylindropuntia californica*) (Rundel 2007).

Maritime sage scrub
Maritime succulent sage scrub habitats include many common species associated with other sage scrub zones, but also feature a variety of endemic succulents (Rundel 2007). Maritime succulent scrub habitat occupies the smallest range in California, extending into Baja California, but has the highest species richness of the sage scrub habitats (Rundel 2007; Westman 1981a).

Management potential
Habitat experts evaluated sage scrub habitats to be of moderate societal value.[25] Sage scrub habitats are valued for their recreation opportunities, rare and endangered species, and aesthetics. Sage scrub habitats provide important ecosystem services, including: recreation, biodiversity, nitrogen retention, carbon sequestration, air quality, and flood and erosion protection (Vulnerability Assessment Reviewers, pers. comm., 2015).

Habitat experts identified that there is moderate potential for managing or alleviating climate impacts for sage scrub habitats.[26] Habitat experts identified the following actions as potential management options for sage scrub habitats: weed management; restoration (although success may depend on annual precipitation; DeSimone 2011); mitigating fire and pollution problems that facilitate invasive species establishment and dominance; practicing climate-informed planting (i.e., planting species that will be able to tolerate future conditions); and promoting landscape connectivity to facilitate migration. In addition, the scientific literature identified several strategies for mitigating climate impacts on sage scrub habitats, including: creating new protected areas to accommodate modeled future climate refugia (Beltran et al. 2014); limiting habitat conversion (Riordan and Rundel 2014); and protecting existing habitat (Bonebrake et al. 2014).

Recommended Citation

Reynier, W.A., L.E. Hillberg, and J.M. Kershner. 2016. Southern California Sage Scrub Habitats: Climate Change Vulnerability Assessment Synthesis. Version 1.0. EcoAdapt, Bainbridge Island, WA.

[25] Confidence: Moderate
[26] Confidence: Moderate

This document is available online at the EcoAdapt website (http://ecoadapt.org/programs/adaptation-consultations/socal).

Literature Cited

Allen, E. B., Eliason, S. A., Marquez, V. J., Schultz, G. P., Storms, N. K., Stylinski, C. D., . . . Allen, M. F. (2000). What are the limits to restoration of coastal sage scrub in southern California? In J. E. Keeley, M. Baer-Keeley, & C. J. Fotheringham (Eds.), *2nd interface between ecology and land development in California* (pp. 253–262). (Open File Report 00-62). Sacramento, CA: U.S. Geological Survey, Western Ecological Research Center.

Allen, E. B., Padgett, P. E., Bytnerowicz, A., & Minnich, R. (1998). Nitrogen deposition effects on coastal sage vegetation of southern California. In A. Bytnerowicz, M. J. Arbaugh, & S. L. Schilling (Eds.), *Proceedings of the international symposium on air pollution and climate change effects on forest ecosystems, Riverside, California, February 5-9, 1996* (pp. 131-140). (Gen. Tech. Rep. PSW-GTR-166). Albany, CA: USDA Forest Service, Pacific Southwest Research Station. Retrieved from http://www.treesearch.fs.fed.us/pubs/26950

Beltrán, B. J., Franklin, J., Syphard, A. D., Regan, H. M., Flint, L. E., & Flint, A. L. (2014). Effects of climate change and urban development on the distribution and conservation of vegetation in a Mediterranean type ecosystem. *International Journal of Geographical Information Science, 28*(8), 1561-1589.

Bonebrake, T. C., Syphard, A. D., Franklin, J., Anderson, K. E., Akçakaya, H. R., Mizerek, T., . . . Regan, H. M. (2014). Fire management, managed relocation, and land conservation options for long-lived obligate seeding plants under global changes in climate, urbanization, and fire regime. *Conservation Biology*, *28*(4), 1057–1067.

Boorse, G. C., Ewers, F. W., & Davis, S. D. (1998). Response of chaparral shrubs to below-freezing temperatures: Acclimation, ecotypes, seedlings vs. adults. *American Journal of Botany, 85*(9), 1224-1230.

Callaway, R. M., & Davis, F. W. (1993). Vegetation dynamics, fire, and the physical environment in coastal central California. *Ecology, 74*(5), 1567-1578.

Cox, R. D., & Allen, E. B. (2008). Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. *Plant Ecology, 198*(1), 37-46.

Cox, R. D., Preston, K. L., Johnson, R. F., Minnich, R. A., & Allen, E. B. (2014). Influence of landscape-scale variables on vegetation conversion to exotic annual grassland in southern California, USA. *Global Ecology and Conservation, 2*, 190-203.

Davis, F. W., Stine, P. A., & Stoms, D. M. (1994). Distribution and conservation status of coastal sage scrub in southwestern California. *Journal of Vegetation Science, 5*, 743-756.

de Becker, S. (1988). Coastal scrub. In K. E. Mayer & W. F. Laudenslayer Jr. (Eds.), *A guide to wildlife habitats of California*. Sacramento, CA: State of California, Resources Agency, Department of Fish and Game.

DeSimone, S. A. (2011). Balancing active and passive restoration in a nonchemical, research-based approach to coastal sage scrub restoration in southern California. *Ecological Restoration, 29*(1-2), 45-51.

DeSimone, S. A. (1995). California's coastal sage scrub. *Fremontia*, *23*, 3-8.

DeSimone, S. A., & Burk, J. H. (1992). Local variation in floristics and distributional factors in Californian coastal sage scrub. *Madroño, 39*(3), 170-188.

DeSimone, S. A., & Tang, M. (2015). *Small mammals act as invasion filters in southern Californian coastal sage scrub restoration*. Paper presented at the California Native Plant Society Conservation Conference, January 13-17, 2015, San Jose, CA. Retrieved from https://www.cnps.org/cnps/conservation/conference/2015/pdf/cnps2015_oral_abstracts.pdf

DeSimone, S. A., & Zedler, P. H. (1999). Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. *Ecology, 80*(6), 2018-2032.

DeSimone, S. A., & Zedler, P. H. (2001). Do shrub colonizers of southern Californian grassland fit generalities for other woody colonizers? *Ecological Applications, 11*(4), 1101-1111.

Dickens, S. J. M., & Allen, E. B. (2014). Soil nitrogen cycling is resilient to invasive annuals following restoration of coastal sage scrub. *Journal of Arid Environments, 110*, 12-18.

Diffendorfer, J. E., Chapman, R. E., Duggan, J. M., Fleming, G. M., Mitrovitch, M., Rahn, M. E., & del Rosario, R. (2002). Coastal sage scrub response to disturbance. A literature review and annotated bibliography. Prepared for the California Department of Fish and Game. San Diego, CA: San Diego State University, Department of Biology. Retrieved from https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=26433

Eliason, S. A., & Allen, E. B. (1997). Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology, 5*(3), 245-255.

Fay, P. A., Carlisle, J. D., Danner, B. T., Lett, M. S., McCarron, J. K., Stewart, C., . . . Collins, S. L. (2002). Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences*, *163*(4), 549–557.

Fenn, M., Allen, E., Weiss, S., Jovan, S., Geiser, L., Tonnesen, G., . . . Yuan, F. (2010). Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. *Journal of Environmental Management, 91*(12), 2404-2423.

Goldstein, L. J., & Suding, K. N. (2014a). Intra-annual rainfall regime shifts competitive interactions between coastal sage scrub and invasive grasses. *Ecology, 95*(2), 425-435.

Goldstein, L. J., & Suding, K. N. (2014b). Applying competition theory to invasion: Resource impacts indicate invasion mechanisms in California shrublands. *Biological Invasions, 16*(1), 191-203.

Joint Fire Science Program (2008). When chaparral and coastal sage scrub burn: Consequences for mammals, management, and more. *Fire Science Brief,* 28, 6. Retrieved from https://www.firescience.gov/projects/briefs/04-2-1-94_FSBrief28.pdf

Keeley, J. E. (2005). Fire as a threat to biodiversity in fire-type shrublands. In B. E. Kus & J. L. Beyers (Eds.), *Planning for biodiversity: Bringing research and management together. Proceedings of a symposium for the south coast ecoregion. February 9-March 2, 2000. Pomona, CA* (pp. 97-106). (Gen. Tech. Rep. PSW-GTR-195). Albany, CA: USDA Forest Service, Pacific Southwest Research Station. Retrieved from http://www.fs.fed.us/psw/publications/documents/psw_gtr195/psw_gtr195_2_97_Keeley.pdf

Keeley, J. E., Baer-Keeley, M., & Fotheringham, C. (2005a). Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications, 15*(6), 2109-2125.

Keeley, J. E., Fotheringham, C., & Baer-Keeley, M. (2005b). Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecological Applications, 15*(5), 1515-1534.

Keeley, J. E., Fotheringham, C., & Baer-Keeley, M. (2006). Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs, 76*(2), 235-255.

Keeley, J. E., & Keeley, S. C. (1984). Postfire recovery of California coastal sage scrub. *American Midland Naturalist, 111*(1), 105-117

Keeley, J. E., & Swift, C. C. (1995). Biodiversity and ecosystem functioning in Mediterranean-climate California. In D. G. W. Davis & D. D. M. Richardson (Eds.), *Mediterranean-type ecosystems* (pp. 121–183). Springer Berlin Heidelberg.

Kimball, S., Goulden, M. L., Suding, K. N., & Parker, S. (2014). Altered water and nitrogen input shifts succession in a southern California coastal sage community. *Ecological Applications, 24*(6), 1390-1404.

Langan, S., Ewers, F., & Davis, S. (1997). Xylem dysfunction caused by water stress and freezing in two species of co-occurring chaparral shrubs. *Plant, Cell & Environment, 20*(4), 425-437.

Lenihan, J. M., Bachelet, D., Neilson, R. P., & Drapek, R. (2008). Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. *Climatic Change, 87*(1), 215-230.

Levine, J. M., McEachern, A. K., & Cowan, C. (2008). Rainfall effects on rare annual plants. *Journal of Ecology, 96*(4), 795-806.

Levine, J. M., McEachern, A. K., & Cowan, C. (2011). Seasonal timing of first rain storms affects rare plant population dynamics. *Ecology, 92*(12), 2236-2247.

Lloret, F., & Zedler, P. H. (1991). Recruitment pattern of Rhus integrifolia populations in periods between fire in chaparral. *Journal of Vegetation Science, 2*(2), 217-230.

Louda, S. M. (1995). Effect of seed predation on plant regeneration: Evidence from Pacific Basin Mediterranean scrub communities. In M. T. K. Arroyo, P. H. Zedler, & M. D. Fox (Eds.), *Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia* (pp. 311–344). Springer New York.

Malanson, G. P. (1985). Fire management in coastal sage-scrub, southern California, USA. *Environmental Conservation*, *12*(02), 141–146.

Malanson, G. P., & O'Leary, J. F. (1982). Post-fire regeneration strategies of Californian coastal sage shrubs. *Oecologia, 53*(3), 355-358.

Malanson, G. P., & O'Leary, J. F. (1985). Effects of fire and habitat on post-fire regeneration in Mediterranean-type ecosystems: Ceanothus spinosus chaparral and Californian coastal sage scrub. *Acta Oecologica. Oecologia Plantarum, 6*(2), 169-181.

Malanson, G. P., & Westman, W. E. (1985). Postfire succession in Californian coastal sage scrub: The role of continual basal sprouting. *American Midland Naturalist, 113*(2), 309-318.

Malanson, G. P., & Westman, W. E. (1991). Modeling interactive effects of climate change, air pollution, and fire on a California shrubland. *Climatic Change, 18*(4), 363-376.

Minnich, R. A., & Dezzani, R. J. (1998). Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds, 29*(4), 366-391.

Noss, R. F., Laroei, E. T., & Scott, J. M. (1995). *Endangered ecosystems of the United States: A preliminary assessment of loss and degradation.* (Biological Report 28). Washington, D.C.: U.S. National Biological Service. Retrieved from http://biology.usgs.gov/pubs/ecosys.htm.

O'Leary, J. F., & Westman, W. E. (1988). Regional disturbance effects on herb succession patterns in coastal sage scrub. *Journal of Biogeography, 15*(5), 775-786.

Padgett, P. E., Allen, E. B., Bytnerowicz, A., & Minnich, R. A. (1999). Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. *Atmospheric Environment, 33*(5), 769-781.

Padgett, P. E., Kee, S. N., & Allen, E. B. (2000). The effects of irrigation on revegetation of semi-arid coastal sage scrub in southern California. *Environmental Management, 26*(4), 427-435.

Pratt, J. D., & Mooney, K. A. (2013). Clinal adaptation and adaptive plasticity in Artemisia californica: Implications for the response of a foundation species to predicted climate change. *Global Change Biology, 19*(8), 2454-2466.

Preston, K. L., Redak, R. A., Allen, M. F., & Rotenberry, J. T. (2012). Changing distribution patterns of an endangered butterfly: Linking local extinction patterns and variable habitat relationships. *Biological Conservation*, *152*, 280–290.

Preston, K. L., Rotenberry, J. T., Redak, R. A., & Allen, M. F. (2008). Habitat shifts of endangered species under altered climate conditions: Importance of biotic interactions. *Global Change Biology*, *14*(11), 2501–2515.

Preston, K. P. (1988). Effects of sulphur dioxide pollution on a Californian coastal sage scrub community. *Environmental Pollution*, *51*(3), 179–195.

Principe, Z. A., MacKenzie, J. B., Cohen, B., Randall, J. M., Tippets, W., Smith, T., & Morrison, S. A. (2013). *50-year climate scenarios and plant species distribution forecasts for setting conservation priorities in Southwestern California*. San Francisco, CA: The Nature Conservancy of California. Retrieved from http://scienceforconservation.org/dl/SW_CA_Climate_Report_v1_Oct_2013.pdf

Riordan, E. C., & Rundel, P. W. (2009). Modelling the distribution of a threatened habitat: The California sage scrub. *Journal of Biogeography, 36*(11), 2176-2188.

Riordan, E. C., & Rundel, P. W. (2014). Land use compounds habitat losses under projected climate change in a threatened California ecosystem. *PloS ONE, 9*(1), e86487.

Rundel, P. W. (2007). Sage scrub. In M. G. Barbour, T. Keeler-Wolf, & A. A. Schoenner (Eds.), *Terrestrial vegetation of California* (pp. 208-228). Berkeley, CA: University of California Press.

Safford, H. D., & Van de Water, K. M. (2014). *Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California.* (Res. Pap. PSW-RP-266). Albany, CA:

USDA Forest Service, Pacific Southwest Research Station. Retrieved from http://www.fs.fed.us/psw/publications/documents/psw_rp266/

Sher, A. A., Goldberg, D. E., & Novoplansky, A. (2003). The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. *Oecologia*, *141*(2), 353–362.

Sleeter, B. M., Sohl, T. L., Bouchard, M. A., Reker, R. R., Soulard, C. E., Acevedo, W., . . . Zhu, Z. (2012). Scenarios of land use and land cover change in the conterminous United States: Utilizing the special report on emission scenarios at ecoregional scales. *Global Environmental Change*, *22*(4), 896–914.

Syphard, A. D., Clarke, K. C., & Franklin, J. (2007). Simulating fire frequency and urban growth in southern California coastal shrublands, USA. *Landscape Ecology, 22*(3), 431-445.

Syphard, A. D., Radeloff, V. C., Hawbaker, T. J., & Stewart, S. I. (2009). Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conservation Biology, 23*(3), 758-769.

Syphard, A. D., Regan, H. M., Franklin, J., Swab, R. M., & Bonebrake, T. C. (2013). Does functional type vulnerability to multiple threats depend on spatial context in Mediterranean-climate regions? *Diversity and Distributions, 19*(10), 1263-1274.

Talluto, M. V., & Suding, K. N. (2008). Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. *Landscape Ecology, 23*(7), 803-815.

Taylor, R. S., Jr. (2005). A new look at coastal sage scrub: What 70-year-old VTM plot data tell us about southern California shrublands. In B.E Kus and J.L Beyers (Eds.), *Planning for biodiversity: Bringing research and management together. Proceedings of a symposium for the south coast ecoregion. February 9-March 2, 2000. Pomona, CA.* (pp. 57-77). (Gen. Tech. Rep. PSW-GTR-195). Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Retrieved from http://www.fs.fed.us/psw/publications/documents/psw_gtr195/psw_gtr195_2_57_Taylor.pdf

U.S. Forest Service (USFS) (2013). *Draft supplemental environmental impact statement: Southern California national forests land management plan amendment*. (R5-MB-250). Vallejo, CA: USDA Forest Service, Pacific Southwest Region. Retrieved from https://www.uschamber.com/sueandsettle/pleadings/CBD%20v.%20USDA%20%28roadless%20rule%29/Draft%20Supplemental%20EIS.pdf

Van de Water, K. M., & Safford, H. D. (2011). A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecology*, *7*(3), 26-58.

Westman, W. E. (1981a). Diversity relations and succession in Californian coastal sage scrub. *Ecology, 62*(1), 170-184.

Westman, W. E. (1981b). Factors influencing the distribution of species of Californian coastal sage scrub. *Ecology*, *62*(2), 439-455.

Westman, W.E. (1983). Xeric Mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. *Vegetation, 52*(1), 3-19.

Willis, K., Gillespie, T., Okin, G., & MacDonald, G. (2013). *Climatic impacts on phenology in chaparral-and coastal sage scrub-dominated ecosystems in southern California using MODIS-derived time series.* Paper presented at the American Geophysical Union Fall Meeting 2013, December 2-9, 2013, San Francisco, CA. Retrieved from http://adsabs.harvard.edu/abs/2013AGUFM.B43C0507W

Zedler, P. H., Gautier, C. R., & McMaster, G. S. (1983). Vegetation change in response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology, 64*(4), 809-818.

Zink, T. A., Allen, M. F., Heindl-Tenhunen, B., & Allen, E. B. (1995). The effect of a disturbance corridor on an ecological reserve. *Restoration Ecology*, *3*(4), 304–310.