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Using Species Distribution Models With Climate Change Scenarios to Aid Ecological Restoration Decisionmaking for Southern California Shrublands

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Abstract

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Sourcing appropriate plant material for restoration within the heterogeneous landscape of southern California is a nuanced task further complicated by climate change. We generated species distribution models (SDMs) that may be useful tools for incorporating climate change scenarios into ecological restoration decisionmaking for southern California scrub and shrubland habitats. We modeled regional patterns of suitable habitat under baseline (1951–1980) and midcentury (2040–2069) climate conditions for 44 focal plant taxa under five future climate scenarios. Projected changes in habitat suitability varied across taxa and climate scenarios. Future climate scenarios with the most extreme directional changes in precipitation (increase or decrease) resulted in the greatest projected loss of suitable habitat for most taxa. The majority of plant taxa we modeled had a high degree of stable future habitat suitability, with 31 taxa projected to have ≥75 percent of baseline suitable habitat maintaining suitability midcentury under at least three future climate scenarios. Infraspecific differences in projected midcentury suitable habitat highlight the importance of considering varieties and subspecies when applying modeling results to conservation and natural resource management decisionmaking. While we did not explicitly model plant communities, multitaxon suitability overlays revealed patterns for alluvial scrub, coastal sage scrub, mixed chaparral-sage scrub, and low-elevation chaparral vegetation groups that were less readily apparent in individual taxon maps. We discuss caveats regarding SDMs and suggest that they could be used as part of an integrated toolset for successful application.

Keywords: Alluvial scrub, chaparral, climate change, coastal sage scrub, ecological restoration, seed transfer, shrubland, southern California, species distribution modeling.

Preface

This study provides the background and methodology for species distribution modeling and habitat suitability maps generated as part of a collaborative effort by the Riverside-Corona Resource Conservation District and the USDA Forest Service Pacific Southwest Research Station to develop decision-support tools for use in ecological restoration within southern California ecosystems. The maps are being incorporated into taxon-specific plant profiles with detailed ecological and genetic information on foundation plant taxa from alluvial scrub, coastal sage scrub, and low-elevation chaparral. The expanded plant profiles will be available online and are intended to help inform species selection, seed sourcing, and decisions about seed transfer for ecological restoration and other native planting projects.

Summary

Sourcing appropriate plant material for restoration within southern California's heterogeneous landscape is a nuanced task further complicated by climate change. It entails a detailed understanding of species distribution, dispersal ecology, population genetics, and biotic and abiotic interactions. Generalized tools used to inform restoration, such as provisional seed zones, are typically static with respect to environmental change and may become less effective in the context of climate change. We generated species distribution models (SDMs) that may be useful tools for incorporating climate change scenarios into recommendations for ecological restoration decisionmaking for southern California scrub and shrubland habitats. We modeled regional patterns of suitable habitat under baseline (1951–1980) and projected midcentury (2040–2069) climate conditions for 44 focal plant taxa under five future climate scenarios. Projected changes in habitat suitability varied across taxa and climate scenarios. Future climate scenarios with the most extreme directional changes in precipitation (projected increase or decrease) had the greatest projected loss of suitable habitat for most taxa. The majority of plant taxa we modeled had a high degree of stable future habitat suitability, with 31 taxa projected to have ≥75 percent of baseline suitable habitat maintaining suitability midcentury under at least three future climate scenarios. Infraspecific differences in midcentury suitable habitat projections highlight the importance of considering within-species variation when applying modeling results to conservation and natural resource management planning, especially in areas of high environmental heterogeneity such as southern California. Although we did not explicitly model plant communities, multitaxon

suitability overlays revealed patterns for alluvial scrub, coastal sage scrub, mixed chaparral-sage scrub, and low-elevation chaparral vegetation groups that were less readily apparent in individual species maps. We discuss caveats regarding SDMs and suggest their use as part of an integrated toolset for successful application. This modeling effort is part of a greater collaborative project between the Riverside-Corona Resource Conservation District and the USDA Forest Service Pacific Southwest Research Station to provide decision-support tools guiding plant selection for use in ecological restorations within southern California shrub-dominated ecosystems.

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Introduction

Land managers in southern California often face the challenge of restoring wildland habitat degraded by various combinations of habitat fragmentation, disruption of dispersal processes and biotic interactions, human-caused disturbance, and human-altered fire regimes. The region's diverse shrubland communities are of particular concern. For example, urbanization, recreational development, and increased fire frequency have contributed to the widespread loss of coastal sage scrub (including alluvial fan scrub), which has as little as 15 percent of its original extent remaining today (O'Leary 1990, 1995; Westman 1981). Restoration efforts to maintain habitat for rare species of these plant communities have been carried out for many years (Allen et al. 2000, Buck-Diaz et al. 2011, DeSimone 2006, Hanes et al. 1989). Low-elevation chaparral has been degraded by nonnative annual grass invasion and reduced shrub density under shortened fire-return intervals (Keeley and Brennan 2012) and by construction projects, leading to more interest in methods to restore chaparral shrubs (Engel 2014, Wilkin et al. 2013) and the important ecosystem services they provide, such as hillslope stability (Gabet and Dunne 2002) and carbon sequestration (Rundel and Vankat 1989). Selecting appropriate species and plant material for restoration in the heterogeneous landscape of southern California is a complex undertaking that entails an understanding of species distribution, habitat relationships, ecological genetics, and biotic and abiotic interactions; this task is further complicated by changing climate.

Scientists have already documented ecological responses to climate change from species to ecosystems (Parmesan and Hanley 2015, Walther 2010). In southern California, Kelly and Goulden (2008) attributed elevational shifts in dominant plant species in the Santa Rosa Mountains to changes in regional climate from 1977 through 2007, though past fire disturbance may have also contributed to the observed shifts (Schwilk and Keeley 2012). In California's forests, climate-driven changes in water balance have been linked to changes in structure and species composition during the 20th century (McIntyre et al. 2015) and increased tree mortality during the 2012–2015 drought (Young et al. 2017). Projected changes in climate are expected to dramatically alter natural systems within the 21st century (Thomas et al. 2004). Many species could face local extirpation, and even extinction, if the rate of climate change exceeds their capacity to adapt locally or migrate to track suitable conditions (Christmas et al. 2016, Corlett and Westcott 2013, Malcolm et al. 2002). Consideration of the potential effects of future climate change on reference or target ecosystems, species, and populations will likely become increasingly important for the long-term success of ecological restoration projects (Breed et al. 2013, Harris et al. 2006, Havens et al. 2015, Jackson and Hobbs 2009).

Climate Change Context

California has experienced an overall warming trend over the past century, although patterns vary spatially and temporally (Cordero et al. 2011, Rapacciuolo et al. 2014). Weather station data show warming trends for statewide minimum and maximum temperatures from 1918 through 2006, accelerating after 1970 to rates of +0.31 °C and +0.27 °C per decade, respectively (Cordero et al. 2011). Southern California has experienced some of the greatest regional increases in temperature across the state, particularly interior mountain areas where minimum and maximum temperatures have increased 0.42 °C and 0.26 °C per decade, respectively, from 1970 through 2006 (Cordero et al. 2011). Intensely urbanized areas have experienced especially large increases in minimum and maximum temperature (LaDochy et al. 2007), in part from a heat island effect (Kalnay and Cai 2003). Los Angeles, for example, experienced as much as a 5 °C increase in minimum temperature and a 2 °C increase in maximum temperature from 1950 to 2000 (LaDochy et al. 2007).

For vegetation, water availability in particular plays a central role in shaping plant distribution (Rehfeldt et al. 2006; Stephenson 1990, 1998; Woodward 1987). Patterns in precipitation have also changed in California, although high spatial and temporal variability make detecting trends difficult. For much of northern and central California, annual precipitation increased in 1970–2009 relative to 1900–1939, whereas precipitation decreased slightly in southern California during the same time period (Rapacciuolo et al. 2014). Shifts in temperature and precipitation affected water balance in southern California, causing large increases in climatic water deficit (CWD) for 1970–2009 relative to 1900–1939 (Rapacciuolo et al. 2014). CWD is the evaporative demand not met by available water, defined as the difference between potential evapotranspiration (PET)—the amount of water that could potentially evaporate or transpire from vegetation given unlimited water—and actual evapotranspiration (AET)—the evaporative water loss from vegetation based on actual water availability (Stephenson 1990). Temperature and precipitation (as it affects soil moisture storage) both influence AET. Together, these variables are important indicators of water availability and climate stress experienced by plants (Stephenson 1998).

Temperatures are projected to continue warming in California throughout the 21st century (Cayan et al. 2008, Hayhoe et al. 2004, Pierce et al. 2013). Statewide mean temperature could increase as much as 5.8 °C by 2070–2099 relative to 1971–2000 under continued high greenhouse gas emissions (Mastrandrea and Luers

2012). In the Los Angeles Basin and surrounding mountains, mean temperature is projected to increase anywhere from 2.8 to 6.2 °C by the end of the 21st century relative to 1981–2000 (Sun et al. 2015). Without measures to reduce greenhouse gas emissions, a new regional climate state could emerge in southern California where average temperatures at the end of the 21st century are outside the range of historical interannual variability (Sun et al. 2015). Future change in precipitation for California is less certain, with both increases and decreases in annual precipitation projected, depending on the general circulation model (GCM) considered (Berg and Hall 2015, Dettinger et al. 2015, Pierce et al. 2013). A recent analysis of many GCMs under a "business-as-usual" (continued high) emission scenario suggests that California will experience precipitation increases, though with less increase toward the south (Allen and Luptowitz 2017). Extreme dry and extreme wet events are projected to increase in frequency by the end of the 21st century (Berg and Hall 2015). Mid-21st-century projected change in precipitation regionally downscaled for the Los Angeles Basin and surrounding mountains ranges from +19 mm to -25 mm relative to 1981–2000 (Berg et al. 2015). Regardless of the direction of precipitation change in southern California, the change will likely be small compared to the naturally high interannual variability (Berg and Hall 2015, Pierce et al. 2013).

Warming temperatures since the mid-20th century are also significantly altering the hydrologic cycle across the Western United States (Barnett et al. 2008, Hamlet et al. 2007) through decreased snowpack (Mote et al. 2005), increased proportion of precipitation falling as rain rather than snow (Knowles et al. 2006), and changes in the timing and variability of spring snowmelt and streamflow (Maurer et al. 2007, Pagano and Garen 2005, Stewart et al. 2005). Projected warming and hydrological shifts will likely increase evaporative demand in the 21st century (Dettinger et al. 2015), while changes in snowmelt, resulting effects on streamflow (Hayhoe et al. 2004), and increases in the frequency of extreme dry and wet hydrological years (Berg and Hall 2015, Kim 2005) could severely stress already-strained water resources and infrastructure. In the mountains of southern California, widespread decline in both snowfall and snowpack are projected for the end of the 21st century (Sun et al. 2016). If greenhouse gas emissions continue to increase at current rates, less than 50 percent of snowfall and 26 percent of snowpack relative to 1981–2010 levels are projected to remain at elevations under 2400 m by the mid-21st century (Sun et al. 2016). Warming-accelerated spring snowmelt and declines in snowpack will likely affect streamflow for the region. Drought risk in California may also increase. Although periodic severe drought is common in California, the recent

2011–2015 drought was exceptionally severe, driven by low, albeit not unprecedented, precipitation and record high temperatures (Griffin and Anchukaitis 2014). Anthropogenic warming is increasing the probability that low-precipitation years will coincide with warm conditions (Diffenbaugh et al. 2015) and contribute to extreme drought (Williams et al. 2015).

A Species Distribution Modeling Approach

When carefully constructed and interpreted, species distribution models (SDMs) can be a useful tool for incorporating climate change into natural resource decisionmaking (Araújo and Peterson 2012, Guisan et al. 2013, Schwartz 2012), including choices of species and source locations for restoration (Havens et al. 2015). Species distribution models correlate species occurrence data with environmental information to predict habitat suitability in space and time (Elith et al. 2006, Guisan and Thuiller 2005). Model algorithms tailored for presence-only data and small sample sizes (e.g., Maxent) (Phillips et al. 2006), combined with statistical techniques addressing sampling bias (e.g., Phillips et al. 2009), allow the investigation of the geographic distribution of suitable habitat for species even with limited or incomplete occurrence information. This is particularly valuable when time or other resource constraints prevent the collection of detailed field data. Gastón et al. (2014) found that SDMs were as effective as local experts in ranking the suitability of different plant taxa at forest restoration sites and proposed SDMs as a fast and cost-effective method to inform species selection.

Some species and plant communities may be affected more than others by changes in climate. A species' vulnerability to climate change can be evaluated based on climate exposure (the degree to which a system is exposed to climate change) and factors related to its sensitivity (how severely it is affected) and adaptive capacity (ability to adjust and maintain fitness), based on life history traits, dispersal capacity, pattern of genetic diversity, and history of population fragmentation (Butt et al. 2016, Dawson et al. 2011, Fordham et al. 2012, Williams et al. 2008). When combined with future climate scenarios, SDMs can provide an estimate of climate exposure, measured in terms of projected change in suitable habitat. These future suitable habitat projections can then help inform various aspects of decisionmaking in restoration. For example, SDMs have recently been applied to improve long-term restoration success by identifying target species having suitable habitat both now and in the future (Butterfield et al. 2016, López-Tirado and Hidalgo 2016). Gelviz-Gelvez et al. (2015) considered ecological characteristics together with SDM-suitable habitat projections under future climate scenarios to select plant

species for restoration in a semiarid region of central Mexico. Species distribution models have also been used to assess the need for and potential success of intervention such as assisted migration (e.g., Hällfors et al. 2016a). If such intervention is warranted, SDM used in concert with maps that show how climate variables may shift spatially can inform the implementation of climate-adjusted provenancing (sourcing) scenarios such as those described by Prober et al. (2015).

Most SDM approaches focus at the species level, pooling occurrence data throughout a species' range and assuming uniform environmental tolerance (Hällfors et al. 2016b). This practice obscures patterns of within-species variation that could be important for restoration success. Modeling approaches that address intraspecific variation in niche structure reveal distinct patterns in predicted distributions as well as forecasts of change under future climate scenarios (Hällfors et al. 2016b, Pearman et al. 2010, Valladares et al. 2014). Ecological and genetics studies that include multiple named infraspecies (variety or subspecies) commonly reveal differences in habitat affinities (Cole 1967, Montalvo and Ellstrand 2000, Stebbins 1942, Wang et al. 1999). In southern California, the presence of geographic variation in environmental tolerance and local adaptation across populations of many plant species suggests that intraspecific variation would be useful to take into account when modeling species distributions to inform restoration decisionmaking. Ideally, information on genetic variation in adaptive traits would be used to delineate populations into groups or ecotypes for modeling at an intraspecific level (e.g., Richardson et al. 2014). However, these data are unavailable for many plant taxa. In the absence of detailed population-level genetic data, infraspecies level models (Pearman et al. 2010, Rehfeldt et al. 2014) or models based on groups of populations delineated by climate or geography (Hällfors et al. 2016b, Hamann and Aitken 2013) may be more informative than pooled species-level models.

Focusing on the South Coast hydrologic region (Calwater 2.2.1) (CIWMC 2004), we used SDMs to create habitat suitability maps to aid species and infraspecies selection and to help inform decisions about seed sourcing for ecological restoration in scrub and shrubland habitats. First, we modeled suitable habitat for 44 focal plant taxa under baseline (1951–1980) climate conditions. We restricted occurrence and climate data to the study area to model regional patterns of habitat suitability and, when possible, modeled at the infraspecific (variety or subspecies) level. We then projected baseline suitability models under five future climate scenarios for mid 21st century (2040–2069) conditions to identify potential shifts in suitable habitat and how the shifts differ in their severity and spatial context under the different climate change scenarios. We also created multitaxon suitability

overlays to highlight potential effects of climate change on southern California alluvial scrub, coastal sage scrub, mixed chaparral-sage scrub, and low-elevation chaparral vegetation groups. Finally, we discuss potential climate change effects in the context of additional nonclimatic drivers known to strongly influence patterns of vegetation structure in southern California and which are expected to interact with climate change—namely fire, invasive species, and land use—and we highlight caveats regarding SDM use in planning and decisionmaking.

Methods

Study Area

Our study area encompasses the South Coast hydrologic region (Calwater 2.2.1) (CIWMC 2004), excluding the Channel Islands but including adjacent hydrologic subareas from the Colorado River hydrologic region plus a 30-km buffer (fig. 1). This region lies within a globally recognized biodiversity hotspot (Myers et al. 2000) where high plant diversity and endemism is intermixed with high human impact. Of California's 39-million population, an estimated 18 million people (46 percent) inhabit Los Angeles, Orange, Riverside, and San Diego Counties (U.S. Census Bureau 2015). Human activities and land use are concentrated in coastal lowland and low-elevation shrubland habitats.

The climate in the region is typical of Mediterranean-type ecosystems with cool moist winters and hot dry summers. Oceanic influences moderate winter and summer temperatures along the coast (fig. 2), and precipitation declines sharply to the east of the mountains in the bordering arid desert ecoregions. Comparisons of 30-year climate averages show recent warming in 1981–2010 relative to 1951–1980 (fig. 2). Although precipitation was variable during this time period, CWD estimated from the California Basin Characterization Model (CA-BCM) (Flint et al. 2013) increased throughout most of our study area because warming temperatures increased evaporative demand. Climatic water deficit, which can be thought of as a measure of drought stress, can increase even with increased precipitation (Thorne et al. 2012).

Focal Taxa and Occurrence Data

We modeled suitable habitat for 44 plant taxa that are characteristic of southern California scrub and shrubland habitats and are important for ecological restoration (table 1). We chose taxa used in habitat restoration that are considered to be foundational: either dominants or codominants, or indicator species of low-elevation shrubland communities. We categorized taxa into vegetation groups based on the

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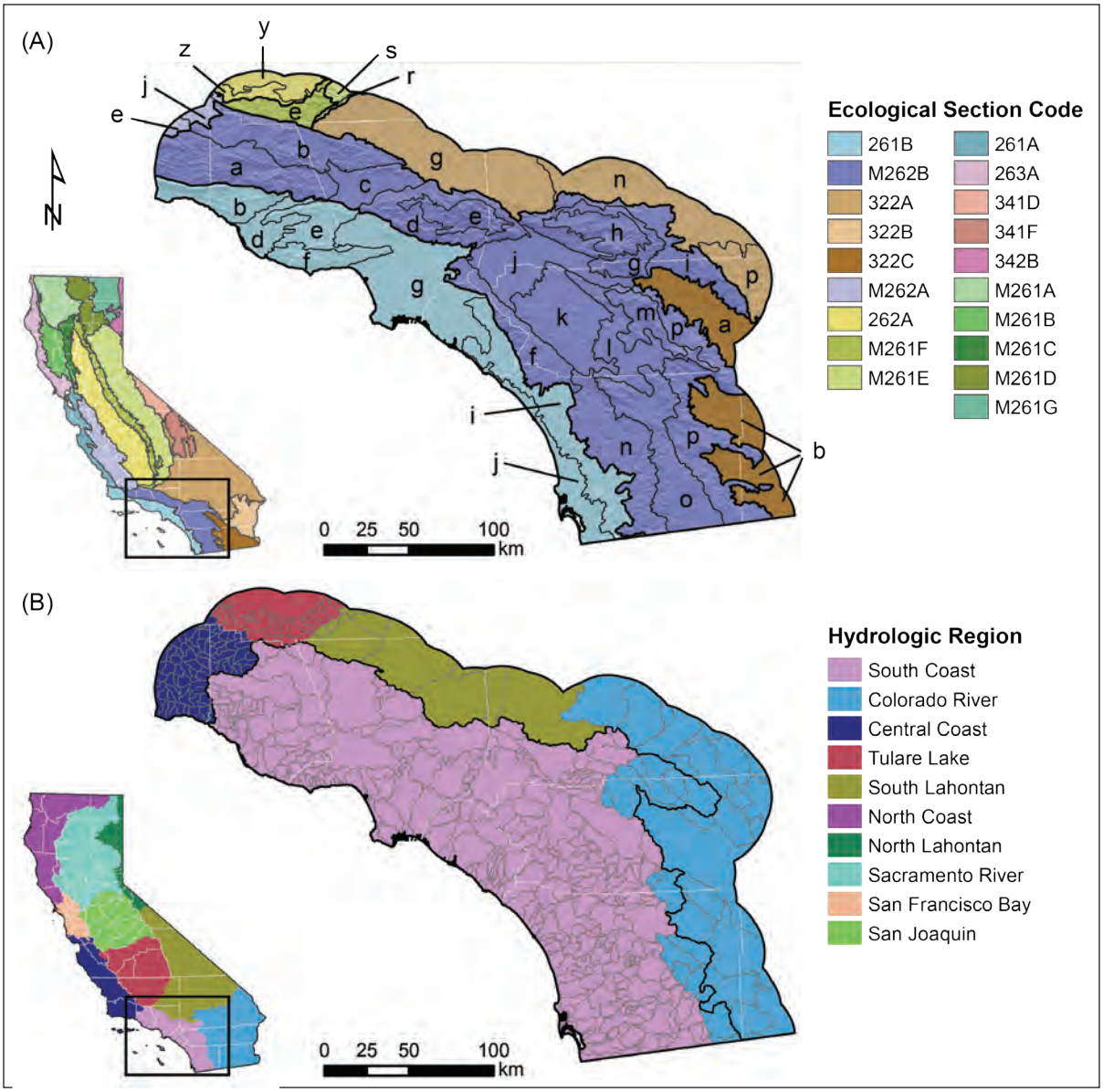

Figure 1—Southern California study area with (A) ecological sections (color key) and subsections (letters) and (B) South Coast hydrologic region and adjacent watersheds with 30-km buffer used for modeling extent. Data sources: ecological sections are from Goudey and Smith (1994) updated by Cleland et al. (2007); hydrologic regions with watersheds are from Calwater 2.2.1 (CIWMC 2004).

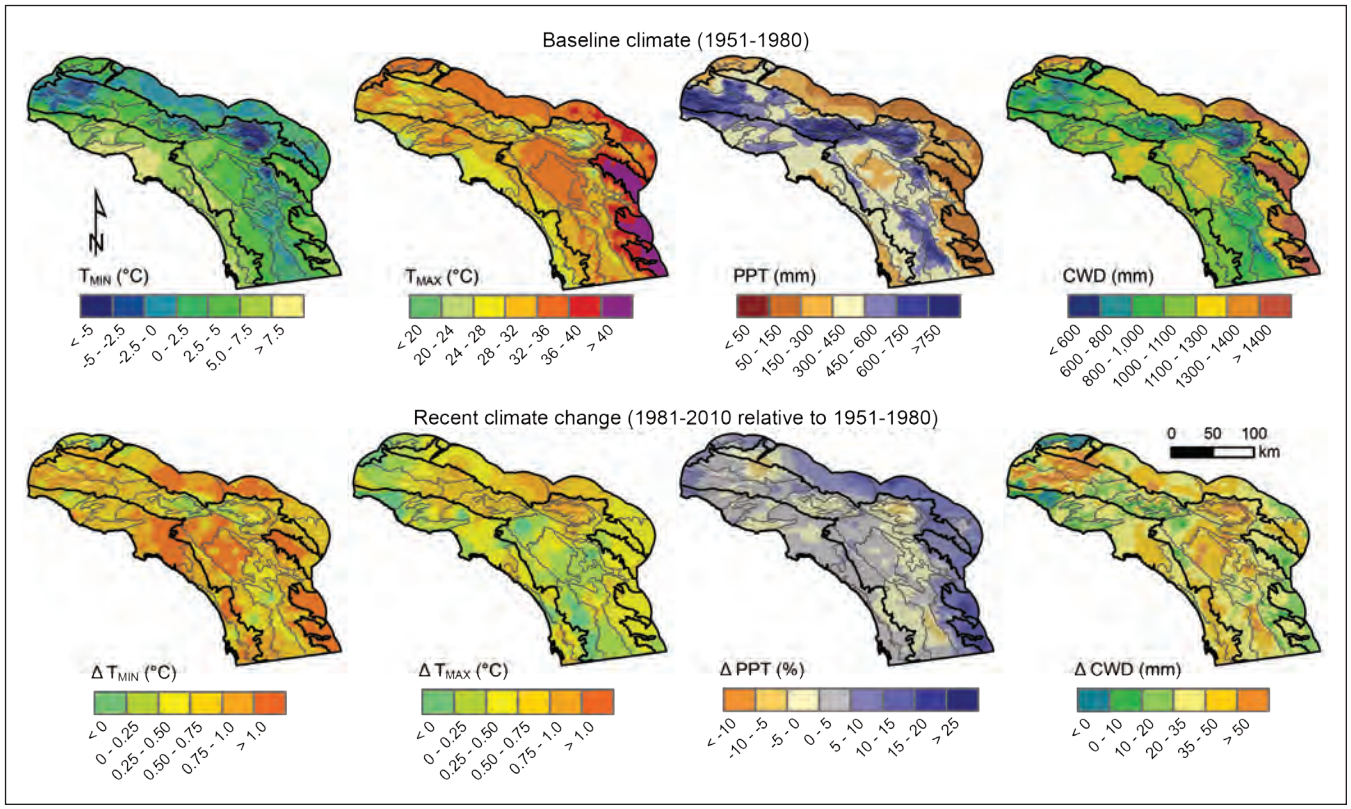

Figure 2—Baseline (1951–1980) climate averages and recent change (1951–1980) relative to baseline in southern California. Climate variables: T_{MIN} = minimum winter temperature December through February, T_{MAX} = maximum summer temperature June through August, PPT = annual precipitation, CWD = climatic water deficit. Black lines indicate ecological section boundaries; dark gray lines indicate ecological subsection boundaries. Climate data are based on PRISM 30-year averages, downscaled by the California Basin Characterization Model (Flint et al. 2013).

Table 1—List of modeled plant taxa

Scientific name[a]	Common name	Family	Life form[b]	Fire response[c]
Acmispon glaber var. *brevialatus* (Ottley) Brouillet	Deerweed, California broom	Fabaceae	Subshrub	S
Acmispon glaber (Vogel) Brouillet var. *glaber*	Deerweed, California broom	Fabaceae	Subshrub	S
Adenostoma fasciculatum Hook. & Arn. var. *fasciculatum*	Chamise	Roseaceae	Shrub	FS
Arctostaphylos glandulosa subsp. *cushingiana* (Eastw.) J.E. Keeley, M.C. Vasey & V.T. Parker	Cushing's manzanita	Ericaceae	Shrub	OR
Arctostaphylos glandulosa Eastw. subsp. *glandulosa*	Eastwood's manzanita	Ericaceae	Shrub	OR(FS[d])
Arctostaphylos glandulosa subsp. *mollis* (J.E. Adams) P.V. Wells	Transverse Range manzanita	Ericaceae	Shrub	OR
Arctostaphylos glauca Lindl.	Big-berry manzanita	Ericaceae	Shrub	S
Artemisia californica Less.	California sagebrush	Asteraceae	Subshrub	FS
Ceanothus crassifolius Torr. var. *crassifolius*	Hoaryleaf ceanothus	Rhamnaceae	Shrub	S
Ceanothus cuneatus (Hook.) Nutt. var. *cuneatus*	Buck brush	Rhamnaceae	Shrub	S
Ceanothus leucodermis Greene	Chaparral whitethorn	Rhamnaceae	Shrub	FS
Ceanothus megacarpus Nutt. var. *megacarpus*	Big-pod ceanothus	Rhamnaceae	Shrub	S
Ceanothus oliganthus Nutt.	Hairy ceanothus	Rhamnaceae	Shrub	S
Ceanothus perplexans Trel.	Cupped leaf ceanothus	Rhamnaceae	Shrub	S
Ceanothus tomentosus Parry	Woolly leaf ceanothus	Rhamnaceae	Shrub	S
Ceanothus vestitus Greene[a]	Mojave ceanothus	Rhamnaceae	Shrub	S
Cercocarpus betuloides Nutt. var. *betuloides*	Birch-leaf mountain mahogany	Rosaceae	Shrub	OR
Corethrogyne filaginifolia (Hook. & Arn.) Nutt.	Common sandaster	Asteraceae	Suffru perennial	OR
Deinandra fasciculata (DC.) Greene	Fascicled tarplant	Boraginaceae	Annual herb	S
Encelia californica Nutt.	California encelia, bush sunflower	Asteraceae	Subshrub	OR
Encelia farinosa A. Gray ex Torr.	Brittlebush, incienso	Asteraceae	Subshrub	FS
Eriodictyon crassifolium Benth. var. *crassifolium*	Thickleaf yerba santa	Boraginaceae	Subshrub	FS
Eriodictyon crassifolium var. *nigrescens* Brand	Bicolored yerba santa	Boraginaceae	Subshrub	FS
Eriodictyon trichocalyx var. *lanatum* (Brand) Jeps.	San Diego yerba santa	Boraginaceae	Subshrub	FS
Eriodictyon trichocalyx A. Heller var. *trichocalyx*	Hairy yerba santa	Boraginaceae	Subshrub	FS
Eriogonum fasciculatum Benth. var. *fasciculatum*	Coastal California buckwheat	Polygonaceae	Subshrub	FS

Table 1—List of modeled plant taxa (continued)

Scientific name[a]	Common name	Family	Life form[b]	Fire response[c]
Eriogonum fasciculatum var. *foliolosum* (Nutt.) Abrams	Leafy California buckwheat	Polygonaceae	Subshrub	FS
Eriogonum fasciculatum var. *polifolium* (Benth.) Torr. & A. Gray	Mojave desert California buckwheat	Polygonaceae	Subshrub	FS
Eriophyllum confertiflorum (DC.) A. Gray var. *confertiflorum*	Golden yarrow	Polygonaceae	Suffru perennial	FS
Hesperoyucca whipplei (Torr.) Trel.	Chaparral yucca	Agavaceae	Suffru rosette	OR
Heteromeles arbutifolia (Lindl.) M. Roem.	Toyon	Roseaceae	Shrub	OR
Lepidospartum squamatum (A. Gray) A. Gray	Scalebroom	Asteraceae	Shrub	OR
Malacothamnus fasciculatus (Nutt. ex Torr. & A. Gray) Greene var. *fasciculatus*	Chaparral mallow	Malvaceae	Subshrub	FS
Malosma laurina (Nutt.) Nutt. ex Abrams	Laurel sumac	Anacardiaceae	Shrub	FS
Phacelia minor (Harv.) Thell. ex F. Zimm.	California bells	Boraginaceae	Annual herb	S
Plantago erecta E. Morris	California plantain, dot-seed plantain	Plantaginaceae	Annual herb	S
Prunus ilicifolia (Nutt. ex Hook. & Arn.) D. Dietr. subsp. *ilicifolia*	Islay, hollyleaf cherry	Roseaceae	Shrub	OR
Quercus berberidifolia Liebm.	Scrub oak	Fagaceae	Shrub	OR
Rhamnus crocea Nutt.	Spiny redberry	Rhamnaceae	Shrub	OR
Rhamnus ilicifolia Kellogg	Hollyleaf redberry	Rhamnaceae	Shrub	OR
Rhus ovata S. Watson	Sugar bush	Anacardiaceae	Shrub	FS
Salvia apiana Jeps.	White sage	Lamiaceae	Subshrub	FS
Salvia mellifera Greene	Black sage	Lamiaceae	Subshrub/ shrub	FS
Stipa pulchra Hitchc.	Purple needlegrass	Poaceae	Bunchgrass	FS

[a] Taxonomy follows the Jepson eFlora (Jepson Flora Project 2017) except for *Ceanothus vestitus*, where we follow the pervious treatment in Baldwin et al. (2012). The most recent eFlora treatment of *Ceanothus vestitus* places the taxon in *Ceanothus pauciflorus* DC. (Jepson Flora Project 2017).

[b] Growth forms: subshrubs are stiff to somewhat woody at base, stems do not die back each year; suffru perennial = suffrutescent perennial, branches stiff and sometimes somewhat woody at base but with substantial annual die-back of stems; suffru rosette = suffrutescent rosette, monocots with stiff leaves in a rosette from a semiwoody crown (no true wood).

[c] Fire response: S = obligate seeder; FS = facultative seeder (both seeds and resprouts); OR = obligate resprouter (seeds killed by fire) (Keeley et al. 2006).

[d] Some populations reseed as well as resprout after fire (Jan Beyers, personal observation).

plant communities with which they are commonly associated (Sawyer et al. 2009): alluvial scrub, coastal sage scrub, mixed chaparral-sage scrub, and low-elevation chaparral (table 2). We define low-elevation chaparral as occurring on the lower slopes of southern California mountains from 300- to 1500-m elevation (lower chaparral sensu Schoenherr 1992) and mixed chaparral-sage scrub where the two communities intergrade along low elevations or south-facing slopes in chaparral. Vegetation groups are not mutually exclusive, and taxa listed in a group do not necessarily occur together in local vegetation alliances or associations. Predominance in a particular vegetation association can depend upon successional stage, postfire disturbance, or both. Additionally, different assemblages within a vegetation group may occur within contrasting exposures or geographic regions.

We obtained occurrence data from the Consortium of California Herbaria, or (CCH) (CCH 2016), Calflora (Calflora 2016), alluvial scrub vegetation surveys from southern California (Buck-Diaz et al. 2011, Wirka 1997), and field surveys in chaparral and coastal sage scrub that we conducted in 2015. CCH provides a record of taxon occurrences based on herbarium specimens for which collection goals and collection intensity vary across taxa and locations. To capture taxon occurrences across ecological gradients, we augmented the CCH data with survey data that recorded the presence of all taxa. For the 2015 surveys, we first mapped the density of herbarium collections of the focal taxa to identify under-collected areas in the lower elevations of the Santa Ana Mountains, San Bernardino Mountains, San Jacinto Mountains, and the Gavilan Hills in Riverside County. We then used provisional seed zone boundaries (Bower et al. 2014) and ecological subsection boundaries (Cleland et al. 2007) to select survey locations that maximized sampling across topographic, climatic, and ecological gradients. At each survey location we recorded geographic coordinates and elevation using a global positioning system (GPS) (Garmin Oregon 600[1]), slope, aspect, and general soil characteristics. We noted the dominant vegetation and presence of any focal taxa within 10 m. We recorded additional focal taxa on contrasting slopes within 250 m, using binoculars for identifications in rugged terrain, and noted the direction and estimated distance from the GPS waypoint.

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture or the Riverside-Corona Resource Conservation District of any product or service.

Table 2—Vegetation group assignments for focal plant taxa

	Vegetation group[a]			
Scientific name	**ALSC**	**CSS**	**CHAP**	**MIXED**
Acmispon glaber var. *brevialatus*[b]	X	X	X	X
Acmispon glaber var. *glaber*[b]	X	X	X	X
Adenostoma fasciculatum var. *fasciculatum*	X		X	X
Arctostaphylos glandulosa subsp. *cushingiana*			X	
Arctostaphylos glandulosa subsp. *glandulosa*			X	
Arctostaphylos glandulosa subsp. *mollis*			X	
Arctostaphylos glauca			X	
Artemisia californica	X	X		X
Ceanothus crassifolius var. *crassifolius*			X	
Ceanothus cuneatus var. *cuneatus*			X	
Ceanothus leucodermis			X	
Ceanothus megacarpus var. *megacarpus*			X	
Ceanothus oliganthus			X	
Ceanothus perplexans			X	
Ceanothus tomentosus			X	
Ceanothus vestitus			X	
Cercocarpus betuloides var. *betuloides*			X	X
Corethrogyne filaginifolia	X	X	X	X
Deinandra fasciculata		X		
Encelia californica		X		
Encelia farinosa		X		
Eriodictyon crassifolium var. *crassifolium*	X		X	X
Eriodictyon crassifolium var. *nigrescens*	X		X	X
Eriodictyon trichocalyx var. *lanatum*			X	X
Eriodictyon trichocalyx var. *trichocalyx*	X		X	X
Eriogonum fasciculatum var. *fasciculatum*		X		X
Eriogonum fasciculatum var. *foliolosum*	X	X	X	X
Eriogonum fasciculatum var. *polifolium*		X		X
Eriophyllum confertiflorum var. *confertiflorum*[b]		X	X	X
Hesperoyucca whipplei	X	X	X	X
Heteromeles arbutifolia			X	X
Lepidospartum squamatum	X			
Malacothamnus fasciculatus var. *fasciculatus*[b]		X	X	X
Malosma laurina	X	X	X	X
Phacelia minor[b]		X	X	X

Table 2—Vegetation group assignments for focal plant taxa (continued)

	Vegetation group[a]			
Scientific name	**ALSC**	**CSS**	**CHAP**	**MIXED**
Plantago erecta		X		
Prunus ilicifolia subsp. *ilicifolia*			X	X
Quercus berberidifolia			X	
Rhamnus crocea	X		X	X
Rhamnus ilicifolia			X	
Rhus ovata			X	X
Salvia apiana	X	X		X
Salvia mellifera	X	X	X	X
Stipa pulchra		X		

[a] Vegetation groups are based upon the plant communities in which each taxon predominantly occurs: ALSC = alluvial scrub, CSS = coastal sage scrub, CHAP = low-elevation chaparral (305 to 1524 m), MIXED = chaparral-sage scrub.

[b] Common in early postfire chaparral.

We used the following criteria to ensure a high quality of occurrence records. We omitted herbarium record occurrences (1) having ≥2.5 km error or uncertainty associated with the geographic coordinates; (2) annotated or otherwise identified as hybrids or having introgression; or (3) planted or cultivated, including suspected roadside revegetation plantings or introductions. We only used Calflora records that were contributed by the rapid vegetation assessments conducted by the California Department of Fish and Wildlife and the U.S. Geological Survey Central Mojave Vegetation Mapping project. Because the majority of taxa modeled are long-lived, we included records collected from 1951 to present, assuming that herbarium collections in years after the 1951–1980 baseline climate period were likely from plants established during or close to the baseline time period. Including these recent collections increased our sample of occurrences with high-quality location data and was necessary to ensure the best possible model accuracy in representing species' climatic niches (e.g., Feeley and Silman 2011). Similarly, we excluded all occurrences collected before 1950 because climate in southern California has already shifted since the early 20th century, increasing the likelihood that older records could reflect climatic conditions at plant establishment that differ from the baseline climate used in SDMs. A more recent time period for the baseline climate (e.g., 1981–2010) could include climate conditions that have already changed since the establishment of the collected specimen and are no longer suitable for successful

reproduction and establishment (Svenning and Sandel 2013). We discuss this issue of vegetation disequilibrium, climate change, and SDM assumptions in appendix 6. We identified climatic outliers as any record occurring in an area of mean annual temperature or annual precipitation greater or equal to five standard deviations from the species' mean. All climatic and geographic outliers were examined and excluded if the mapped coordinates did not reasonably match the locality description in the database.

As species misidentification errors affect the accuracy and spatial predictions of SDMs (Costa et al. 2015), we visited major data contributors to CCH—the University of California and Jepson Herbaria at the University of California, Berkeley; the California Academy of Sciences Herbarium; Rancho Santa Ana Botanic Garden (RSA); and the Herbarium at the University of California, Riverside (UCR)—to verify the identification of the following easily confused *Ceanothus* taxa: *C. cuneatus, C. perplexans, C. vestitus, C. tomentosus,* and *C. oliganthus.* Previous taxonomic treatments list *C. perplexans* and *C. vestitus* as varieties of *C. greggii*. Where possible, we identified records of *C. greggii* missing an infraspecies determination to either *C. perplexans* or *C. vestitus.* At RSA and UCR, we also examined specimens of *C. crassifolius*, *Acmispon glaber,* and *Arctostaphylos glandulosa* to verify varietal status. At these two herbaria, we checked any focal taxa specimens with dubious geographic locations for misidentification or labeling errors. Finally, we assigned infraspecific names for any record missing an infraspecific determination in our occurrence database when the infraspecies could reasonably be inferred from the record's geographic location and the taxon description (app. 2).

Climate Data

We downloaded 30-year averages of baseline (1951–1980) and midcentury (2040–2069) climate data at 270 m resolution from the CA-BCM (Flint et al. 2013). The CA-BCM applies a regional water-balance model to simulate hydrological responses to climate across the California hydrologic region (Flint et al. 2013). Monthly historical temperature and precipitation data are based on Parameter-Elevation Relationships on Independent Slopes Model (PRISM) data (Daly et al. 1994) spatially downscaled by the gradient-inverse distance squared (GIDS) approach. We selected five general circulation models (GCMs) from phase five of the Coupled Model Intercomparison Project (CMIP5) (Taylor et al. 2012) under a business-as-usual greenhouse gas emission scenario, the representative concentration pathway (RCP) 8.5. The RCP 8.5 scenario corresponds to an increase in global radiative forcing of 8.5 W m^{-2} from preindustrial times through 2100 (van Vuuren

et al. 2011) and represents a high greenhouse gas future that most closely tracks our current emissions trajectory. The five GCMs were chosen to represent the range in projected precipitation and temperature change: CCSM4, CNRM-CM5, FGOALS-G2, IPSL-CM5A-LR, and MIROC-ESM (fig. 3, app. 1).

We calculated 19 bioclimatic variables (Busby 1991) from monthly temperature and precipitation 30-year averages. We then examined correlations among bioclimatic and hydrological CA-BCM variables, selecting a subset of variables for modeling that (1) are important in driving plant distributions in the Western United States (Rehfeldt et al. 2006, Stephenson 1998), (2) minimized correlations between variables (Pearson's $|r| < 0.8$) (table 3), and (3) maximized model performance. These variables were minimum winter temperature (T_{MIN}) calculated as the minimum temperature averaged over the coldest months (December through February), summer maximum temperature (T_{MAX}) calculated as the maximum temperature averaged over the hottest months (June through August), temperature seasonality (T_{SEAS}) calculated as the standard deviation of the weekly mean temperatures, precipitation seasonality (PPT_{SEAS}) calculated as the standard deviation of the weekly precipitation estimates expressed as a percentage of the annual mean of those estimates, precipitation of the warmest quarter (PPT_{SUMMER}), precipitation of the coldest quarter (PPT_{WINTER}), CWD, and AET. The last two variables, CWD and AET, reflect biologically relevant estimates of water balance that have been associated with vegetation distribution, structure, and mortality (Das et al. 2013; McIntyre et al. 2015; Stephenson 1990, 1998). We also included a variable for soil parent geology (app. 2). Although different variables within the subset may contribute more or less to the habitat suitability for individual taxa, we included all eight variables for comparability of models across taxa.

Land Use

We obtained contemporary urban and agricultural land use from the California State Department of Forestry and Fire Protection Fire and Resource Assessment Program vegetation map (FRAP 2015). This vegetation map is a compilation of best available land cover data from about 1990 to 2014 and is available as a raster of 30 m resolution. We used spatial overlays to exclude area already converted to human land-cover types from habitat suitability maps and habitat change calculations. We did not include projections for future land use.

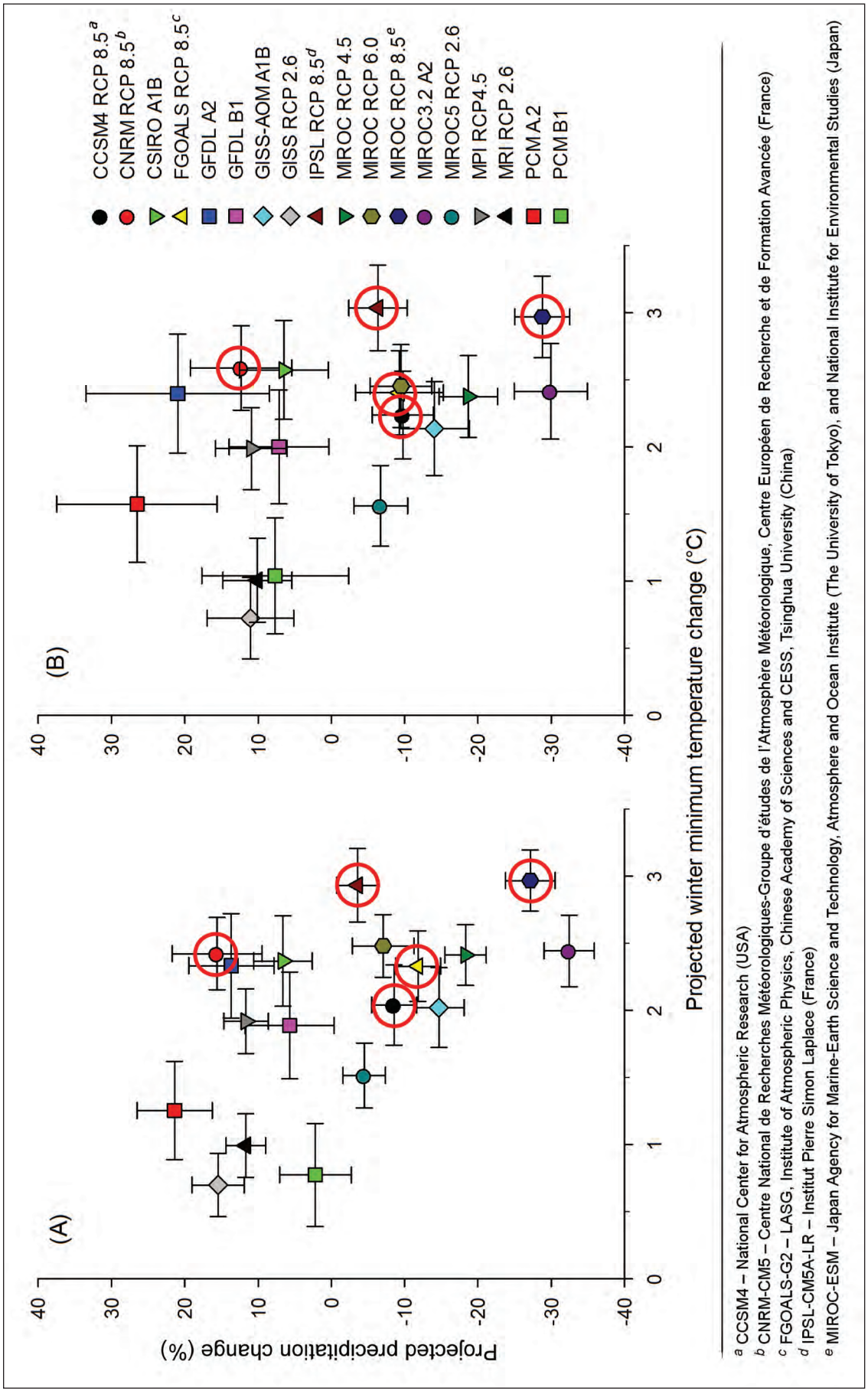

Figure 3—Range of projected midcentury (2040–2069) change in southern California climate relative to baseline (1951–1980) climate averages for 18 climate scenarios downscaled by the California Basin Characterization Model. Points show mean ± standard deviation change in annual precipitation and minimum winter temperature summarized for (A) Southern California Coast (261B) and (B) Southern California Mountains and Valleys (M262B) ecological sections of Goudey and Smith (1994) updated by Cleland et al. (2007). The climate scenarios used for species distribution modeling and climate change visualizations are circled in red.

Table 3—Pairwise Pearson's correlation coefficients for climatic variables used in species distribution modeling

	PPTSEAS	PPTSUMMER	PPTWINTER	TSEAS	AET	CWD	TMIN	TMAX
PPT_{SEAS}	1.000							
PPT_{SUMMER}	-0.699	1.000						
PPT_{WINTER}	0.520	0.075	1.000					
T_{SEAS}	-0.443	0.604	0.133	1.000				
AET	0.231	0.088	0.552	-0.110	1.000			
CWD	0.090	-0.494	-0.589	-0.326	-0.384	1.000		
T_{MIN}	0.511	-0.677	-0.139	-0.777	0.163	0.625	1.000	
T_{MAX}	-0.226	0.060	-0.300	0.405	-0.035	0.449	-0.046	1.000

Pearson's correlation coefficients calculated across occurrence localities. Climate variables: PPTSEAS = precipitation seasonality, PPTSUMMER = precipitation of the warmest quarter, PPTWINTER = precipitation of the coldest quarter, TSEAS = temperature seasonality, AET = actual evapotranspiration, CWD = climatic water deficit, TMIN = minimum winter temperature December–February, TMAX = summer maximum temperature June–August.

Modeling Approach

Species distribution models correlate occurrence data and spatially explicit environmental data to predict species distributions in space and time (Elith and Leathwick 2009, Guisan and Thuiller 2005). Using the modeling algorithm Maxent (version 3.3.3 k) (Phillips et al. 2006), we used the occurrence data and environmental layers described above to predict suitable habitat for focal plant taxa under baseline and midcentury climate conditions. Maxent is a high-performing SDM method tailored to presence-only data (Elith et al. 2006, Merow et al. 2013, Phillips et al. 2006). For each taxon, we modeled the baseline (1951–1980) taxon-climate relationship, then forecast that model onto each of the five future climate scenarios to map future habitat suitability under midcentury (2040–2069) conditions. We ran models with the following settings: (1) linear, quadratic, and product features only; (2) default beta-regularization; (3) 10,000 bias-weighted background points (details below); and (4) logistic output ranging from zero to one. The modeling extent was restricted to the study area described above (fig. 1). We implemented Maxent in R (R Core Team 2016) with the "dismo" package (Hijmans et al. 2016).

Spatial and temporal biases in natural history collections can reduce SDM predictive performance (Kadmon et al. 2004, Kramer-Schadt et al. 2013, Syfert et al. 2013). We corrected for sampling bias by weighting background sampling with a bias grid based on a target group (Phillips et al. 2009) consisting of digitized herbarium records for all vascular plants in southern California collected after 1950

(CCH 2016). Our aim was to produce geographic sampling bias in the background data that was similar to that of the occurrence data. The bias grid was derived from a Gaussian-kernel density map of the target group occurrences with a standard deviation of 100 km, rescaled from 1 to 20 (Elith et al. 2010). We then used this grid to weight background sampling within the study area. We restricted background sampling to within 100 km of known occurrences inside the study area. We investigated two additional methods to control for sampling bias but report results only for the bias grid approach, as it gave the highest performance with the least overfitting for the majority of focal taxa (see app. 2 for a detailed comparison of methods). Model complexity also affects predictive performance and transferability across space and time (Merow et al. 2014, Moreno-Amat et al. 2015, Warren and Seifert 2011). Overly complex (overfit) models produce predictions that reflect noise or sampling idiosyncrasies rather than a species' environmental tolerances. Thus, we used only linear, quadratic, and product features to limit the complexity of the climate response curves created in Maxent.

We calculated future changes in habitat suitability from binary suitable habitat maps created using the maximum sensitivity plus specificity threshold (Jimenez-Valverde and Lobo 2007, Liu et al. 2013). For each taxon by future climate scenario, we calculated the percentage change in suitable habitat relative to baseline. We defined changes in future suitable habitat as stable = suitable under baseline and future conditions, loss = suitable under baseline but unsuitable under future conditions, or gain = unsuitable under baseline and becoming suitable under future conditions (fig. 4). We assumed unlimited dispersal within the study area for projections of suitability gain and assumed no dispersal (species are unable to disperse to new areas of suitable habitat) for projections of suitability loss. These dispersal assumptions are meant to cap the two extremes of potential habitat change under future climate. Expansion into newly suitable habitat will depend on intrinsic species traits and habitat connectivity. We excluded areas already converted to human land cover types from all suitable habitat calculations. To show how forecasted habitat suitability varies with climate scenario, we created consensus maps for each species. Consensus maps show the degree of agreement in future suitable habitat across the five climate scenarios, where values range from 1 (no agreement) to 5 (full agreement). To visualize potential climate change effects on different vegetation groups, we overlaid the suitability maps of the individual taxa associated with each group: alluvial scrub, coastal sage scrub, mixed chaparral-sage scrub, and low-elevation chaparral (table 2). We excluded bunchgrass and annual growth forms from vegetation group maps, as these are not structurally dominant elements of our vegetation groups.

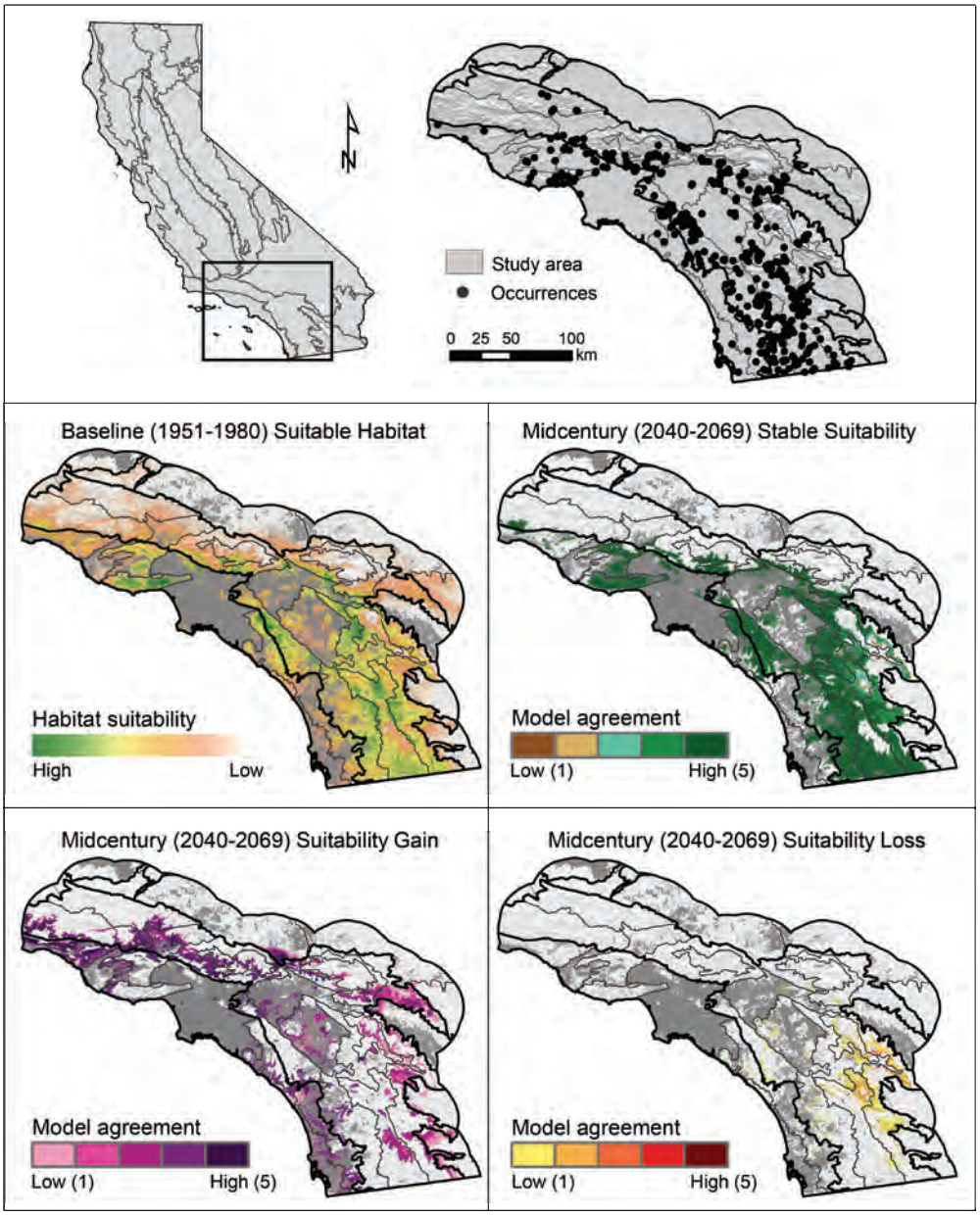

Figure 4—Example of occurrence data and baseline (1951–1980) and projected midcentury (2040–2069) suitable habitat for *Rhus ovata*. Midcentury suitable habitat maps show agreement across the five climate model scenarios and range from one (no agreement) to five (full agreement). Projected change in suitable habitat is defined as follows: stable = suitable under baseline and future conditions; loss = suitable under baseline but unsuitable under future conditions; gain = unsuitable under baseline and becoming suitable under future conditions. In all maps, suitable habitat already converted to human land uses (FRAP 2015) is masked in dark gray.

Model Evaluation

We evaluated overall model performance by the area under the receiver operator curve statistic (AUC) (Fielding and Bell 1997, Lobo et al. 2008) averaged over fivefold cross-validation replicates. AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination between presence and background, 0.5 indicates predictive performance no better than random, and < 0.5 indicates predictive performance worse than random. To evaluate model overfitting, we calculated the difference between the training and test AUC (AUC_{diff}); the smaller the difference, the lesser the degree of overfitting in the model (Warren and Seifert 2011). We also included two threshold-dependent measurements of performance, the omission rate at the 10 percent test threshold (OR_{10p}) and the omission rate at the maximum sensitivity plus specificity threshold (OR_{mSSS}) used to create binary suitability maps. The omission (or false negative) rate is the proportion of test occurrences incorrectly classified and provides information about the discriminatory ability of the model at a particular threshold. We identified important climatic variables from Maxent's percentage of permutation importance metric. Permutation importance is calculated in Maxent by randomly permuting the values of each variable among the training points and measuring the drop in training AUC. A large decrease indicates heavy model dependence on a particular variable and high permutation importance.

Results

Midcentury Climate Exposure in Southern California

Under the five climate scenarios we considered, projected midcentury (2040–2069) increase in minimum winter and summer maximum temperatures averaged across the Southern California Coast (261B) ecological section ranged from 2.0 ± 0.3 °C to 3.0 ± 0.2 °C (mean ±SD) and 2.2 ± 0.3 °C to 3.0 ± 0.3 °C, respectively, relative to 1951–1980 averages (table 4, fig. 3). The direction and magnitude of precipitation change varied across the five climate scenarios, ranging from a 27 ± 3 percent decrease (MIROC-ESM) to a 16 ± 6 percent increase (CNRM-CM5). Projected increases in winter minimum and summer maximum temperatures tended to be slightly higher in the Southern California Mountains and Valleys (M262B) ecological section compared to the Southern California Coast (261B), ranging from 2.2 ± 0.3 °C to 3.0 ± 0.3 °C for winter and 2.4 ± 0.4 °C to 3.6 ± 0.4 °C for summer, relative to 1951–1980 averages. Projected change in precipitation ranged from a 29 ± 4 percent decrease (MIROC-ESM) to a 12 ± 7 percent increase (CNRM-CM5). Climatic water deficit increased in both ecological sections even under scenarios of increased precipitation (table 4, app. 1). The MIROC-ESM scenario had the greatest

Table 4—Recent and projected midcentury (2040–2069) climate change in southern California climate variables relative to baseline (1951–1980) conditions, summarized (mean ± standard deviation) by ecological section

		Change in climate relative to baseline					
	Baseline climate	Historical	Projected midcentury (2040–2069				
Variable	1951–1980	1981–2010	CCSM4	CNRM	FGOALS	IPSL	MIROC
Southern California Coast (261B):							
AET (mm)	322 ± 44	11 ± 7	-12 ± 12	21 ± 15	-12 ± 15	2 ± 12	-57 ± 24
CWD (mm)	1034 ± 70	28 ± 12	82 ± 14	60 ± 17	102 ± 17	101 ± 15	150 ± 24
PPTSEAS	97 ± 5	5 ± 2	-1 ± 2	25 ± 3	3 ± 5	-3 ± 1	-5 ± 3
PPTSUMMER (mm, %)	10 ± 2	-29 ± 12	33 ± 16	24 ± 34	66 ± 36	-1 ± 27	-33 ± 11
PPTWINTER (mm, %)	236 ± 67	8 ± 3	0 ± 5	35 ± 7	-7 ± 6	-6 ± 4	-31 ± 5
TMIN (°C)	6.3 ± 1.5	0.7 ± 0.3	2.0 ± 0.3	2.4 ± 0.3	2.3 ± 0.3	2.9 ± 0.3	3 ± 0.2
TMAX (°C)	27 ± 3.2	0.4 ± 0.4	2.2 ± 0.3	2.5 ± 0.3	2.8 ± 0.3	3.5 ± 0.3	3 ± 0.4
TSEAS	362 ± 77	-3 ± 7	13 ± 9	27 ± 7	27 ± 8	32 ± 8	6 ± 9
Southern California Mountains and Valleys (M262B):							
AET (mm)	291 ± 79	13 ± 11	3 ± 27	31 ± 22	16 ± 26	17 ± 30	-32 ± 42
CWD (mm)	996 ± 167	32 ± 15	96 ± 24	84 ± 27	107 ± 27	123 ± 32	160 ± 33
PPTSEAS	88 ± 11	-16 ± 15	29 ± 12	33 ± 21	83 ± 33	-10 ± 11	-9 ± 22
PPTSUMMER (mm, %)	24 ± 14	9 ± 7	-1 ± 6	33 ± 8	-9 ± 6	-8 ± 5	-35 ± 4
PPTWINTER (mm, %)	256 ± 122	19 ± 12	-4 ± 15	83 ± 47	-21 ± 18	-22 ± 17	-89 ± 43
TMIN (°C)	2.0 ± 3.0	0.7 ± 0.3	2.2 ± 0.3	2.6 ± 0.3	2.4 ± 0.3	3.0 ± 0.3	3.0 ± 0.3
TMAX (°C)	31.2 ± 3.3	0.3 ± 0.3	2.4 ± 0.4	2.6 ± 0.4	2.8 ± 0.4	3.6 ± 0.4	2.9 ± 0.4
TSEAS	591 ± 75	-1 ± 9	14 ± 10	25 ± 8	24 ± 8	31 ± 8	3 ± 9

Ecological sections from Goudey and Smith (1994) updated by Cleland et al. (2007).

Climate variables: AET = actual evapotranspiration, CWD = climatic water deficit, PPTSEAS = precipitation seasonality, PPTSUMMER = precipitation of the warmest quarter, PPTWINTER = precipitation of the coldest quarter, TMIN = minimum winter temperature December–February, TMAX = maximum summer temperature June–August, TSEAS = temperature seasonality.

Change in annual precipitation is calculated as the percentage of change relative to baseline.

Global circulation models used: CCSM4, CNRM (= CNRM-CM5 in text), FGOALS (= FSGOALS-G2 in text), IPSL (= IPSL-CM5A-LR in text), and MIROC (= MIROC-ESM in text).

projected increase in CWD throughout our southern California study area. Across all the future scenarios we considered, CWD increased notably in section M262B subsections g, h–San Gorgonio Mountains, l–San Jacinto Foothills-Cahuilla Mountains (eastern portion), m–San Jacinto Mountains, and o–Palomar-Cuyamaca Peak (eastern portion of the Peninsular Ranges, especially the Laguna Mountains).

Species Distribution Model Performance

Overall, Maxent models had high performance (app. 3). For the 44 taxa modeled, AUC_{test} scores ranged from 0.728 to 0.959 with a median score of 0.830. Omission rate at the 10 percent test threshold (OR_{10p}) ranged from 0.10 to 0.18. Higher AUC_{test} scores did not necessarily translate to higher model performance in terms of omission rate. For example, *Arctostaphylos glandulosa* subsp. *mollis* had among the highest overall model performance in terms of AUC_{test} (0.926) but lowest performance in terms of omission rate at the 10 percent test threshold (0.18). The importance of environmental variables in models varied across taxa (app. 3). Temperature seasonality (TSEAS) was most frequently important, ranking most important for 13 taxa. Climatic water deficit ranked most important for nine taxa, and winter rainfall (PPTWINTER) ranked most important for six taxa. Also worth noting is precipitation seasonality (PPTSEAS). Although ranked most important for only three species, two of those species were projected to have among the greatest losses in habitat suitability (*Ceanothus perplexans* and *Eriodictyon trichocalyx* var. *lanatum*).

Baseline suitable habitat maps generally matched the known distribution of most taxa, with a few exceptions (app. 4). Models of *Eriodictyon crassifolium* var. *nigrescens* predicted baseline suitable habitat in areas of San Diego County where occurrence data were excluded from our models and where *E. crassifolium* var. *crassifolium* occurs (see app. 2). The model of *Ceanothus vestitus* may overpredict baseline suitable habitat in the Peninsular Ranges or may reflect the taxonomic uncertainty between *C. vestitus* and *C. perplexans* in the area. Previously considered varieties of *C. greggii*, these taxa are now treated as separate species. Herbarium records suggest *C. perplexans* is more common in the Peninsular Ranges, but the degree to which the species overlap in this region has not yet been closely studied. Therefore, it is unclear whether our model is picking up suitable habitat in the Peninsular Ranges that is indeed occupied by the *C. vestitus* or overpredicting into the range of *C. perplexans*. In both cases, taxonomic uncertainties may be affecting model predictions. Two of the 44 taxa, *Encelia farinosa* and *Eriogonum fasciculatum* var. *polifolium*, have geographic distributions that extend significantly into desert ecoregions much more arid than the portion of the species range we model in our study area. These range truncations, as well as those to the north and

south of the study area, may affect future habitat suitability projections. Lastly, suitable habitat maps for *Lepidospartum squamatum* should be interpreted with caution. *Lepidospartum squamatum* is sensitive to the substrate and fluvial dynamics of alluvial fans and confined outwashes, factors that were not directly measured by our environmental predictors.

Projected Changes in Habitat Suitability

Projected midcentury (2040–2069) changes in suitable habitat varied widely across taxa and climate scenarios (table 5, apps. 3 and 4), including among taxa in the same genus and family. For example, in the family Rhamnaceae, the chaparral shrub *C. crassifolius* var. *crassifolius* was projected to have among the highest degree of stable suitable habitat of all modeled taxa, with >90 percent of baseline habitat maintaining future suitability under all five GCMs. In contrast, *C. perplexans* was projected to have among the greatest losses of suitable habitat, >50 percent, under three of five GCMs. *Rhamnus ilicifolia*, another chaparral shrub, had highly variable suitability projections (32 to 99 percent stable) (fig. 5). *Rhamnus crocea*, which occurs in alluvial scrub, chaparral, and mixed chaparral-sage scrub, had even greater variability in suitability projections (2 to 99 percent stability) across the GCMs we considered.

The climate scenarios with the greatest projected loss of suitable habitat for most taxa were the two scenarios with the most extreme directional changes in precipitation: CNRM-CM5 (wettest) and MIROC-ESM (driest). Taxa differed in the direction of the precipitation shift that resulted in the greatest loss of suitable habitat. Twelve taxa showed projected losses of ≥50 percent under the driest climate scenario, most of which were woody chaparral shrubs (app. 3). Fourteen taxa showed projected losses of ≥50 percent under the wettest climate scenario, including a number of taxa associated with coastal sage scrub such as *Acmispon glaber* var. *glaber, Encelia californica, Eriogonum fasciculatum* var. *fasciculatum, Deinandra fasciculata,* and *Salvia apiana*.

Overall, the majority of plant taxa we modeled had a high degree of stable future suitable habitat, with 31 taxa projected to have ≥75 percent of baseline suitable habitat maintaining suitability midcentury under at least three future climate scenarios (table 5). Eleven taxa had ≥75 percent of baseline suitable habitat maintaining suitability across all five GCMs (*Artemisia californica, Ceanothus crassifolius* var. *crassifolius, Encelia farinosa, Eriodictyon crassifolium* var. *crassifolium, Eriogonum fasciculatum* var. *foliolosum, Hesperoyucca whipplei, Malosma laurina, Phacelia minor, Quercus berberidifolia, Rhus ovata,* and *Salvia mellifera*). Seven taxa had projected losses of baseline suitable habitat of >50 percent under at

Table 5—Baseline (1951–1980) climatically suitable habitat and percentage of change in suitable habitat under projected midcentury (2040–2069) climate scenarios for taxa arranged from highest to lowest percentage loss of suitable habitat[a]

	Baseline suitable habitat[b]		Projected percentage of change in suitable habitat[c]		
	Unconverted	Converted	Stable	Loss	Gain
	Square kilometers		*Percent*		
Eriodictyon trichocalyx var. *lanatum*	3 563	7	16 (0–64)	84 (36–100)	0 (0–21)
Acmispon glaber var. *glaber*	4 572	53	37 (1–58)	63 (42–99)	0 (0–23)
Corethrogyne filaginifolia	13 041	35	38 (21–50)	62 (50–79)	0 (0–0)
Ceanothus vestitus	10 857	9	38 (26–47)	62 (53–74)	0 (0–5)
Eriophyllum confertiflorum var. *confertiflorum*	13 482	25	39 (4–58)	61 (42–96)	0 (0–1)
Arctostaphylos glandulosa subsp. *cushingiana*	4 922	4	44 (29–58)	56 (42–71)	3 (0–9)
Ceanothus perplexans	6 392	10	48 (1–67)	52 (33–99)	9 (0–16)
Eriodictyon crassifolium var. *nigrescens*	8 553	22	51 (34–84)	49 (16–66)	1 (1–9)
Ceanothus cuneatus var. *cuneatus*	8 558	19	58 (27–82)	42 (18–73)	15 (12–53)
Ceanothus oliganthus	8 078	23	67 (31–91)	33 (9–69)	18 (13–37)
Deinandra fasciculata	6 001	62	68 (11–93)	32 (7–89)	0 (0–24)
Arctostaphylos glandulosa subsp. *mollis*	8 022	8	68 (49–91)	32 (9–51)	2 (1–38)
Arctostaphylos glauca	18 060	11	71 (41–96)	29 (4–59)	2 (1–14)
Arctostaphylos glandulosa subsp. *glandulosa*	8 751	20	75 (17–95)	25 (5–83)	4 (0–16)
Eriodictyon trichocalyx var. *trichocalyx*	6 171	21	77 (27–91)	23 (9–73)	28 (10–181)
Stipa pulchra	6 486	56	77 (64–94)	23 (6–36)	8 (6–38)
Ceanothus leucodermis	8 542	12	78 (35–91)	22 (9–65)	7 (3–15)
Plantago erecta	4 607	62	79 (36–89)	21 (11–64)	6 (1–47)
Rhamnus ilicifolia	13 131	22	80 (32–99)	20 (1–68)	16 (15–45)
Eriogonum fasciculatum var. *fasciculatum*	4 133	60	81 (8–100)	19 (0–92)	6 (0–68)
Ceanothus megacarpus var. *megacarpus*	3 471	52	82 (58–100)	18 (0–42)	4 (2–67)
Encelia farinosa	7 204	33	84 (79–95)	16 (5–21)	155 (95–175)
Eriogonum fasciculatum var. *polifolium*	16 033	11	86 (62–95)	14 (5–38)	9 (4–26)
Ceanothus tomentosus	3 300	42	89 (50–98)	11 (2–50)	27 (1–61)
Eriodictyon crassifolium var. *crassifolium*	8 073	28	89 (81–92)	11 (8–19)	64 (42–90)
Acmispon glaber var. *brevialatus*	8 459	33	90 (65–98)	10 (2–35)	20 (13–32)
Lepidospartum squamatum	6 143	51	92 (12–100)	8 (0–88)	55 (7–329)

Table 5—Baseline (1951–1980) climatically suitable habitat and percentage of change in suitable habitat under projected midcentury (2040–2069) climate scenarios for taxa arranged from highest to lowest percentage loss of suitable habitat[a] (continued)

	Baseline suitable habitat[b]		Projected percentage of change in suitable habitat[c]		
	Unconverted	Converted	Stable	Loss	Gain
	Square kilometers		*Percent*		
Rhamnus crocea	5 532	63	95 (2–99)	5 (1–98)	26 (0–60)
Cercocarpus betuloides var. *betuloides*	16 762	11	96 (53–100)	4 (0–47)	13 (3–50)
Encelia californica	3 560	67	97 (33–100)	3 (0–67)	8 (0–96)
Prunus ilicifolia subsp. *ilicifolia*	10 889	28	98 (57–100)	2 (0–43)	24 (11–34)
Adenostoma fasciculatum var. *fasciculatum*	12 064	32	99 (53–100)	1 (0–47)	29 (6–44)
Heteromeles arbutifolia	6 961	43	99 (69–100)	1 (0–31)	43 (3–56)
Malacothamnus fasciculatus var. *fasciculatus*	7 422	59	99 (69–100)	1 (0–31)	15 (5–21)
Hesperoyucca whipplei	9 406	29	99 (81–100)	1 (0–19)	56 (33–94)
Eriogonum fasciculatum var. *foliolosum*	11 751	47	99 (84–100)	1 (0–16)	13 (4–24)
Rhus ovata	10 492	29	99 (85–99)	1 (1–15)	49 (28–55)
Salvia apiana	10 461	36	100 (48–100)	0 (0–52)	46 (15–54)
Quercus berberidifolia	13 145	28	100 (75–100)	0 (0–25)	30 (11–44)
Ceanothus crassifolius var. *crassifolius*	7 768	35	100 (93–100)	0 (0–7)	92 (20–219)
Malosma laurina	6 310	58	100 (95–100)	0 (0–5)	24 (7–33)
Artemisia californica	8 411	58	100 (96–100)	0 (0–4)	72 (37–88)
Phacelia minor	7 802	41	100 (96–100)	0 (0–4)	147 (82–247)
Salvia mellifera	5 600	55	100 (97–100)	0 (0–3)	70 (53–97)

[a] Converted is the area of baseline habitat that is climatically suitable but has already been converted to human land uses. Unconverted is the area of baseline suitable habitat on land cover types.

[b] Reported percentage of change of suitable habitat where at least three climate scenarios are in agreement with the range (minimum–maximum) across all five scenarios.

All habitat suitability calculations exclude areas that have already been converted to human land uses (FRAP 2015).

Stable suitable habitat can also be interpreted as the percentage of spatial overlap of suitable area under baseline and future climate conditions.

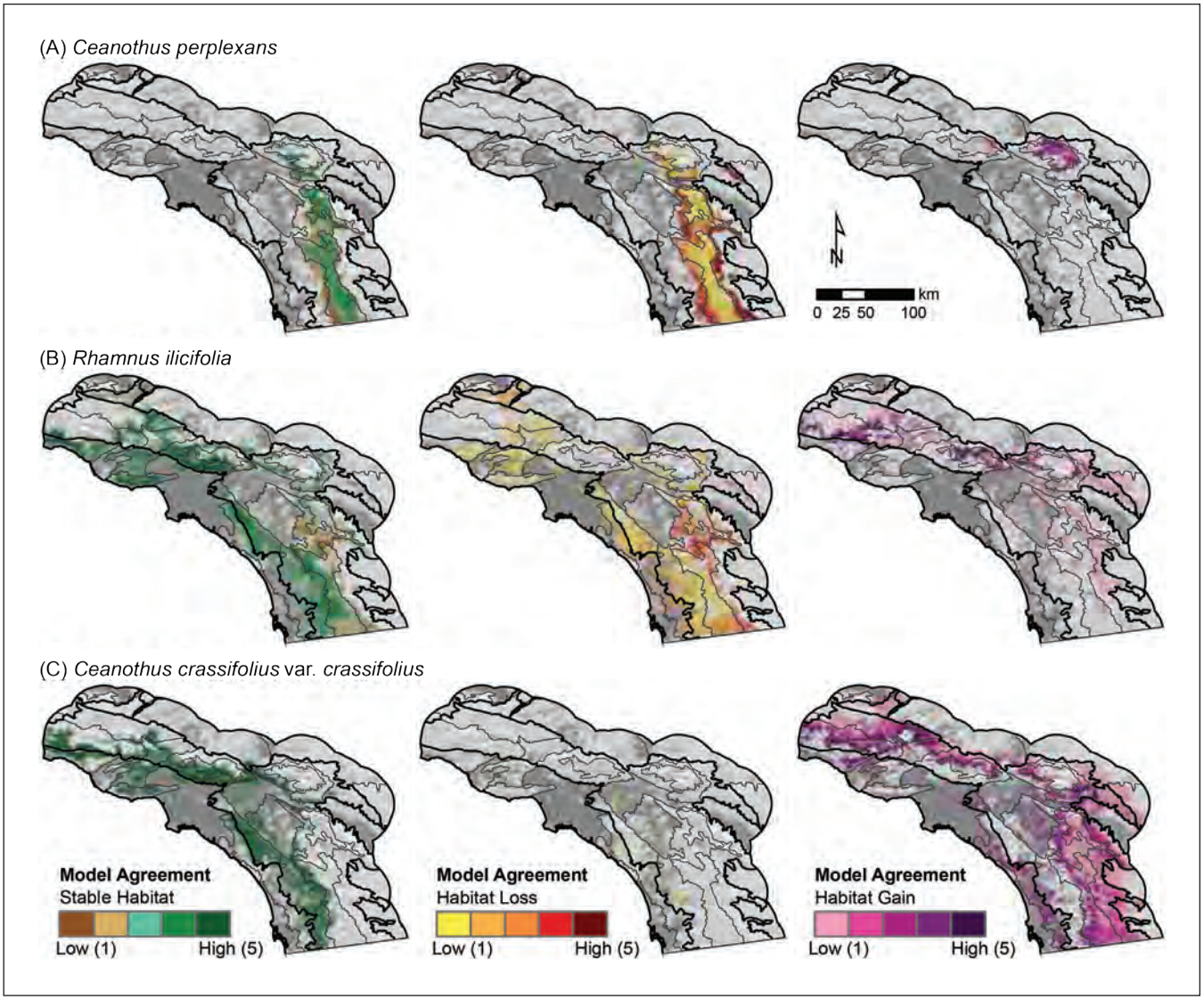

Figure 5—Examples of contrasting patterns of projected change in suitable habitat under midcentury (2040–2069) climate for three species, (A) *Ceanothus perplexans* (high loss), (B) *Rhamnus ilicifolia* (variable), and (C) *C. crassifolius* var. *crassifolius* (high stability). Maps show agreement across the five climate model scenarios and range from one (no agreement) to five (full agreement). Projected change in suitable habitat is defined as follows: stable = suitable under baseline and future conditions; loss = suitable under baseline but unsuitable under future conditions; gain = unsuitable under baseline and becoming suitable under future conditions. In all maps, suitable habitat already converted to human land uses (FRAP 2015) is masked in dark gray.

least three GCMs (*Acmispon glaber* var. *glaber, Arctostaphylos glandulosa* subsp. *cushingiana, Ceanothus perplexans, C. vestitus, Corethrogyne filaginifolia, E. trichocalyx* var. *lanatum, Eriophyllum confertiflorum* var. *confertiflorum*). Some of these taxa with large losses in suitable habitat also occur in areas of high CWD exposure (e.g., ecological section M262B subsection near the Palomar Mountains and Cuyamaca Peak), such as *Ceanothus perplexans* and *Eriodictyon trichocalyx* var. *lanatum*. *Corethrogyne filaginifolia*, however, is widespread in our study area, yet had among the greatest projected loss in suitable habitat of all modeled taxa (50 to 79 percent loss).

We found examples of contrasting patterns of projected habitat suitability change for varieties within the same species. *Acmispon glaber* var. *glaber* had much greater projected loss of suitable habitat (42 to 99 percent) compared to *A. glaber* var. *brevialatus* (2 to 35 percent). Both varieties had the greatest loss of suitable habitat under the wettest climate scenario, but *A. g.* var. *brevialatus* fared better with 35 percent loss compared to 99 percent loss for *A. g.* var. *glaber.* Similarly, *Eriodictyon trichocalyx* var. *lanatum* had a much greater loss in suitable habitat (36 to 100 percent) compared to *E. trichocalyx* var. *trichocalyx* (9 to 73 percent). Interestingly, these varieties strongly differed as to which climate scenario resulted in the greatest suitable habitat loss. The wettest scenario resulted in 100 percent loss of suitable habitat for *E. t.* var. *lanatum,* but only 9 percent loss for *E. t.* var. *trichocalyx*, while the driest scenario resulted in 36 percent loss for *E. t.* var. *lanatum* and 73 percent loss of suitable habitat for *E. t.* var. *trichocalyx.*

Although we did not explicitly model plant communities, the multitaxon suitable habitat overlays revealed patterns for associated vegetation groups that were less readily apparent in maps of individual taxa (fig. 6, app. 5). Spatial patterns of projected suitable habitat loss, or climate exposure, varied across future climate scenarios and vegetation groups. All vegetation groups—alluvial scrub, coastal sage scrub, low-elevation chaparral, and mixed chaparral-sage scrub—had large projected suitability losses under the wettest future climate scenario (CNRM-CM5). Many taxa associated with low-elevation chaparral also had large projected suitable habitat losses under the driest scenario (MIROC-ESM). For low-elevation chaparral, suitable habitat losses were most pronounced in the low elevations of the Southern California Mountains and Valleys (M262B) ecological section. Coastal sage scrub taxa, in contrast, had the most pronounced suitable habitat losses in the Southern California Coast (261B) ecological section. Baseline and future suitable habitat for coastal sage scrub taxa also coincided geographically with a high degree of human land use. Larger unconverted areas of stable habitat suitability occurred

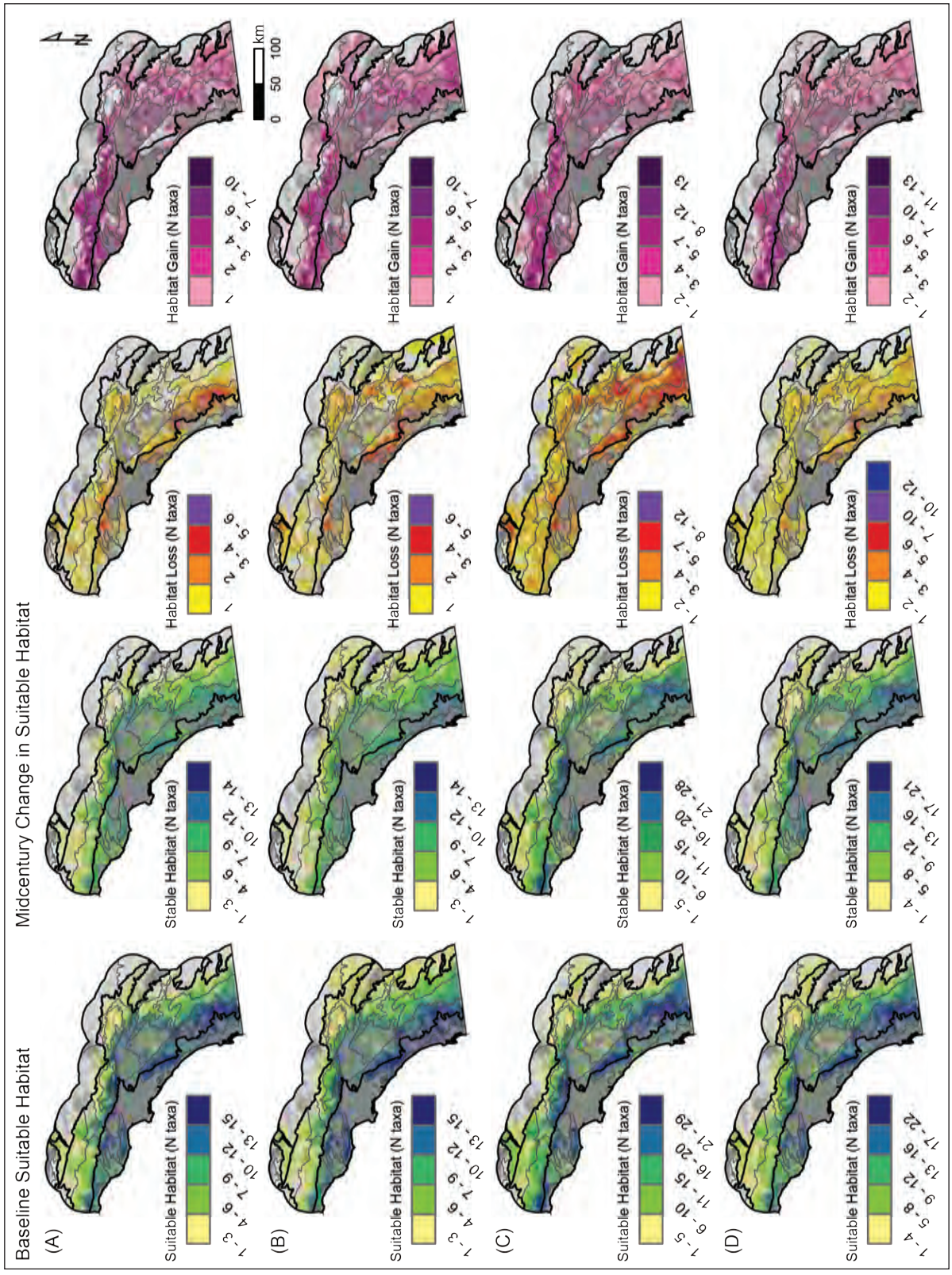

Figure 6—Number of taxa with suitable habitat under baseline (1951–1980) and midcentury (2040–2060) climate conditions for (A) alluvial scrub, (B) coastal sage scrub, (C) low-elevation chaparral, and (D) mixed chaparral-sage scrub vegetation groups. Midcentury maps show areas of agreement for least three of the five future climate scenarios. Projected change in suitable habitat is defined as stable = suitable under baseline and future conditions; loss = suitable under baseline but unsuitable under future conditions; gain = unsuitable under baseline and becoming suitable under future conditions. See appendix 5 for maps for individual climate scenarios. Vegetation group assignments are not mutually exclusive (see table 2). In all maps, suitable habitat already converted to human land uses (FRAP 2015) is masked in dark gray.

in coastal Orange and San Diego Counties for alluvial scrub and coastal sage scrub taxa and in portions of the Santa Monica, San Gabriel, and Santa Ana Mountains for low-elevation chaparral and mixed chaparral-sage scrub taxa. Overlays for all vegetation groups showed potential gains in suitable habitat with increasing elevation in the Transverse and Peninsular Ranges under all five future climate scenarios (app. 5).

Discussion

Species distribution models can be a valuable tool for conservation and natural resource management decisionmaking when applied thoughtfully and in concert with expert knowledge about the biology, ecological relationships, population dynamics, and demographics of the species of interest. Habitat suitability maps provide insights about which species might be used most successfully for restoration in the face of an uncertain future, and, when paired with climate-adjusted provenancing strategies (e.g., Prober et al. 2015), provide information on where one might collect material for any particular restoration site. One of the largest hurdles to incorporating climate change into decisionmaking is the uncertainty in future climate. We explored this uncertainty by considering five scenarios that span a range of future conditions for southern California, including both increases and decreases in precipitation. Note, however, that the actual climate conditions at midcentury may not be encompassed by these five scenarios.

Habitat suitability forecasts are best interpreted as an estimate of potential climate exposure (the nature and degree of projected change in climate at midcentury), as our models focus on climatic predictors rather than other factors that may influence species distribution, such as biotic interactions or disturbance regime. Projected loss in suitability suggests high future climate stress or exposure, but inferring extinction risk or population persistence requires coupling SDMs with demographic models (Dawson et al. 2011; Franklin et al. 2014, 2016), which we were unable to do given the lack of detailed demographic data for nearly all taxa. Climate exposure estimates from SDM projections can be evaluated in combination with factors related to the sensitivity and adaptive capacity of a species to assess vulnerability under climate change (Butt et al. 2016, Estrada et al. 2015). However, we caution against transferring our regional model results outside our focal area, as those taxon-climate relationships may differ from the ones we modeled. Additionally, our restricted occurrence dataset could result in underpredicting suitable climate space and overpredicting climate-driven suitability loss (e.g., Barbet-Massin

et al. 2010). Finally, there are a number of methodological assumptions for SDMs that should be taken into consideration when using modeling results for practical applications. These are explicitly recognized in appendix 6.

Habitat Suitability Under Projected Climate Change

In California's environmentally heterogeneous landscapes, the geographic ranges of species can vary tremendously in extent and habitat attributes. Our regional models focus on projected changes in suitable habitat under climate change specifically for southern California. Projections of future habitat suitability for focal shrubland taxa varied widely depending on the climate scenario considered. Future climate scenarios with the most extreme directional changes in precipitation at midcentury had the greatest projected losses of suitable habitat for most taxa. The wettest scenario (CNMR-CM5) had the greatest departure from baseline conditions with respect to novel climate combinations. Our choice to limit SDM extrapolation in areas of novel climates may have contributed to the high projected losses for some taxa under this scenario. The driest scenario (MIROC-ESM) produced high losses of suitable habitat for many plant taxa. It also had the greatest increase in climatic water deficit (CWD) of all five future climate scenarios.

Given the strong association between water availability and vegetation structure and composition in California (e.g., Jin and Goulden 2014), shifts toward a hotter, drier climate like that projected by MIROC-ESM could be expected to have large effects on southern California vegetation. The majority of taxa with high suitability loss under the MIROC-ESM scenario were woody chaparral shrubs, suggesting that low-elevation chaparral shrublands may be vulnerable to increased drought stress in southern California. Thorne et al. (2016) also predicted high climate exposure and loss of suitability for chaparral at the macro-group level, particularly in low-elevation areas in southern California. Differential response to drought stress among chaparral species (Coates et al. 2015, Frazer and Davis 1988, Venturas et al. 2016) may result in changes in chaparral structure and composition as climate shifts. Future increases in precipitation extremes and interannual variability (Berg and Hall 2015, Berg et al. 2015) may also strongly affect southern California vegetation, although we did not directly address these changes in our modeling. SDM overlays of multiple taxa provide a first pass at predicting climate change effects on shrubland vegetation groups. Areas that maintain suitable habitat for a large number of taxa in vegetation groups may act as important refugia under future climate change. Individualistic shifts of taxa in response to climate change (Huntley 1991), however, will have implications for the structure and composition of plant communities and

ecosystems, such as the potential for emergent novel species assemblages with no modern analog or novel biotic interactions (Jackson and Overpeck 2000, Williams and Jackson 2007).

Many of the taxa we modeled showed high stability in future suitable habitat under projected midcentury climate conditions, which contrasts with recent modeling studies predicting large habitat losses for southern California plant taxa under climate change (e.g., Principe et al. 2013, Riordan and Rundel 2014). For example, we predicted a high degree of stable future suitable habitat under midcentury climate for *Artemisia californica* in southern California (92 to 100 percent of baseline suitable habitat), while Principe et al. (2013) predicted a 78 precent loss. Thorne et al. (2016) and Riordan and Rundel (2014) also predicted greater losses of suitable habitat for dominant coastal sage scrub taxa both at mid and late 21st century compared to our regional modeling results. Factors that may have contributed to the differences between studies include, but are not limited to, GCM and emission scenario selection, study area extent, source of occurrence data, and spatial resolution of climatic data. Our models used higher resolution (270 m) climate data that may better identify topographically buffered areas maintaining stable climate conditions (Dobrowski et al. 2009, Franklin et al. 2013, Meineri and Hylander 2017) compared to models built on coarser 1 km resolution climate data, such as Riordan and Rundel (2014) and Principe et al. (2013).

The infraspecific differences in projected midcentury suitable habitat that we found highlight the need to consider within-species variation when forecasting future climate change effects in southern California. Modeling at the infraspecies level can improve model performance, revealing divergent patterns of potential effects of climate change that are masked when modeling at the species level (e.g., Pearman et al. 2010). Furthermore, incorporating intraspecific genetic information into SDMs can provide more realistic distribution models and improve forecasts of range shifts, especially if infraspecies are adapted to different environments (Gotelli and Stanton-Geddes 2015, Marcer et al. 2016). Plant populations are often adapted to their local environments and can vary in genetic structure and traits across even relatively short distances within a species' range (reviewed in Linhart and Grant 1996). Valladares et al. (2014) showed that when population differentiation (phenotypic plasticity and local adaptation) and dispersal restrictions are accounted for in SDMs, models predict greater losses in suitable habitat under climate change than when assuming a homogenous species range with unlimited dispersal. Species' traits and interactions with dispersal agents also ought to be considered, as both can profoundly affect migration rates, isolation, expansion of species range, and the extent to which populations can adapt to new conditions

(Aitken et al. 2008). Although we were unable to incorporate population-level genetic variation in our SDMs, we emphasize the importance of considering genetic variation and dispersal ability, where available, when applying modeling results for restoration in areas of high environmental heterogeneity like southern California. For example, Richardson et al. (2014) showed that genetically distinct warm- and cold-adapted ecotypes in blackbrush (*Coleogyne ramosissima* Torr.) differed in their predicted occupancy of contemporary and future climate space, with the warm-adapted ecotype dominating contemporary climate space and the cold-adapted ecotype dominating future climate space and newly suitable habitat that became available at higher latitudes and elevations.

Climate Change, Land Use, and Fire

Fire, invasive species, and human land use are major drivers of vegetation change in southern California. For example, a combination of human land use, frequent fire, invasion by exotic annuals, grazing, and air pollution have greatly reduced coastal sage scrub (Minnich and Dezzani 1998; O'Leary 1990, 1995; Westman 1981). In southern California, contemporary fire-return intervals for coastal sage scrub and chaparral are 30 to 40 years (Keeley and Fotheringham 2001), which is already shorter than pre-European settlement return intervals (Safford and Van de Water 2014). Too-frequent fires and other human disturbance can lead to a shift in dominance to nonnative annual grasses (Fleming et al. 2009, Talluto and Suding 2008). Nitrogen deposition from air pollution and severe drought enhance these shifts in coastal sage scrub, slowing postfire succession and increasing nonnative grass cover (Kimball et al. 2014). Once established, nonnative grasses can further promote high fire frequencies by carrying fire easily where ignitions are plentiful, as they are in most of southern California (D'Antonio and Vitousek 1992, Faivre et al. 2014, Keeley and Syphard 2017). In addition, interacting drivers of vegetation change such as fire can complicate and confound climate change signals (e.g., Schwilk and Keeley 2012). Thus, fire, land use, and invasive species could interact with changing climate to cause vegetation change, even if the projected vulnerability to climate change alone is relatively low. Novel climate conditions may also facilitate new invasive species or affect existing biotic interactions (Schweiger et al. 2010).

In the Western United States, warming temperatures exacerbate water deficit and drought (Williams et al. 2015), which may affect fuel conditions and increase wildfire activity (Westerling et al. 2006), including fire severity and intensity (van Mantgem et al. 2013). In southern California, the worst fire conditions occur during Santa Ana wind events in autumn, but projected warmer and drier conditions mid-century could lead to a longer fire season and cause an increase in the area burned

by fire, whether or not it occurs during a Santa Ana event (Jin et al. 2015, Yue et al. 2014). Because climatic conditions are already suitable for massive fires most years in southern California, human activity has a large effect on ignition frequency and wildfire activity (Faivre et al. 2014, Keeley and Syphard 2016). A projected increase in southern California's population of over 50 percent by midcentury (Sanstad et al. 2011) will likely further alter fire regimes and contribute to additional habitat loss and fragmentation, all of which could affect vegetation response to climate change.

Habitat fragmentation poses a significant threat to many species' persistence. Much of the lower elevation of the southern California landscape has a high degree of habitat conversion and fragmentation, the result of interrelated effects of urbanization, altered fire regimes, and invasive species (especially nonnative grasses and forbs). Local extinctions can stem from direct habitat loss owing to land development, but also indirectly from the effects of habitat degradation and fragmentation. Reduced population sizes in habitat fragments are more susceptible to inbreeding depression and extirpation from demographic stochasticity (Frankham 1995, Neel 2008, Richards 2000). The high degree of human land use in southern California is a considerable barrier to dispersal and gene flow and could negatively affect the adaptive capacity and ability of some species to move across the landscape in response to changing conditions (Fahrig 1997, Krosby et al. 2010).

Life history traits, especially postfire regeneration response, are also important in understanding the influence of different environmental drivers of vegetation change (Swab et al. 2012, Syphard et al. 2013). In southern California, seedling recruitment of many shrubs is stimulated by fire (Keeley et al. 2006, Keeley and Keeley 1981, Keeley and Zedler 1978). Obligate resprouters regenerate after fire solely by vegetative resprouts, while postfire seeders can either be obligate seeders that cannot resprout after fire or facultative seeders that recruit postfire through seeds and resprouting (Keeley et al. 2012). Too-frequent fires can cause shifts in dominance by reducing obligate seeders on a site (Syphard et al. 2006, Zedler et al. 1983) or lead to type conversion to grass-dominated vegetation (Haidinger and Keeley 1993, Lippitt et al. 2013). Modeling studies linking population dynamics, climate change, land use, and fire highlight the substantial threat of short-interval fire regimes on obligate seeder persistence in southern California (Syphard et al. 2013). The interaction between fire and drought can also affect postfire regeneration in chaparral. Facultative seeding and obligate resprouting shrub species may be able to tolerate shorter fire-return intervals than obligate seeding species (Lucas et al. 2013), but they are susceptible to severe drought following fire that causes high seedling mortality (Frazer and Davis 1988) as well as increased mortality

of resprouts (Pratt et al. 2014). Seedlings of obligate seeders have comparatively higher tolerance to water stress and postfire drought (Pratt et al. 2008), but they are particularly vulnerable to short fire-return intervals.

Despite uncertainty in projections of future drought and precipitation, warming temperatures are predicted to increase annual climatic water deficits regardless of the direction in future precipitation change (Thorne et al. 2012). Recent extreme and prolonged drought in California could be indicative of a trend of continuing hot droughts in the Anthropocene characterized by high plant mortality rates as physiological thresholds are exceeded (Allen et al. 2015, Overpeck 2013). Although our modeling approach is best used to understand potential shifts in climate exposure, rather than to infer mechanisms of species response to climate change, high projected losses in habitat suitability may suggest increased mortality for some chaparral species. Chaparral shrubs tend to have lower drought tolerance and to occur in more mesic and higher elevation areas than drought-deciduous sage scrub species (Harrison et al. 1971, Miller and Poole 1979, Mooney and Dunn 1970). Thus high projected habitat suitability losses for low-elevation chaparral species under the driest future scenario may translate to future increases in mortality. Structure and composition within vegetation types may shift depending on differential species tolerance to drought (Pratt et al. 2007, 2014; Venturas et al. 2016), as well as differential responses to changes in wildfire frequency and intensity (Keeley et al. 2005, 2006).

Spatial context is also important when evaluating the vulnerability of southern California plant species to multiple interacting threats. At high fire-return intervals, fire tends to be the most serious threat for obligate seeding shrub species, compared to projected land use or climate change (Franklin et al. 2014, Regan et al. 2010, Syphard et al. 2013). At longer fire-return intervals, however, the rankings of projected threats vary by species and depend on the spatial context (Syphard et al. 2013). Regan et al. (2010) found that a small degree of habitat fragmentation may actually be beneficial for the obligate seeder *Ceanothus perplexans* if it spatially and temporally decouples fire events, though the negative impact of habitat loss typically outweighed this benefit as fragmentation increased. For species that are already embedded in urban landscapes, such as the rare obligate seeder *C. verrucosus* (not modeled in our study), climate change may pose the greatest threat, resulting in population decline and increased local extirpation (Lawson et al. 2010). It is also possible that climate change may benefit some plant taxa. Our modeling results suggest that many southern California shrub taxa may retain and even gain suitable habitat under projected climate change. Drought-tolerant species such as *C. crassifolius*, whose seedlings are particularly tolerant of water stress (Pratt et al. 2008, 2014), may be able to expand with moderate increases in temperature and climatic

water deficit so long as fire frequencies do not exceed the threshold needed for the species to reach reproductive maturity. Therefore, it is important to consider SDM results such as ours within a broader spatial framework of environmental change.

Management Implications

Effective land management under rapid environmental change may call for managers to consider multiple spatial and temporal scales, address diverse threats and drivers of environmental change, and incorporate scenarios of climate change into many aspects of planning and action (e.g., Abrahms et al. 2017, Heller and Zavaleta 2009, Lawler 2009). For ecological restoration, practitioners are beginning to redefine project goals and procedures in the context of recent and projected future climate change, from the selection of reference targets to sourcing of plant material (Breed et al. 2013, Harris et al. 2006, Havens et al. 2015, Jackson and Hobbs 2009). Understanding how climate is projected to change in southern California and the potential effects on target species are important considerations for restoration efforts in the region. Fortunately, a variety of tools and frameworks have been developed to help facilitate the incorporation of climate change into planning and decisionmaking (reviewed in Abrahms et al. 2017). The SDM results from this study can be consulted to address some important questions raised in the Abrahms et al. (2017) review, including (1) how climate is projected to change in the project area, (2) how the suitable habitat of a potential project taxon is expected to shift, (3) how vulnerable potential combinations of taxa are to the projected changes, (4) what suite of taxa is projected to remain or become appropriate for the project site, (5) and what management strategies might affect project outcomes.

Uncertainty, whether from a lack of knowledge in how species and ecosystems will respond to change (e.g., Walther 2010) or due to uncertainty about the magnitude and direction of future climate change itself (e.g., Stott and Kettleborough 2002), can impede decisionmaking. Scenario planning facilitates incorporating uncertainty into decisionmaking by providing a framework to evaluate the robustness of a decision across a range of plausible but contrasting futures (Peterson et al. 2003). Considering multiple climate scenarios allows planners to address uncertainty about future climate change and identify strategies that are successful across a range of future conditions. Our projections of future suitable habitat provide information about possible climate change effects on focal shrubland plant taxa that can be incorporated into a scenario planning framework. For example, taxa projected to maintain suitability at a site under all future scenarios may have high restoration value even given uncertain future conditions. For taxa with high projected suitable habitat loss and climate exposure, evaluation of their ecological

relationships, genetics, and life-history traits will help estimate vulnerability to climate change and guide the development of taxon- and site-specific sourcing strategies. Because nonclimatic factors are important drivers of southern California vegetation distribution, we suggest that SDM outputs could be used in a broader context that combines future habitat suitability under climate change with alternative futures of varying stressors (e.g., fire, land use, invasive species) and species response (e.g., dispersal capacity, physiological tolerances).

Species distribution model forecasts can be used to inform restoration goals and reference targets, as well as to evaluate restoration feasibility, under projected climate change. Setting realistic and effective goals for ecological restoration under changing environmental conditions remains a significant challenge, despite numerous recent advancements in the field (Hobbs 2007, Perring et al. 2015). Ecological restoration in the United States has often used historical data from the site to be restored and contemporary data from pristine analogous sites to establish reference conditions for restoration (Moore et al. 1999, White and Walker 1997). Although this approach may lose effectiveness under mounting climate and environmental change, restoring historical ecosystems may remain a viable goal in some areas (Jackson and Hobbs 2009). For example, historical targets may remain useful at sites projected to maintain suitability for many species across a range of future scenarios, whereas sites projected to lose suitability may be more difficult to restore or necessitate greater human intervention for success. Managers may want to consider alternative restoration goals as well as more dynamic targets in areas of high future climate exposure, especially if other ecological stressors (e.g., invasive species, disturbance) are also high. Species distribution models can also help managers to evaluate species-site suitability and identify specific taxa with projected high stability of suitable habitat, or the reverse, under climate change to aid in species selection (Butterfield et al. 2016, Gelviz-Gelvez et al. 2015, López-Tirado and Hidalgo 2016).

For SDMs to most effectively assist restoration efforts, we recommend that models take into account intraspecific variability. As found in our study, this often leads to very different predictions of risk and vulnerability under projected climate change, compared to traditional SDM approaches that pool records across a species' range (Hällfors et al. 2016b, Pearman et al. 2010, Valladares et al. 2014). By partitioning species' ranges into groups of populations at landscape units, Hamann and Aitken (2013) showed that climate change could negatively affect populations throughout a species' range, not just at the leading or trailing edges. When Valladares et al. (2014) accounted for population-level differentiation and restricted dispersal capacity, they

forecasted greater losses under climate change compared to conventional forecasts assuming uniformly high plasticity across a species' range. Wherever possible, we recommend interpreting SDM results in a broader context that combines variation in habitat attributes, genetics, and adaptive and life-history traits.

One of the biggest challenges in ecological restoration is accounting for variation among populations within taxa. Our study takes a step toward incorporating such variation by modeling at the level of infraspecies over a limited ecological region. Within a species' range, natural plant populations are often adapted to their local environments and can differ in genetic structure and phenotypic characters over large or small spatial scales (reviewed in Linhart and Grant 1996). This variation has implications both for sourcing appropriate plant material for restoration and for understanding how a species may respond to changing climate. In the absence of taxon-specific seed transfer guidelines, using local seed sources for restoration has been recommended to minimize the risk of maladaptation and outbreeding depression to the extent that the deleterious effects of small populations and inbreeding can be avoided (Hufford and Mazer 2003, McKay et al. 2005, Rogers 2004, Rogers and Montalvo 2004). Rapidly changing environmental conditions, however, can threaten the adaptive capacity of species at local spatial scales (Christmas et al. 2016, Nicotra et al. 2015), suggesting a more complex, but carefully determined, form of seed sourcing may be needed on a case-by-case basis (Havens et al. 2015, Prober et al. 2015). Population-level genetic variation is also important in understanding species vulnerability to climate change. Variation in adaptive traits and intrinsic traits can profoundly affect migration rates, isolation, expansion of species range, and the extent to which populations migrate to suitable conditions or adapt to new conditions (Aitken et al. 2008, Estrada et al. 2015). Any guidelines for determining the direction and extent of expanded seed sourcing areas will need to consider the risks of moving too far or too soon. The SDM results we provide can be combined with other information to begin the genesis of such guidelines and stimulate research to test their utility.

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U.S. Equivalents

When you know:	Multiply by:	To find:
Millimeters (mm)	0.0394	Inches
Meters (m)	3.28	Feet
Kilometers (km)	0.621	Miles
Square kilometers (km^2)	.386	Square miles
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

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Appendix 1: Projected Midcentury Change in Southern California Climate

Appendix 1 provides maps (fig. 7 A–E) of projected midcentury climate change relative to baseline climate conditions. Change in climatic variables was calculated as the difference between midcentury (2040–2069) and baseline (1951–1980) 30-year climate averages under five climate scenarios. Change in annual precipitation was calculated as percentage of change relative to baseline. Abbreviations: TMIN = minimum winter temperature (December through February); TMAX = maximum summer temperature (June through August); PPT = annual precipitation; CWD = climatic water deficit. Black lines indicate ecological section boundaries; dark gray lines indicate ecological subsection boundaries. Climate data are from the Basin Characterization Model (CA-BCM) (Flint et al. 2013). See figure 3 for full name and source of the general circulation models for the five climate scenarios.

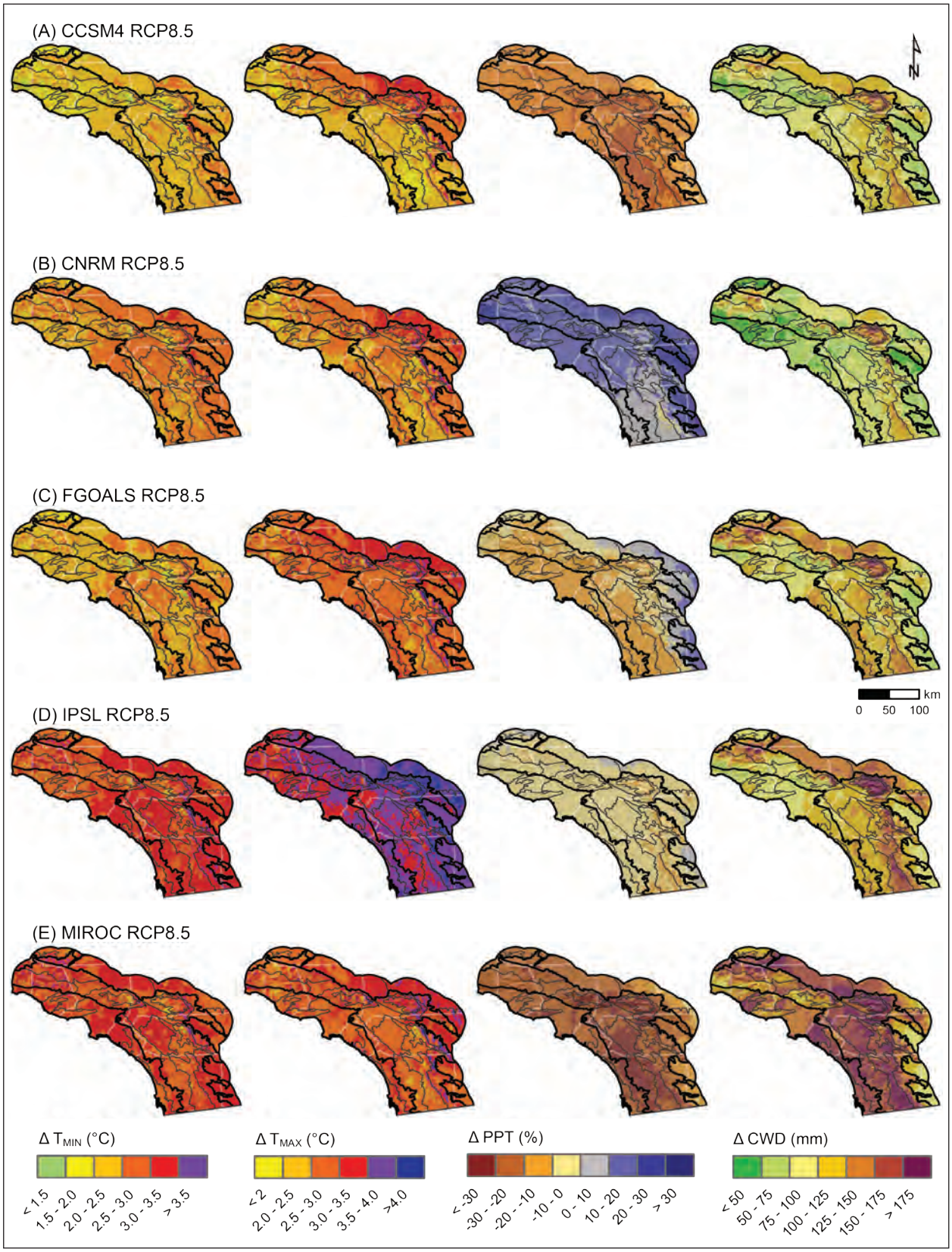

Figure 7—Projected midcentury (2040–2069) change in climate under five future climate scenarios (A-E) relative to baseline (1951–1980) climate.

Appendix 2: Detailed Species Distribution Modeling Methods

Infraspecies Name Assignments

Species distribution models (SDMs) use locality data from species occurrences and spatially explicit environmental layers to predict species distributions in space and time (Elith and Leathwick 2009, Guisan and Thuiller 2005). Spatial and temporal biases in natural history collections (e.g., Kadmon et al. 2004) can affect model performance, requiring more collections than previously thought to accurately represent a species range or climatic niche (Feeley and Silman 2011). To maximize the number of occurrence records used in infraspecies models, we assigned missing infraspecific names where the variety or subspecies could reasonably be inferred from the geographic location of the occurrence data based on the taxonomic description. For some taxa, we also checked herbarium specimens at the Herbarium at the University of California, Riverside (UCR). Taxonomy and nomenclature follow Baldwin et al. (2012), unless otherwise noted.

***Acmispon glaber*—**

Two varieties are recognized for *Acmispon glaber*: *A. g.* var. *brevialatus* and *A. g.* var. *glaber*. *Acmispon g.* var. *brevialatus* is restricted to southern California and Baja California unless planted or introduced, whereas *A. g.* var. *glaber* occurs not just in southern California, but also in coastal portions of northern California, the North Coast Ranges, and the Sierra Nevada foothills. In southern California, *A. g.* var. *brevialatus* occurs primarily in hotter and drier interior regions of Riverside, Los Angeles, western San Bernardino, and eastern San Diego Counties, and *A. g.* var. *glaber* primarily occurs in coastal southern California, the western Transverse Ranges, and Peninsular Ranges. After checking and annotating herbarium specimens at UCR, we assigned other records missing a variety determination that occurred outside southern California and were not obvious roadside plantings or introductions to *A. g.* var. *glaber* (north of the western Transverse Ranges, including the Tehachapi Mountains, Sierra Nevada foothills, Coast Ranges, and the central and northern California coast). We did not use *A. glaber* records lacking variety determinations that were collected in southern California where both varieties occur.

***Adenostoma fasciculatum* var. *fasciculatum*—**

There are three varieties recognized in *Adenostoma fasciculatum*: *A. f.* var. *fasciculatum*, *A. f.* var. *prostratum*, and *A. f.* var. *obtusifolium*. *Adenostoma f.* var. *fasciculatum* is common and broadly distributed throughout shrublands below 1830 m in the California Floristic Province. After checking specimens at UCR, we

assigned all records missing a variety determination to *A. f.* var. *fasciculatum*. This may include a small number of records from two other less common varieties, *A. f.* var. *prostratum* (restricted to a limited area in the central coast and outside our study extent) and *A. f.* var. *obtusifolium* (occurring in the south coast and southwest Peninsular Ranges in San Diego County).

***Ceanothus crassifolius* var. *crassifolius*—**
There are two varieties recognized in *Ceanothus crassifolius*: *C. c.* var. *crassifolius* and *C. c.* var. *planus.* The varieties intergrade in Santa Barbara and Ventura Counties and may represent the extremes of an intergrading network that needs more study to see if varietal rank is appropriate. We included all records missing varietal determination as *C. c.* var. *crassifolius,* but recognize this may include some records near the northern limit of our study area that either are *C. c.* var. *planus* or have introgression with *C. c.* var. *planus.*

***Ceanothus cuneatus* var. *cuneatus*—**
There are three varieties in *Ceanothus cuneatus*: *C. c.* var. *cuneatus, C. c.* var. *fascicularis,* and *C. c.* var. *ramulosus. C. c.* var. *cuneatus* is widespread throughout the California Floristic Province below 2133 m. The two other varieties are restricted to the central coast (*C. c.* var. *fascicularis* in Santa Barbara and San Luis Obispo Counties) and the Coast Ranges from the San Francisco Bay Area south into the western Transverse Ranges (*C. c.* var. *ramulosus*), outside the geographic extent of this study. We assigned records missing a variety determination collected outside these areas of overlap to *C. c.* var. *cuneatus.*

***Ceanothus megacarpus* var. *megacarpus*—**
There are two varieties recognized in *Ceanothus megacarpus*: *C. m.* var. *insularis,* which is restricted to the Channel Islands, and *C. m.* var. *megacarpus,* which occurs in southern California. We assigned records missing variety determination collected on the mainland to *C. m.* var. *megacarpus.*

***Cercocarpus betuloides* var. *betuloides*—**
There are three varieties recognized in *Cercocarpus betuloides*: *C. b.* var. *betuloides, C. b.* var. *blanchaea,* and *C. b.* var. *macrourus. Cercocarpus. b.* var. *betuloides* overlaps in distribution with *C. b.* var. *blanchaea* in the Chanel Islands and the southern western Transverse Ranges and with *C. b.* var. *macrourus* in northern California in the Klamath Ranges, Cascade Range, and Modoc Plateau. We assigned records missing a variety determination collected outside these areas of overlap to *C. b.* var. *betuloides.*

***Eriodictyon crassifolium*—**

There are two varieties recognized in *Eriodictyon crassifolium*: *E. c.* var. *crassifolium* and *E. c.* var. *nigrescens. Eriodictyon c.* var. *crassifolium* occurs in cismontane southern California, including the South Coast Ranges and drainages, from eastern Santa Barbara County to northwestern Baja California. *Eriodictyon c.* var. *nigrescens* also occurs in cismontane southern California, but primarily in the western Transverse Ranges and southern South Coast Ranges. However, there are specimens from areas of southern California that are hard to place into either variety; and there are some specimens from the southwestern Peninsular Ranges that have been identified as *E. c.* var. *nigrescens.* We assigned all southern California records missing variety determination collected from San Bernardino, Riverside, Orange, and San Diego Counties to *E. c.* var. *crassifolium.* We excluded records of *E. c.* var. *nigrescens* collected in the southwestern Peninsular Ranges in San Diego County from models, but recognize this may truncate the taxon's range if those collections are indeed correct and if the range description in the current taxonomic treatment needs to be updated.

***Malacothamnus fasciculatus* var. *fasciculatus*—**

There are four varieties currently recognized in *Malacothamnus fasciculatus,* including *M. f.* var. *fasciculatus,* which is most common and widespread in southern California. Two subspecies, *M. f.* var. *catalinensis* and *M. f.* var. *nesioticus,* occur only on Catalina and Santa Cruz Islands, respectively. One variety, *M. f.* var. *nuttallii*, overlaps with *M. f.* var. *fasciculatus* on the mainland in the South Coast Ranges and western Transverse Ranges in Santa Barbara and Ventura Counties. We include all mainland records missing a variety determination as *M. f.* var. *fasciulatus*, but recognize that this may include a few records of *M. f.* var. *nuttallii* within a small zone of overlap for the study extent.

***Prunus ilicifolia* subsp. *ilicifolia*—**

There are two subspecies recognized in *Prunus ilicifolia*: *P. i.* subsp. *ilicifolia* and *P. i.* subsp. *lyonii.* As *P. i.* subsp. *lyonnii* is restricted to the Channel Islands, we assigned any records missing a subspecies determination occurring on the mainland to *P. i.* subsp. *ilicifolia.*

Parent Geology

The parent geology data included in SDMs (fig. 8) were obtained from the California Basin Characterization Model (CA-BCM) (Flint et al. 2013), based on the Geologic Map of California (Jennings et al. 2010). We simplified the CA-BCM parent geology layer into 18 categories. All different types of alluvium parent

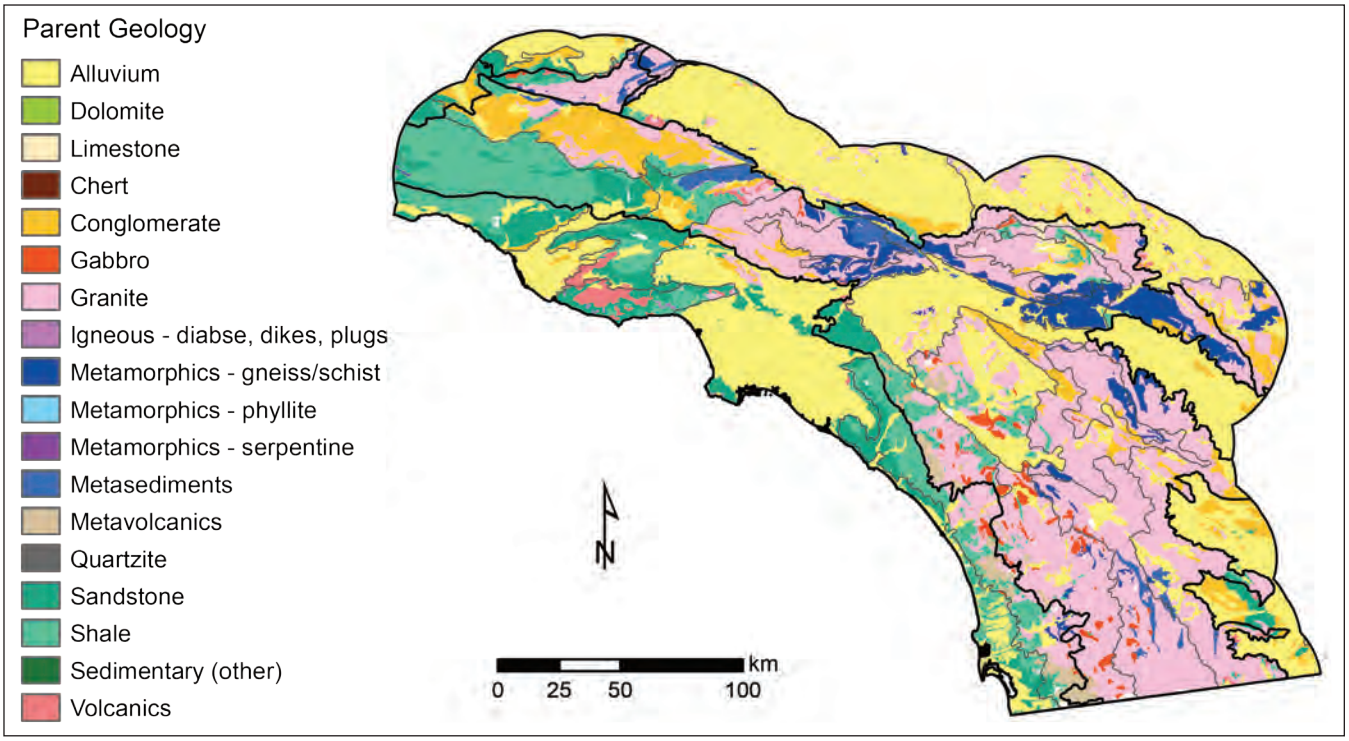

Figure 8—Parent geology map simplified to 18 categories used in species distribution models.

geology, such as playas, valley fill, and channels, were grouped into a single "alluvium" category. Different types of granites, volcanics, and sandstone were also combined into single groups by those names.

Treatment of Sampling Bias

We compared three methods for correcting sampling bias based on the manipulation of background data to produce geographical sampling bias similar to that of our occurrence data. Each approach used target group sampling (Phillips et al. 2009) of digitized herbarium records for all vascular plants in southern California collected after 1950 (CCH 2016). In the first method, "target background," we substituted all target group occurrences thinned to one record per environmental grid cell for Maxent's default random background. In the second method, "target-weighted," we created a grid of relative sampling frequency by summing the number of occurrences in each grid cell and dividing by the total number of occurrences (Merow et al. 2013). We then used this grid to weight background sampling in proportion to the relative sampling frequency of our target group. In the third method, "bias grid," we created a bias grid derived from a Gaussian-kernel density map of the target group, rescaled from 1 to 20 (Elith et al. 2010). As in the second method, we

used this grid to weight background sampling. We tested model performance of six different bias grids of varying standard deviation distances of the Gaussian-kernel (15 km, 20 km, 30 km, 50 km, 75 km, and 100 km). To evaluate model performance, we ran each modeling method with fivefold cross validation and compared three evaluation metrics: sample size corrected Akaike information criterion (AICc) (Akaike 1974, Burnham and Anderson 2002), area under the receiver operating curve of the test data (AUC_{test}) and the difference between the calibration and test AUC (AUC_{diff}). We included AICc as an additional measure of overall model performance when comparing methods because AUC can produce inflated estimates of model performance when both training and test data are spatially biased, non-independent, or both (Hijmans 2012, Veloz 2009). We calculated AICc in R by the *calc.aicc* function in the ENMeval package (Muscarella et al. 2014). Of the different distance-based bias grids, the 100 km standard deviation distance produced models with the lowest AICc (highest model performance) for the majority of taxa modeled. When compared to the target background and target weighted methods, the 100 km bias grid had significantly higher performance, as measured by AICc and AUC_{test} (all $P < 0.0001$; paired Student's t-test), and less overfitting, as measured by AUC_{diff} (all $P < 0.0001$; paired Student's t-test).

Appendix 3: Detailed Species Distribution Modeling Results

Detailed model performance metrics and summaries of projected habitat suitability change are presented for all focal plant taxa. Table 6 reports model performance (mean ± standard deviation) summarized across fivefold cross-validation replicates for four different metrics: area under the receiver operator curve for the test data (AUC_{test}); difference between the calibration and test AUC (AUC_{diff}); omission rate at the 10 percent test threshold (OR_{10P}); and the omission rate at the maximum sensitivity plus specificity threshold (OR_{mSSS}). AUC_{test} provides a threshold-independent measures of overall model performance. AUC_{diff} measures model overfitting with high values indicate high overfitting to the calibration data. The omission (or false negative) rate gives the proportion of test occurrences incorrectly identified and provides information about the discriminatory ability of the model at a particular threshold. Table 7 reports the relative significance of individual environmental variables to Maxent models for each taxon. Variable significance is estimated as the percentage of permutation importance. A high value of permutation importance indicates a strong model dependence on that particular variable. Bold font indicates the variable with the greatest permutation importance. Table 8 reports the percentage of change in suitable habitat under projected midcentury (2040–2069) climate conditions relative to baseline (1951–1980) suitable habitat for each of the five climate scenarios. Projected change in suitable habitat is defined as follows: stable = suitable under baseline and future conditions; loss = suitable under baseline but unsuitable under future conditions; gain = unsuitable under baseline and becoming suitable under future conditions.

Table 6—Model performance metrics (mean ± standard deviation) for focal taxa

Scientific name	N	AUC_{test} [a]	AUC_{diff} [b]	OR_{10P} [c]	OR_{mSSS} [d]
Acmispon glaber var. *brevialatus*	303	0.780 ± 0.027	0.014 ± 0.035	0.13 ± 0.06	0.20 ± 0.09
Acmispon glaber var. *glaber*	246	0.859 ± 0.021	0.003 ± 0.026	0.11 ± 0.03	0.24 ± 0.08
Adenostoma fasciculatum var. *fasciculatum*	609	0.762 ± 0.014	0.001 ± 0.017	0.11 ± 0.04	0.18 ± 0.02
Arctostaphylos glandulosa subsp. *cushingiana*	39	0.914 ± 0.014	0.023 ± 0.016	0.13 ± 0.09	0.15 ± 0.14
Arctostaphylos glandulosa subsp. *glandulosa*	204	0.899 ± 0.014	0.006 ± 0.017	0.13 ± 0.09	0.12 ± 0.08
Arctostaphylos glandulosa subsp. *mollis*	137	0.926 ± 0.023	0.011 ± 0.027	0.18 ± 0.11	0.15 ± 0.11
Arctostaphylos glauca	503	0.785 ± 0.012	0.006 ± 0.013	0.12 ± 0.03	0.21 ± 0.06
Artemisia californica	345	0.825 ± 0.020	0.003 ± 0.023	0.12 ± 0.03	0.06 ± 0.03
Ceanothus crassifolius var. *crassifolius*	357	0.873 ± 0.013	-0.002 ± 0.016	0.12 ± 0.05	0.22 ± 0.07
Ceanothus cuneatus var. *cuneatus*	135	0.827 ± 0.040	0.033 ± 0.049	0.16 ± 0.11	0.24 ± 0.14
Ceanothus leucodermis	404	0.842 ± 0.019	0.001 ± 0.021	0.12 ± 0.04	0.20 ± 0.09
Ceanothus megacarpus var. *megacarpus*	88	0.959 ± 0.029	0.001 ± 0.035	0.13 ± 0.16	0.07 ± 0.13
Ceanothus oliganthus	235	0.913 ± 0.017	0.001 ± 0.021	0.11 ± 0.04	0.12 ± 0.06
Ceanothus perplexans	229	0.881 ± 0.023	0.004 ± 0.028	0.11 ± 0.05	0.14 ± 0.05
Ceanothus tomentosus	201	0.917 ± 0.011	0.001 ± 0.014	0.11 ± 0.05	0.11 ± 0.05
Ceanothus vestitus	97	0.916 ± 0.032	0.013 ± 0.039	0.17 ± 0.11	0.09 ± 0.10
Cercocarpus betuloides var. *betuloides*	398	0.792 ± 0.019	0.006 ± 0.022	0.12 ± 0.06	0.19 ± 0.09
Corethrogyne filaginifolia	456	0.728 ± 0.022	0.007 ± 0.028	0.12 ± 0.03	0.27 ± 0.09
Deinandra fasciculata	347	0.841 ± 0.013	-0.002 ± 0.016	0.11 ± 0.05	0.17 ± 0.08
Encelia californica	195	0.915 ± 0.024	0.001 ± 0.030	0.13 ± 0.07	0.14 ± 0.09
Encelia farinosa	256	0.890 ± 0.017	-0.002 ± 0.021	0.12 ± 0.05	0.10 ± 0.03
Eriodictyon crassifolium var. *crassifolium*	274	0.818 ± 0.029	0.008 ± 0.036	0.11 ± 0.01	0.26 ± 0.10
Eriodictyon crassifolium var. *nigrescens*	121	0.854 ± 0.023	0.025 ± 0.026	0.17 ± 0.09	0.18 ± 0.09
Eriodictyon trichocalyx var. *lanatum*	62	0.862 ± 0.040	0.029 ± 0.046	0.13 ± 0.09	0.19 ± 0.11
Eriodictyon trichocalyx var. *trichocalyx*	148	0.880 ± 0.022	0.018 ± 0.025	0.13 ± 0.07	0.24 ± 0.07
Eriogonum fasciculatum var. *fasciculatum*	79	0.934 ± 0.012	0.010 ± 0.013	0.18 ± 0.08	0.18 ± 0.08
Eriogonum fasciculatum var. *foliolosum*	477	0.770 ± 0.025	0.004 ± 0.028	0.12 ± 0.06	0.21 ± 0.05
Eriogonum fasciculatum var. *polifolium*	426	0.740 ± 0.027	0.011 ± 0.033	0.13 ± 0.03	0.27 ± 0.06
Eriophyllum confertiflorum var. *confertiflorum*	478	0.751 ± 0.021	0.002 ± 0.026	0.10 ± 0.04	0.26 ± 0.06
Hesperoyucca whipplei	459	0.763 ± 0.036	0.005 ± 0.046	0.11 ± 0.04	0.30 ± 0.12

Table 6—Model performance metrics (mean ± standard deviation) for focal taxa (continued)

Scientific name	N	AUC_{test} [a]	AUC_{diff} [b]	OR_{10P} [c]	OR_{mSSS} [d]
Heteromeles arbutifolia	361	0.836 ± 0.012	0.002 ± 0.015	0.11 ± 0.03	0.20 ± 0.03
Lepidospartum squamatum	338	0.757 ± 0.041	0.016 ± 0.050	0.14 ± 0.07	0.33 ± 0.10
Malacothamnus fasciculatus var. *fasciculatus*	346	0.789 ± 0.018	0.007 ± 0.021	0.12 ± 0.03	0.21 ± 0.09
Malosma laurina	365	0.871 ± 0.007	-0.003 ± 0.008	0.12 ± 0.04	0.11 ± 0.05
Phacelia minor	282	0.801 ± 0.025	0.009 ± 0.030	0.12 ± 0.03	0.36 ± 0.14
Plantago erecta	274	0.830 ± 0.018	0.008 ± 0.021	0.12 ± 0.07	0.21 ± 0.07
Prunus ilicifolia subsp. *ilicifolia*	377	0.751 ± 0.019	0.010 ± 0.021	0.13 ± 0.03	0.29 ± 0.01
Quercus berberidifolia	386	0.782 ± 0.018	0.010 ± 0.020	0.11 ± 0.03	0.19 ± 0.07
Rhamnus crocea	229	0.815 ± 0.025	0.015 ± 0.030	0.13 ± 0.12	0.15 ± 0.13
Rhamnus ilicifolia	471	0.766 ± 0.021	0.007 ± 0.027	0.13 ± 0.03	0.27 ± 0.13
Rhus ovata	512	0.798 ± 0.037	-0.003 ± 0.043	0.11 ± 0.07	0.22 ± 0.08
Salvia apiana	435	0.752 ± 0.012	0.013 ± 0.016	0.12 ± 0.06	0.22 ± 0.07
Salvia mellifera	470	0.838 ± 0.025	-0.005 ± 0.030	0.13 ± 0.06	0.23 ± 0.07
Stipa pulchra	187	0.831 ± 0.014	0.020 ± 0.017	0.11 ± 0.05	0.28 ± 0.10

N = total number of taxon occurrences.

[a] AUC_{test} = area under the receiver operator curve for the test data.

[b] AUC_{diff} = difference between the calibration and test AUC.

[c] OR_{10P} = omission rate at the 10 percent test threshold.

[d] OR_{mSSS} = omission rate at the maximum sensitivity plus specificity threshold.

Table 7—Relative significance of individual environmental variables to Maxent models measured as percentage of permutation importance

Scientific name	AET	CWD	PPTSEAS	PPTSUMMER	PPTWINTER	TSEAS	TMIN	TMAX	GEOL
Acmispon glaber var. *brevialatus*	2	3	7	15	3	**38**	5	25	2
Acmispon glaber var. *glaber*	2	21	13	12	2	4	**38**	4	5
Adenostoma fasciculatum var. *fasciculatum*	5	14	19	0	20	5	**25**	9	4
Arctostaphylos glandulosa subsp. *cushingiana*	0	**67**	0	12	2	6	8	0	5
Arctostaphylos glandulosa subsp. *glandulosa*	10	**21**	8	1	13	7	**21**	2	16
Arctostaphylos glandulosa subsp. *mollis*	0	20	0	2	**27**	23	14	12	2
Arctostaphylos glauca	2	**26**	9	5	19	14	17	0	8
Artemisia californica	1	9	7	7	3	**41**	23	8	2
Ceanothus crassifolius var. *crassifolius*	0	6	24	11	4	8	**25**	15	8
Ceanothus cuneatus var. *cuneatus*	24	6	7	14	**27**	5	10	5	2
Ceanothus leucodermis	1	19	2	5	**37**	16	9	3	9
Ceanothus megacarpus var. *megacarpus*	4	8	1	9	17	**38**	13	1	9
Ceanothus oliganthus	5	26	1	1	**33**	7	23	2	3
Ceanothus perplexans	4	25	**24**	2	8	6	22	10	1
Ceanothus tomentosus	10	23	4	4	0	**35**	15	7	2
Ceanothus vestitus	6	5	3	11	6	22	**27**	20	1
Cercocarpus betuloides var. *betuloides*	4	16	7	**29**	10	12	16	2	4
Corethrogyne filaginifolia	4	**36**	8	3	9	13	4	14	8
Deinandra fasciculata	5	1	4	10	3	**63**	3	2	9
Encelia californica	0	5	7	17	1	**54**	13	0	4
Encelia farinosa	5	9	11	5	2	8	14	**43**	4
Eriodictyon crassifolium var. *crassifolium*	16	**25**	2	12	0	12	19	12	2
Eriodictyon crassifolium var. *nigrescens*	1	**22**	0	41	11	6	2	4	13
Eriodictyon trichocalyx var. *lanatum*	3	21	**40**	0	0	9	16	1	10
Eriodictyon trichocalyx var. *trichocalyx*	13	8	22	**24**	7	6	5	6	10
Eriogonum fasciculatum var. *fasciculatum*	4	20	13	10	1	**20**	27	4	1
Eriogonum fasciculatum var. *foliolosum*	2	11	9	4	8	**36**	22	5	3
Eriogonum fasciculatum var. *polifolium*	3	**35**	6	16	2	10	11	14	2
Eriophyllum confertiflorum var. *confertiflorum*	3	**37**	19	6	8	15	6	1	5
Hesperoyucca whipplei	**40**	3	9	4	12	1	10	17	3

Table 7—Relative significance of individual environmental variables to Maxent models measured as percentage of permutation importance (continued)

Scientific name	AET	CWD	PPTSEAS	PPTSUMMER	PPTWINTER	TSEAS	TMIN	TMAX	GEOL
Heteromeles arbutifolia	2	22	7	3	3	22	**34**	1	6
Lepidospartum squamatum	11	1	**33**	15	4	10	7	9	12
Malacothamnus fasciculatus var. *fasciculatus*	0	0	7	1	1	**77**	2	4	7
Malosma laurina	7	15	4	2	1	**43**	19	6	3
Phacelia minor	7	11	18	18	0	14	4	**21**	7
Plantago erecta	1	0	2	7	20	**55**	7	1	8
Prunus ilicifolia subsp. *ilicifolia*	1	6	2	7	**23**	18	19	9	14
Quercus berberidifolia	3	10	1	12	24	8	**29**	6	7
Rhamnus crocea	1	1	13	2	3	**56**	5	16	3
Rhamnus ilicifolia	1	**28**	7	9	14	0	25	2	13
Rhus ovata	5	14	8	15	8	18	12	**19**	1
Salvia apiana	2	0	18	8	13	**31**	12	13	3
Salvia mellifera	8	4	8	2	2	**31**	30	4	11
Stipa pulchra	15	4	2	8	**26**	14	7	4	19

Environmental variables: AET = actual evapotranspiration; CWD = climatic water deficit; PPTSEAS = precipitation seasonality; PPTSUMMER = precipitation of warmest quarter; PPTWINTER = precipitation of coldest quarter; TSEAS, temperature seasonality; TMIN = winter minimum temperature over the coldest months (December through February); TMAX = summer maximum temperature over the warmest months (June through August); GEOL = soil parent geology.

Bold font = variable with greatest permutation importance.

Table 8—Percentage of change in suitable habitat under projected midcentury (2040–2069) climate conditions relative to baseline (1951–1980) suitable habitat for each of five climate scenarios

	CCSM4			CNRM			FGOALS			IPSL			MIROC		
Scientific name	**S**	**L**	**G**	**S**	**L**	**G**	**S**	**L**	**G**	**S**	**L**	**G**	**S**	**L**	**G**
Acmispon glaber var. *brevialatus*	98	2	32	65	35	13	74	26	28	83	17	28	83	17	26
Acmispon glaber var. *glaber*	39	61	0	1	99	0	6	94	0	56	44	4	58	42	23
Adenostoma fasciculatum var. *fasciculatum*	100	0	34	53	47	6	99	1	18	100	0	44	97	3	27
Arctostaphylos glandulosa subsp. *cushingiana*	45	55	3	58	42	9	29	71	0	52	48	6	33	67	1
Arctostaphylos glandulosa subsp. *glandulosa*	95	5	16	17	83	0	69	31	3	78	22	6	72	28	9
Arctostaphylos glandulosa subsp. *mollis*	69	31	2	91	9	38	62	38	1	74	26	4	49	51	1
Arctostaphylos glauca	75	25	2	96	4	14	64	36	1	62	38	7	41	59	8
Artemisia californica	100	0	88	96	4	80	97	3	37	100	0	84	100	0	64
Ceanothus crassifolius var. *crassifolius*	100	0	111	100	0	219	100	0	93	100	0	92	93	7	20
Ceanothus cuneatus var. *cuneatus*	59	41	12	56	44	21	50	50	13	82	18	53	27	73	46
Ceanothus leucodermis	87	13	9	91	9	15	77	23	5	63	37	9	35	65	3
Ceanothus megacarpus var. *megacarpus*	85	15	5	100	0	67	58	42	3	80	20	3	80	20	2
Ceanothus oliganthus	82	18	22	91	9	37	66	34	20	64	36	17	31	69	13
Ceanothus perplexans	63	37	10	1	99	0	67	33	9	44	56	9	48	52	16
Ceanothus tomentosus	98	2	61	50	50	1	89	11	41	79	21	14	90	10	53
Ceanothus vestitus	41	59	0	47	53	0	43	57	0	33	67	5	26	74	3
Cercocarpus betuloides var. *betuloides*	98	2	15	100	0	50	86	14	27	87	13	6	53	47	3
Corethrogyne filaginifolia	50	50	0	28	72	0	21	79	0	47	53	0	32	68	0
Deinandra fasciculata	68	32	0	11	89	0	40	60	0	86	14	7	93	7	24
Encelia californica	97	3	8	33	67	0	65	35	0	100	0	42	100	0	96
Encelia farinosa	88	12	148	84	16	95	95	5	170	79	21	175	81	19	162
Eriodictyon crassifolium var. *crassifolium*	92	8	80	81	19	42	85	15	90	90	10	57	91	9	59
Eriodictyon crassifolium var. *nigrescens*	48	52	1	60	40	4	34	66	1	84	16	7	54	46	9
Eriodictyon trichocalyx var. *lanatum*	15	85	0	0	100	0	34	66	2	13	87	0	64	36	21
Eriodictyon trichocalyx var. *trichocalyx*	85	15	60	91	9	181	64	36	102	76	24	15	27	73	10
Eriogonum fasciculatum var. *fasciculatum*	81	19	6	8	92	3	21	79	0	98	2	31	100	0	68
Eriogonum fasciculatum var. *foliolosum*	100	0	20	84	16	4	85	15	5	100	0	24	98	2	15
Eriogonum fasciculatum var. *polifolium*	95	5	17	79	21	19	62	38	26	84	16	10	64	36	4

Table 8—Percentage of change in suitable habitat under projected midcentury (2040–2069) climate conditions relative to baseline (1951–1980) suitable habitat for each of five climate scenarios (continued)

	CCSM4			CNRM			FGOALS			IPSL			MIROC		
Scientific name	**S**	**L**	**G**	**S**	**L**	**G**	**S**	**L**	**G**	**S**	**L**	**G**	**S**	**L**	**G**
Eriophyllum confertiflorum var. *confertiflorum*	47	53	0	4	96	0	12	88	0	58	42	0	58	42	1
Hesperoyucca whipplei	100	0	64	88	12	41	81	19	49	100	0	94	97	3	33
Heteromeles arbutifolia	100	0	56	69	31	3	97	3	42	99	1	46	98	2	46
Lepidospartum squamatum	96	4	71	100	0	329	86	14	147	70	30	37	12	88	7
Malacothamnus fasciculatus var. *fasciculatus*	100	0	17	69	31	5	97	3	8	98	2	19	98	2	21
Malosma laurina	100	0	30	95	5	7	95	5	10	100	0	25	100	0	33
Phacelia minor	100	0	143	100	0	247	96	4	185	100	0	119	96	4	82
Plantago erecta	89	11	14	36	64	1	85	15	13	58	42	5	86	14	47
Prunus ilicifolia subsp. *ilicifolia*	100	0	30	99	1	34	87	13	21	94	6	24	57	43	11
Quercus berberidifolia	100	0	32	96	4	44	100	0	32	100	0	26	75	25	11
Rhamnus crocea	95	5	28	2	98	0	68	32	2	97	3	51	99	1	60
Rhamnus ilicifolia	85	15	15	99	1	45	72	28	19	72	28	16	32	68	15
Rhus ovata	99	1	55	95	5	48	85	15	55	99	1	48	96	4	28
Salvia apiana	100	0	54	48	52	15	93	7	41	99	1	49	100	0	51
Salvia mellifera	100	0	66	97	3	66	100	0	53	100	0	97	100	0	72
Stipa pulchra	81	19	8	68	32	38	94	6	32	64	36	6	72	28	23

Climate scenarios CCSM4, CNRM, FGOALS, IPSL, and MIROC represent a range of midcentury climate conditions with MIROC and CCSM4 models spanning the largest directional changes in precipitation increase and decrease, respectively (table 4, fig. 3).

Percentage of habitat change categories: S = percentage of stable suitable habitat, L = percentage of loss in suitable habitat, G = percentage of gain in suitable habitat.

Habitat suitability calculations exclude areas that have already been converted to human land uses (FRAP 2015).

Appendix 4: Baseline and Projected Midcentury Suitable Habitat Maps for Focal Species

Baseline maps illustrate areas with suitable habitat in southern California under historical (1951–1980) climate conditions. Midcentury (2040–2069) suitable habitat maps show projected changes in suitable habitat under each of five future climate scenarios relative to baseline suitable habitat. Projected change in suitable habitat is defined as stable = suitable under baseline and future conditions; loss = suitable under baseline but unsuitable under future conditions; gain = unsuitable under baseline and becoming suitable under future conditions. Climate model consensus maps show agreement in projected suitable habitat change across the five climate scenarios and range from one (no agreement) to five (full agreement). In all maps, suitable habitat that has already been converted to urban and agriculture land uses is masked in dark gray (FRAP 2015). Projections for future land use change were not included.

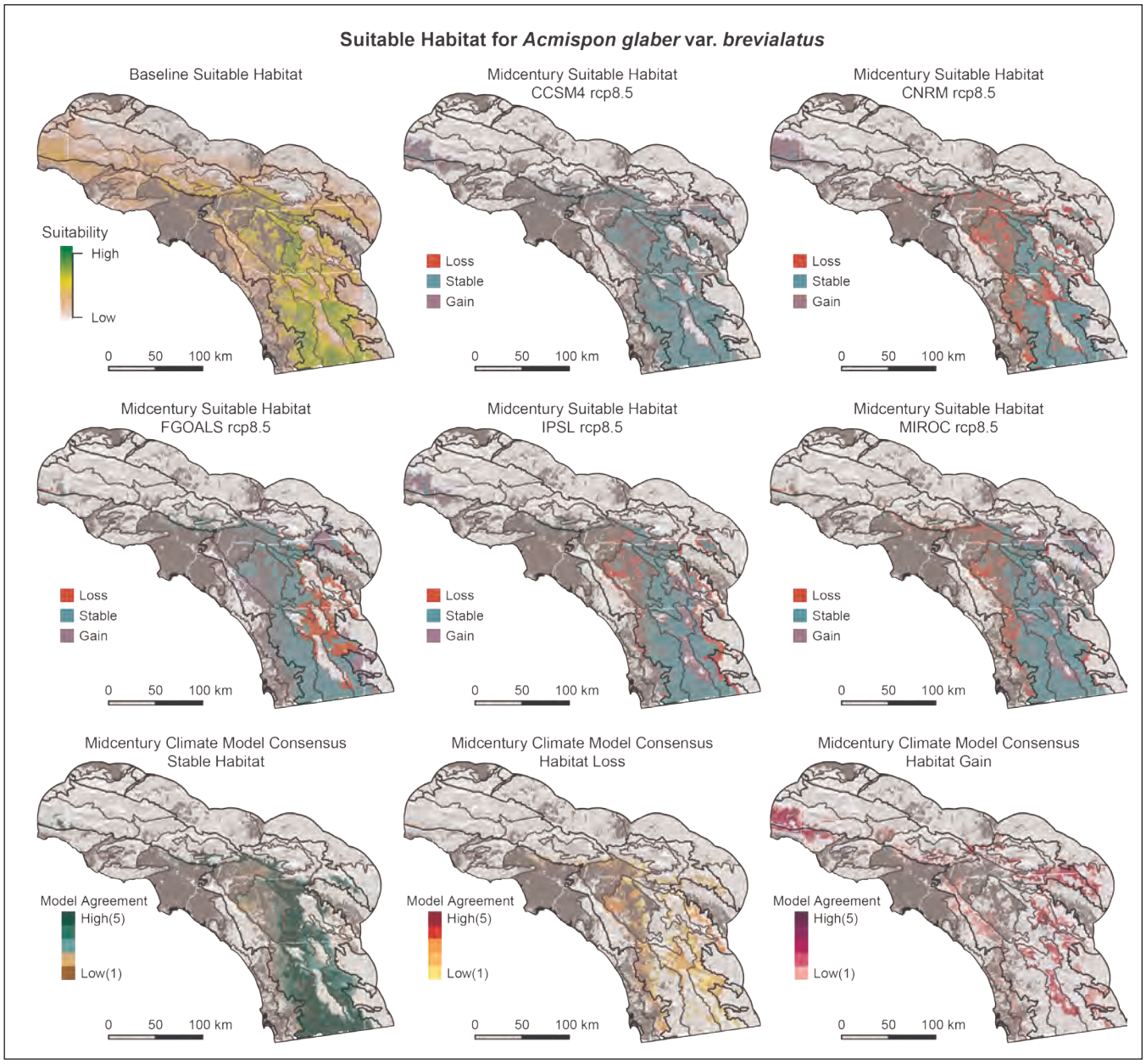

Figure 9—*Acmispon glaber* var. *brevialatus* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

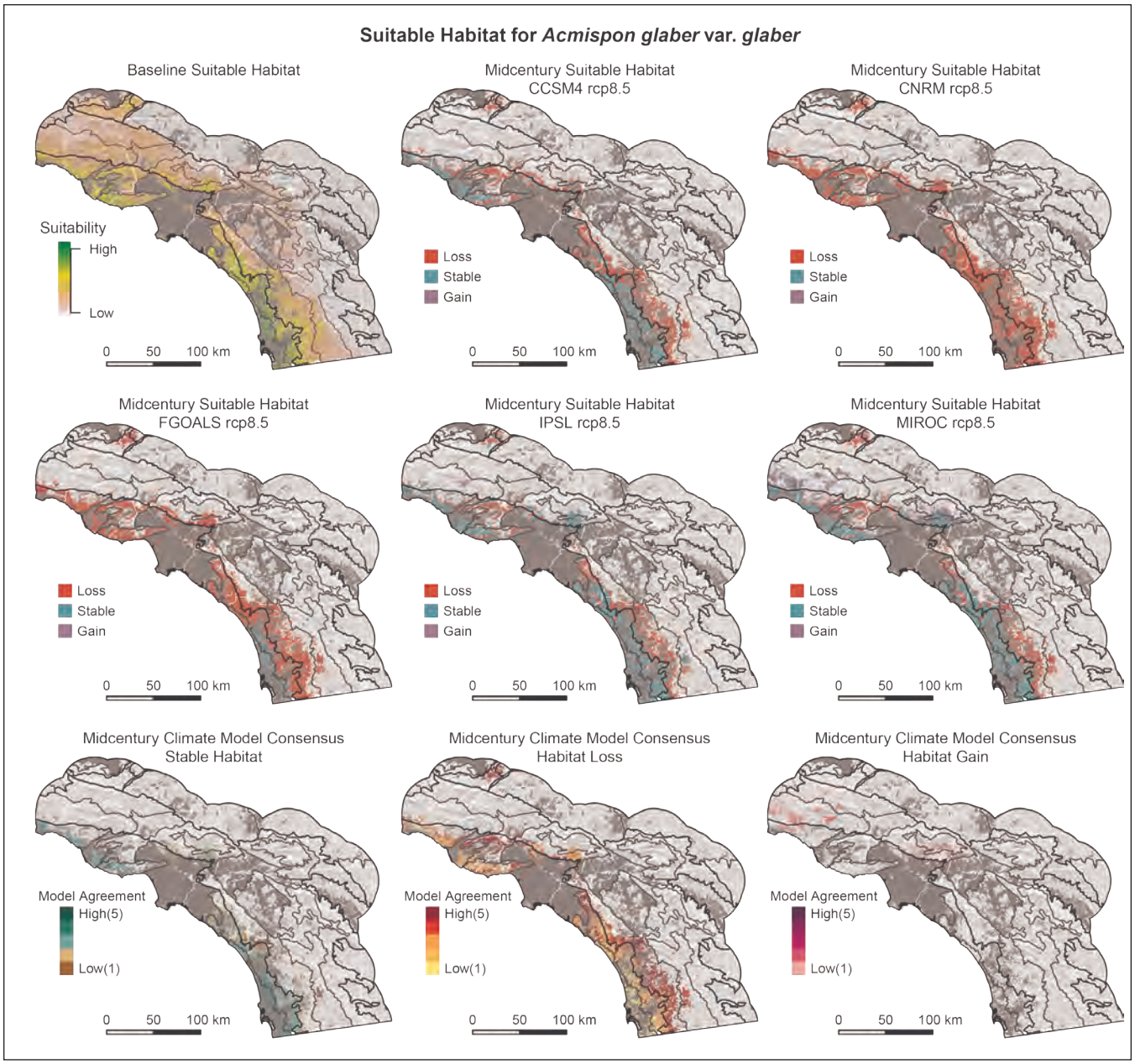

Figure 10—*Acmispon glaber* var. *glaber* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

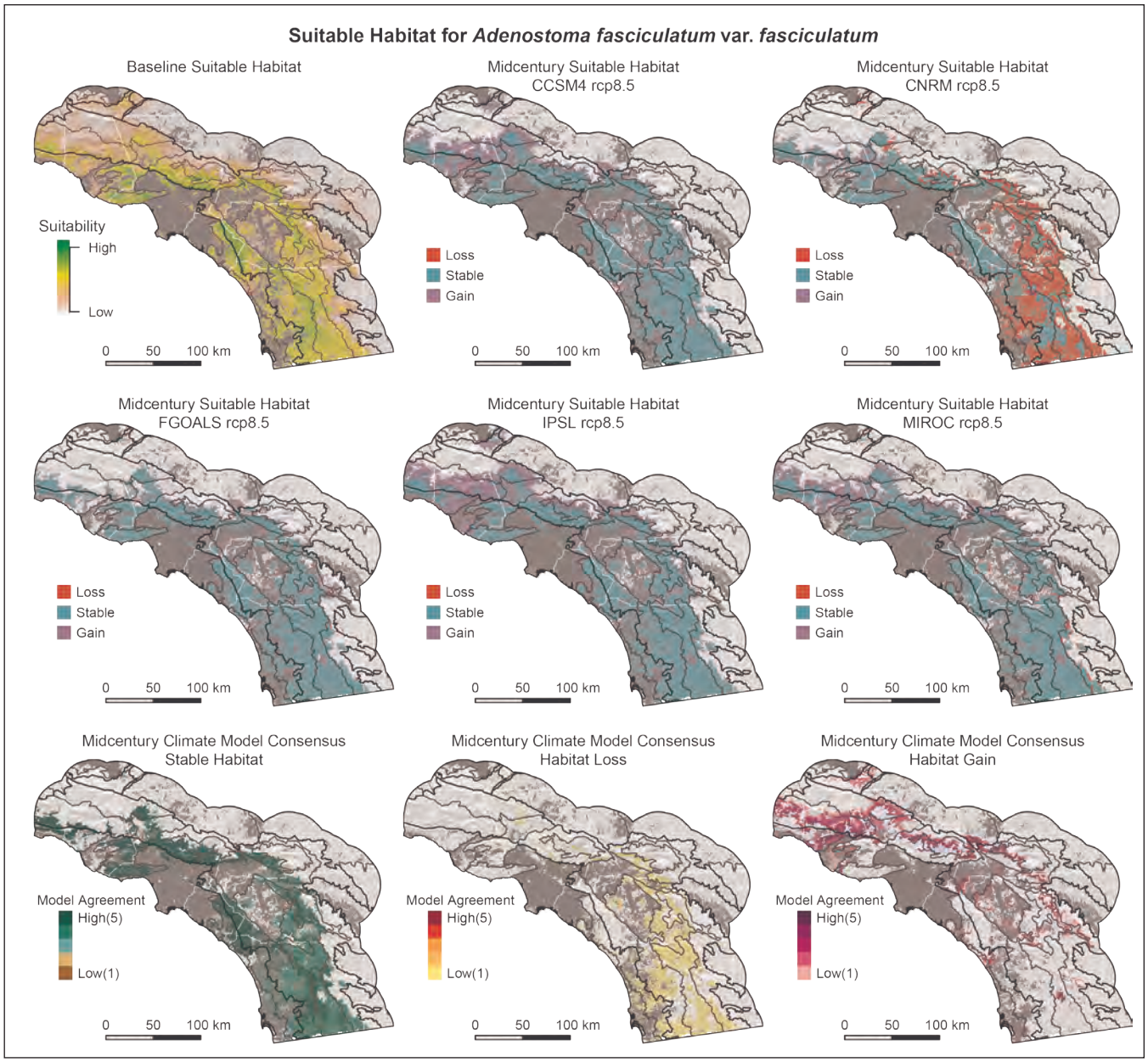

Figure 11—*Adenostoma fasciculatum* var. *fasciculatum* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

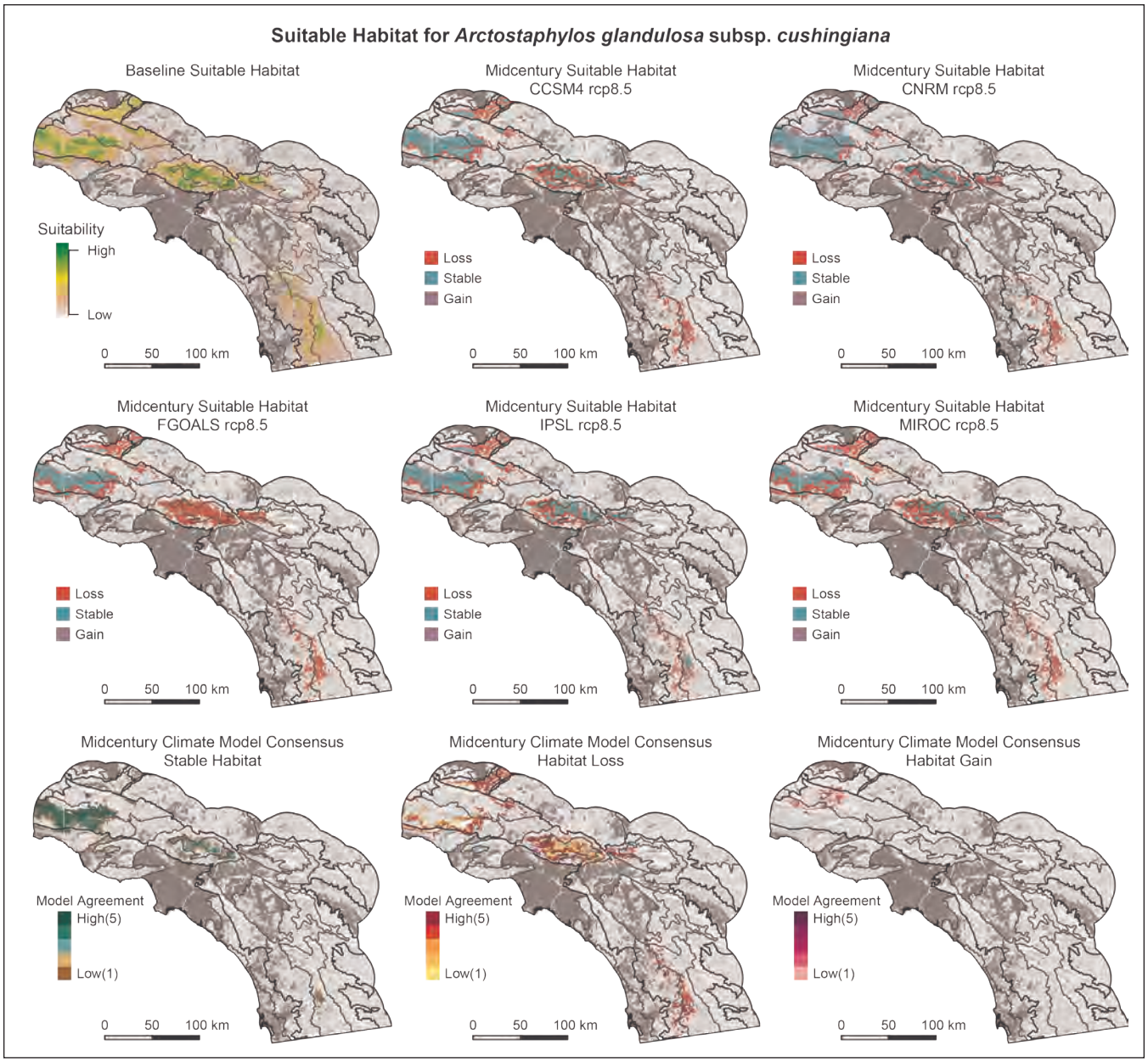

Figure 12—*Arctostaphylos glandulosa* subsp. *cushingiana* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps

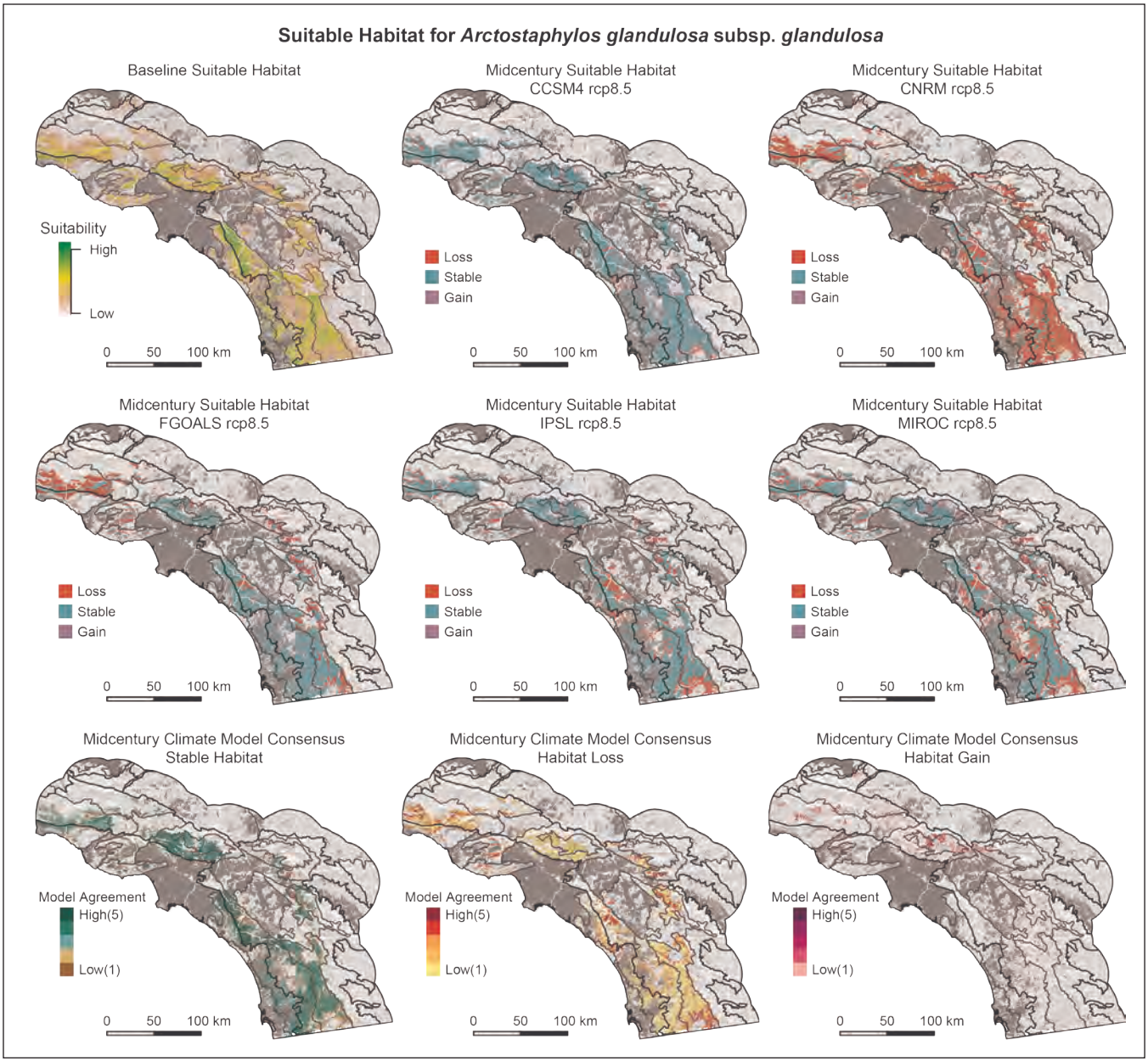

Figure 13—*Arctostaphylos glandulosa* subsp. *glandulosa* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps

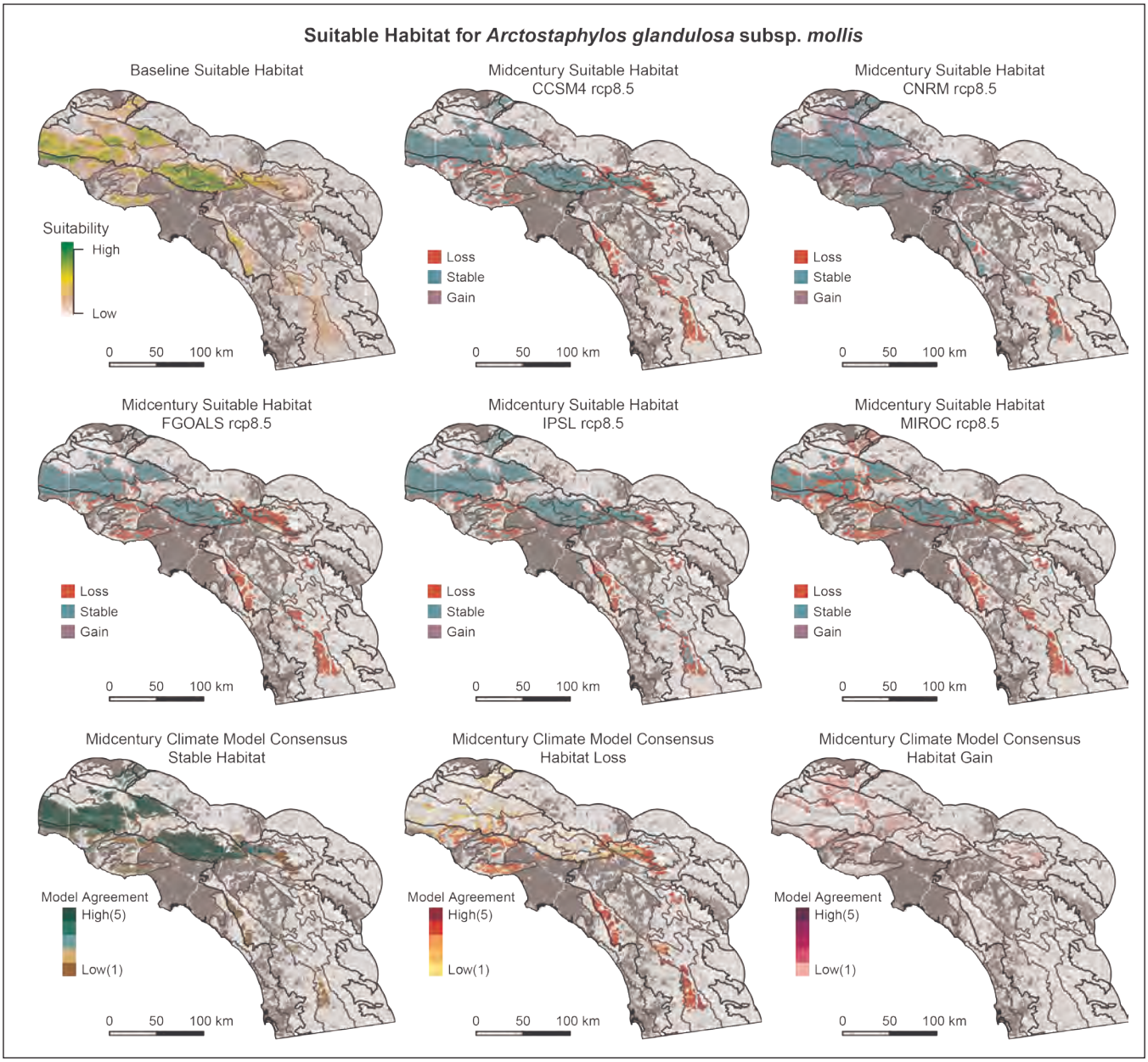

Figure 14—*Arctostaphylos glandulosa* subsp. *mollis* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

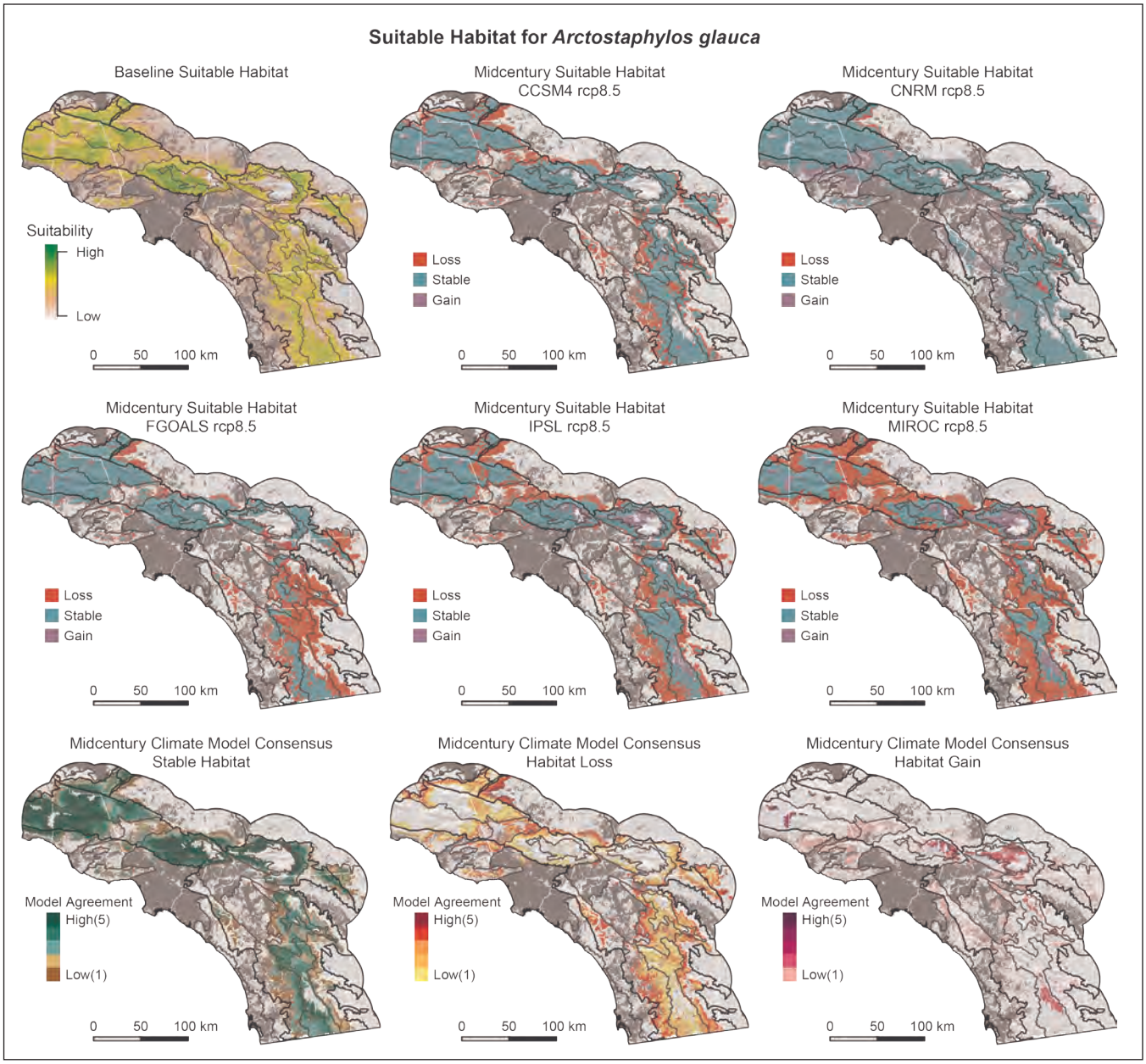

Figure 15—*Arctostaphylos glauca* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

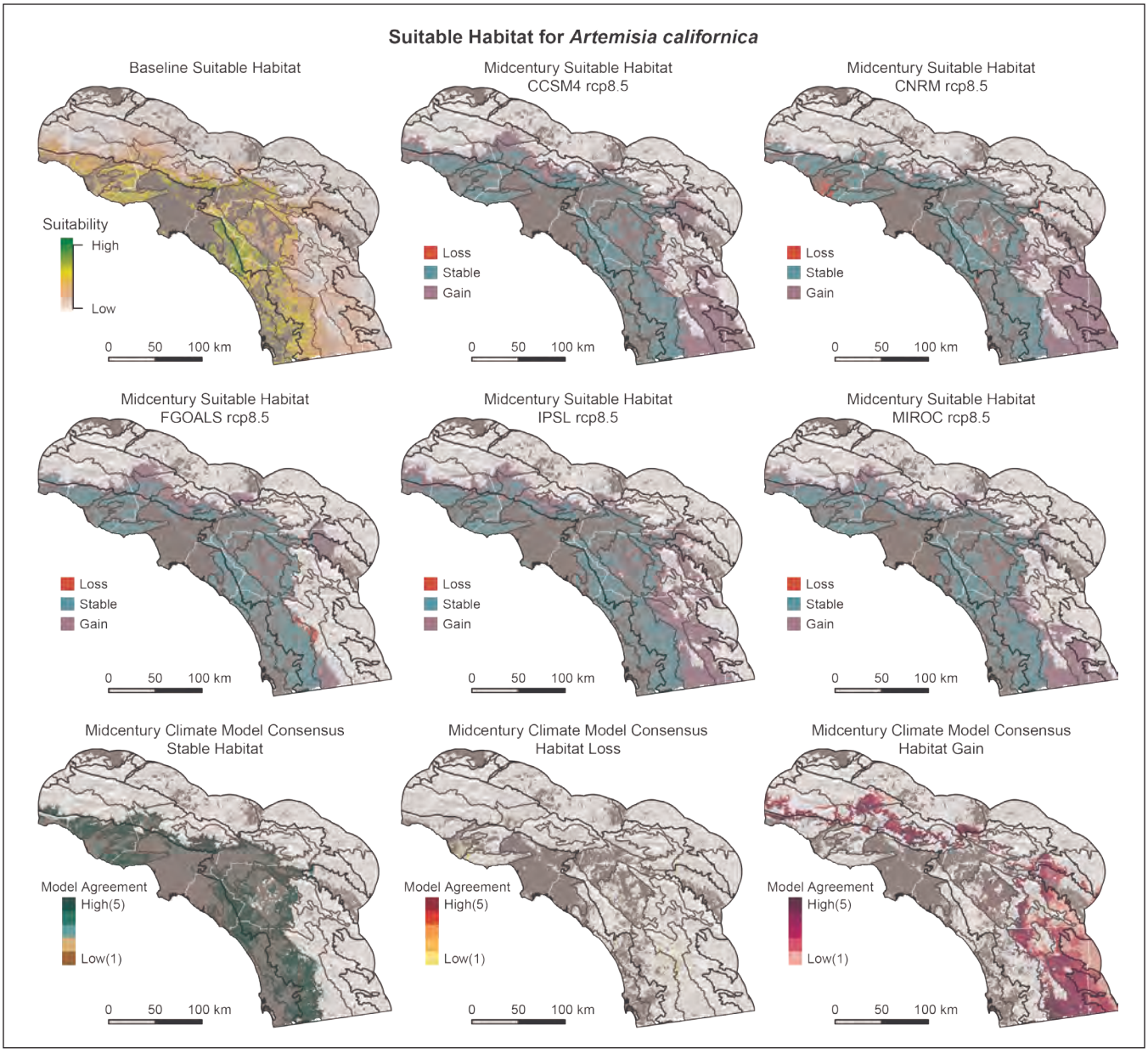

Figure 16—*Artemisia californica* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

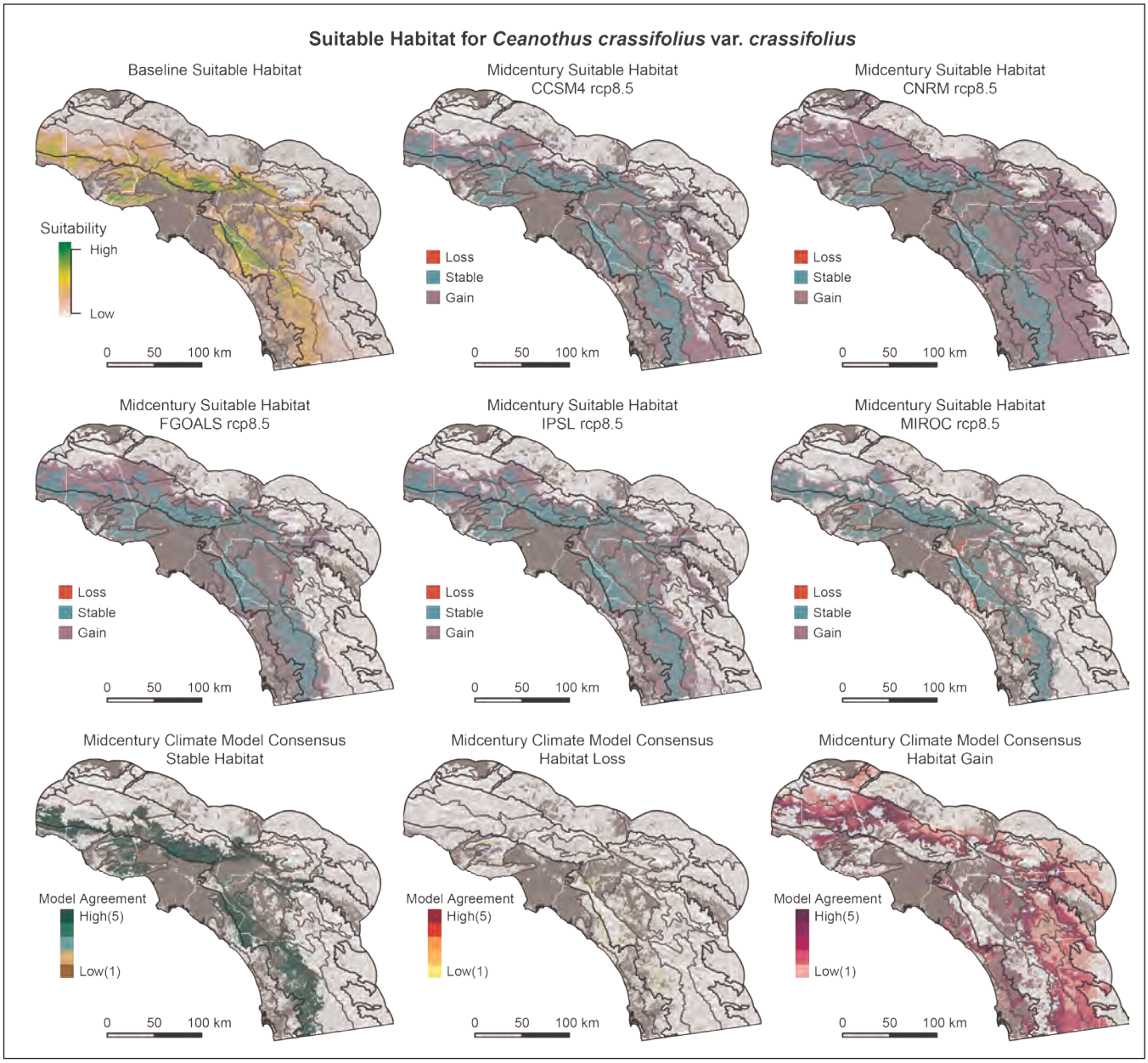

Figure 17—*Ceanothus crassifolius* var. *crassifolius* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

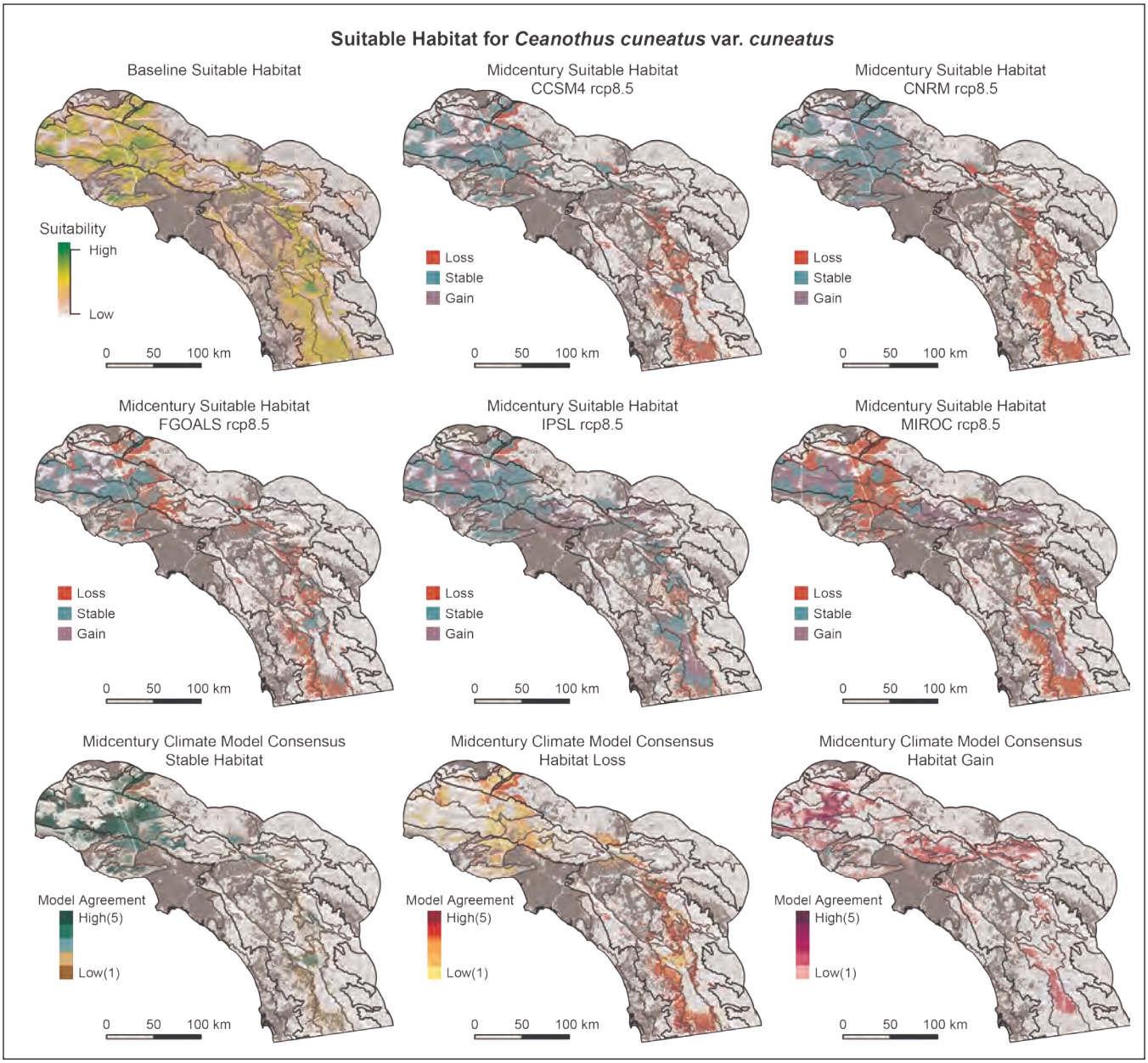

Figure 18—*Ceanothus cuneatus* var. *cuneatus* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

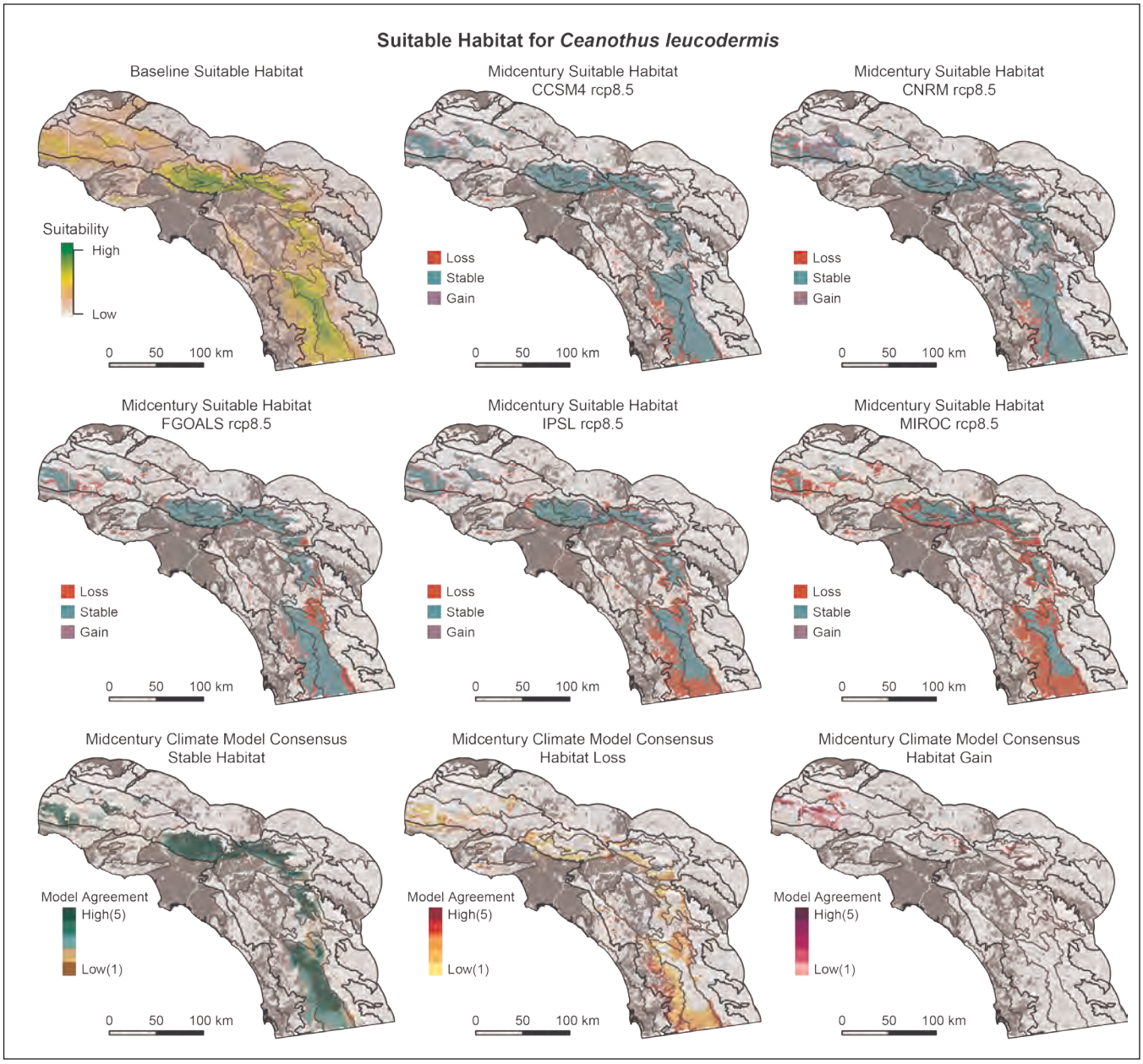

Figure 19—*Ceanothus leucodermis* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

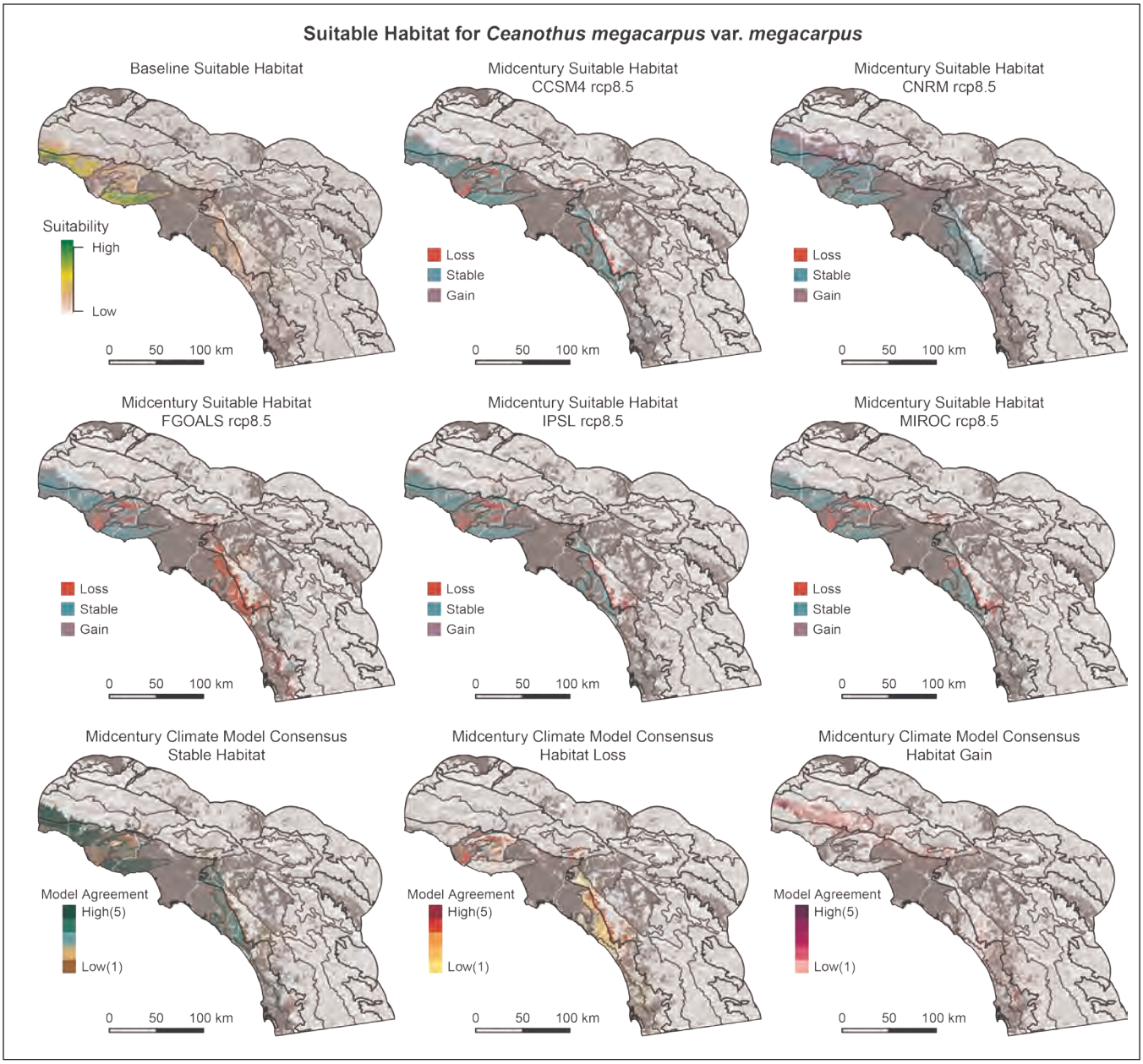

Figure 20—*Ceanothus megacarpus* var. *megacarpus* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

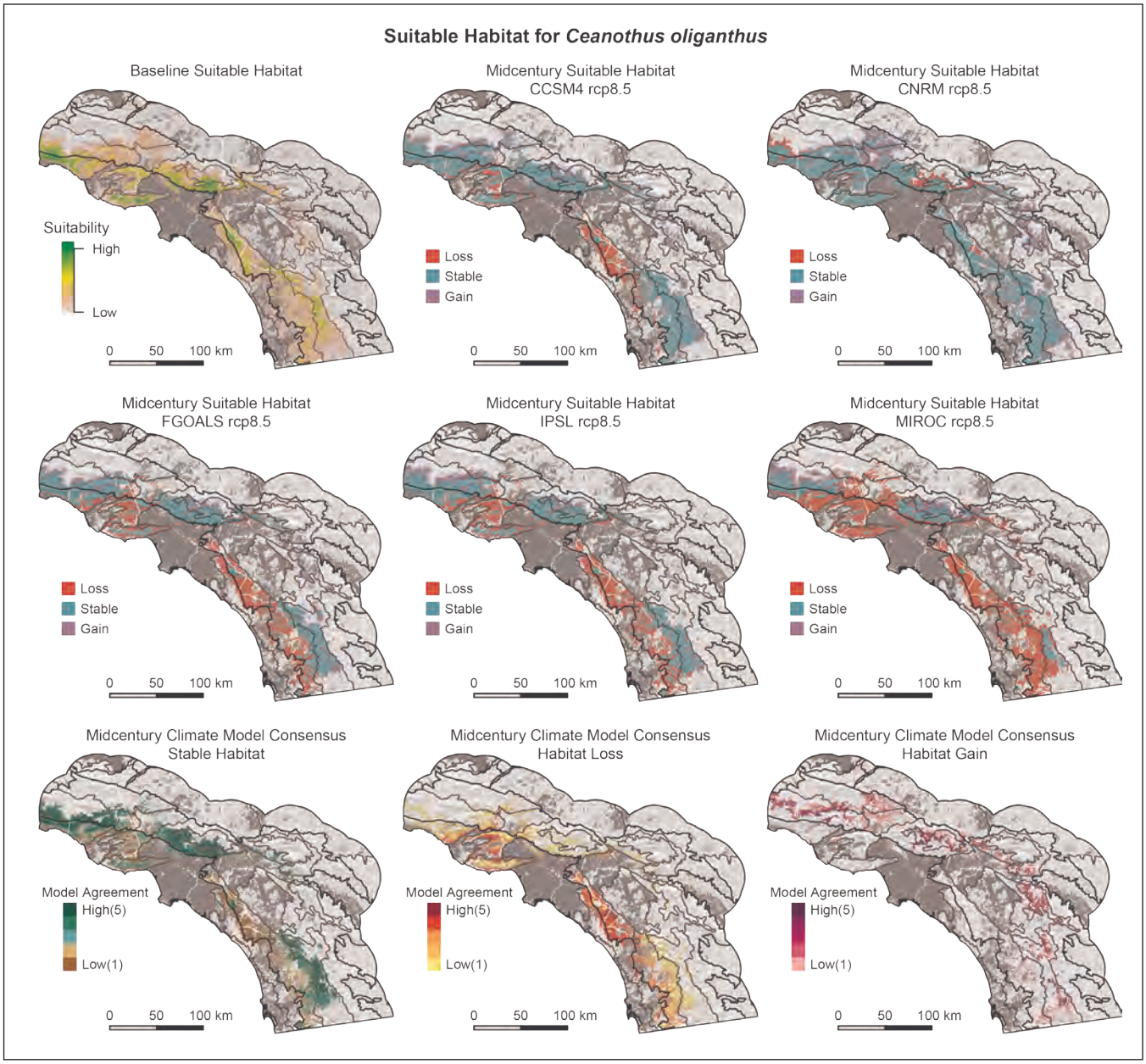

Figure 21—*Ceanothus oliganthus* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

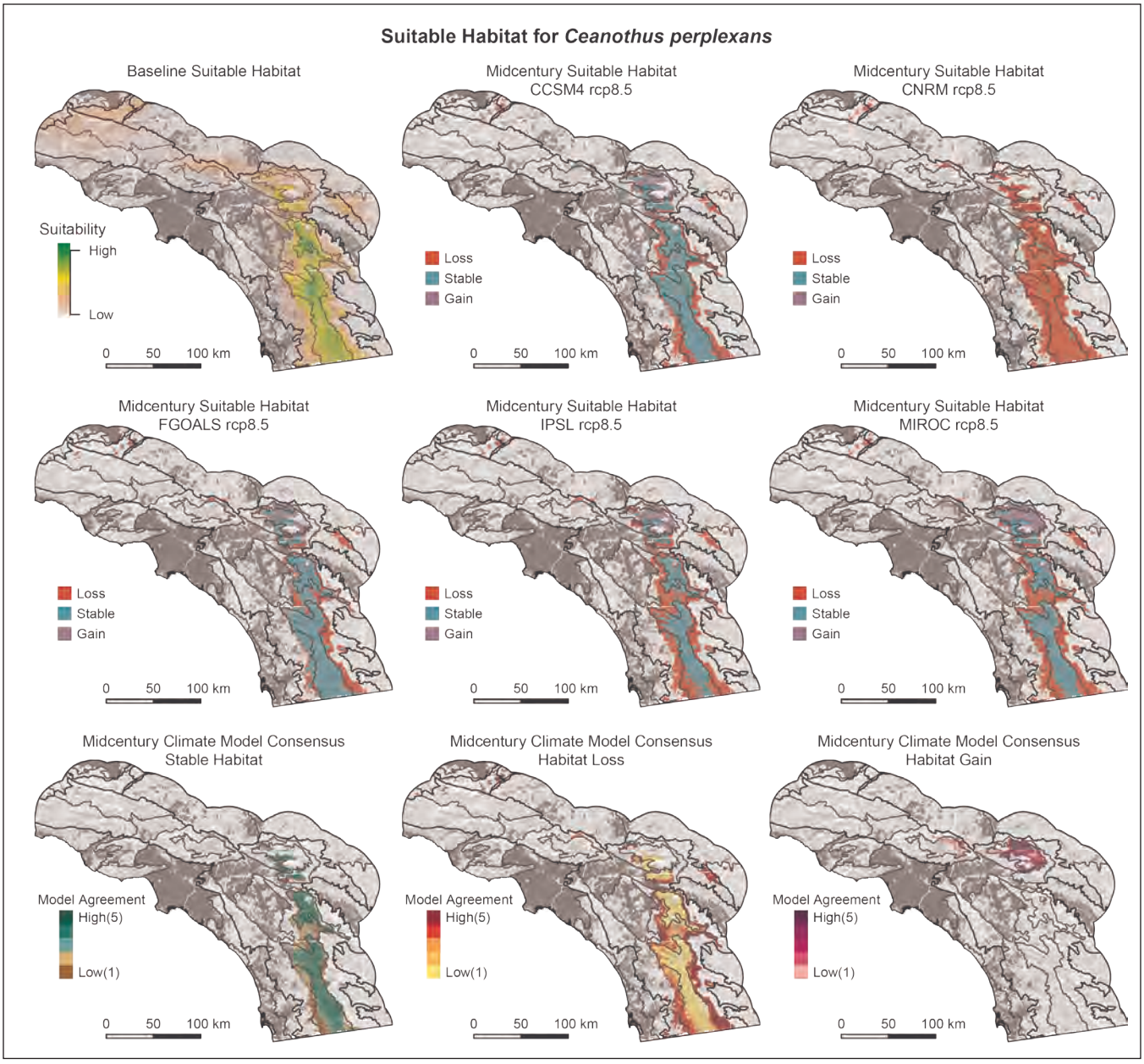

Figure 22—*Ceanothus perplexans* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

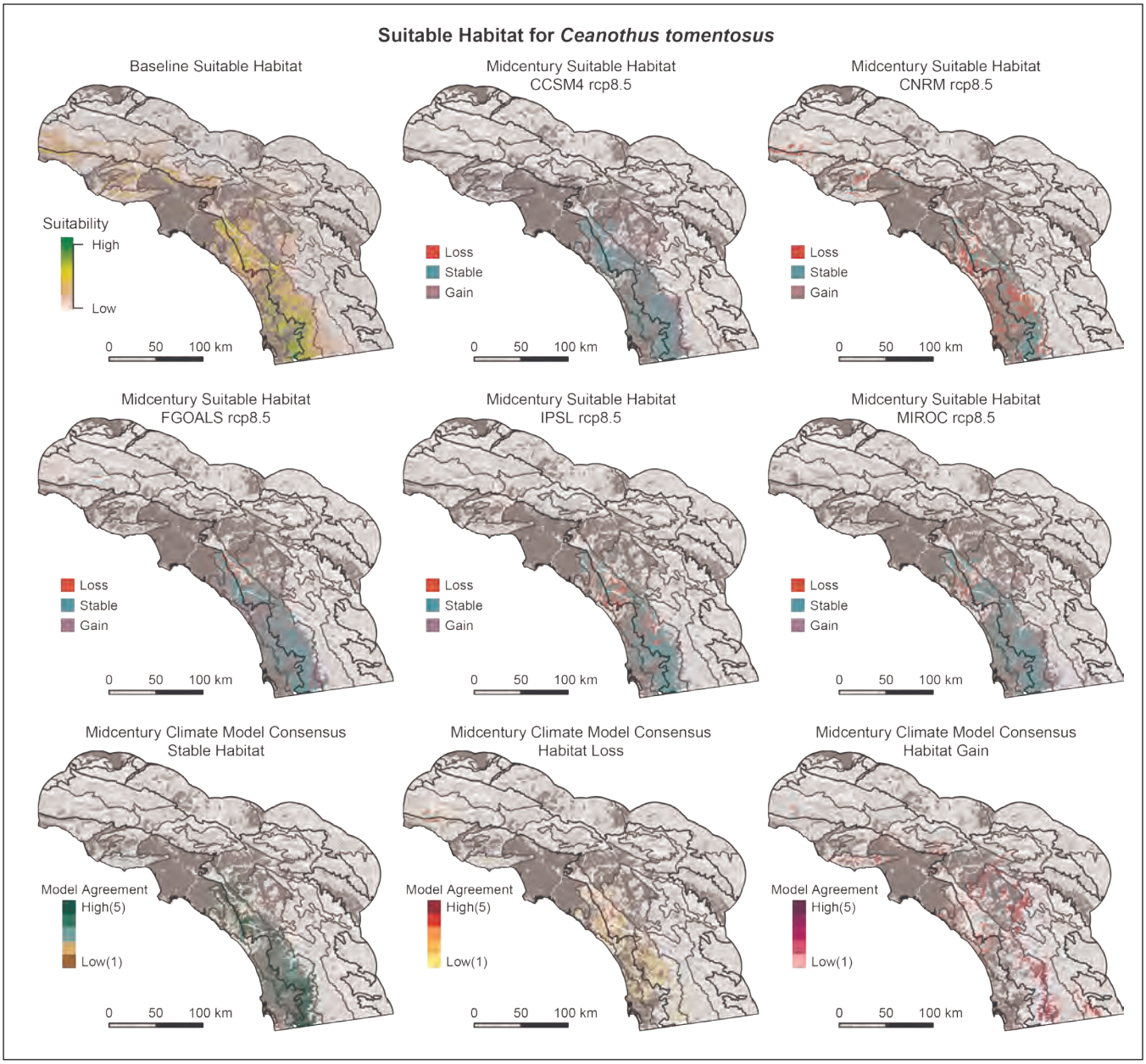

Figure 23—*Ceanothus tomentosus* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

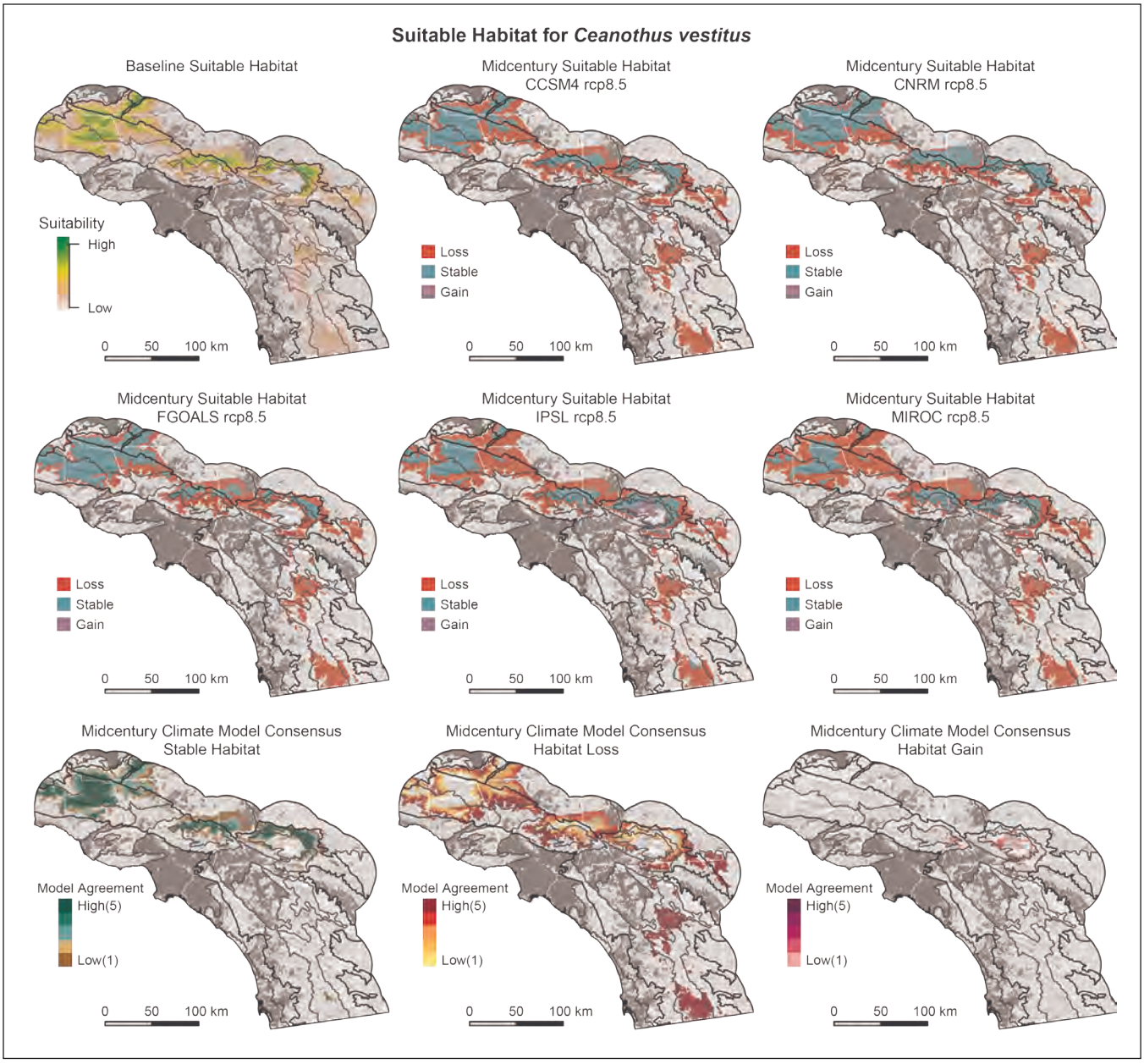

Figure 24—*Ceanothus vestitus* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

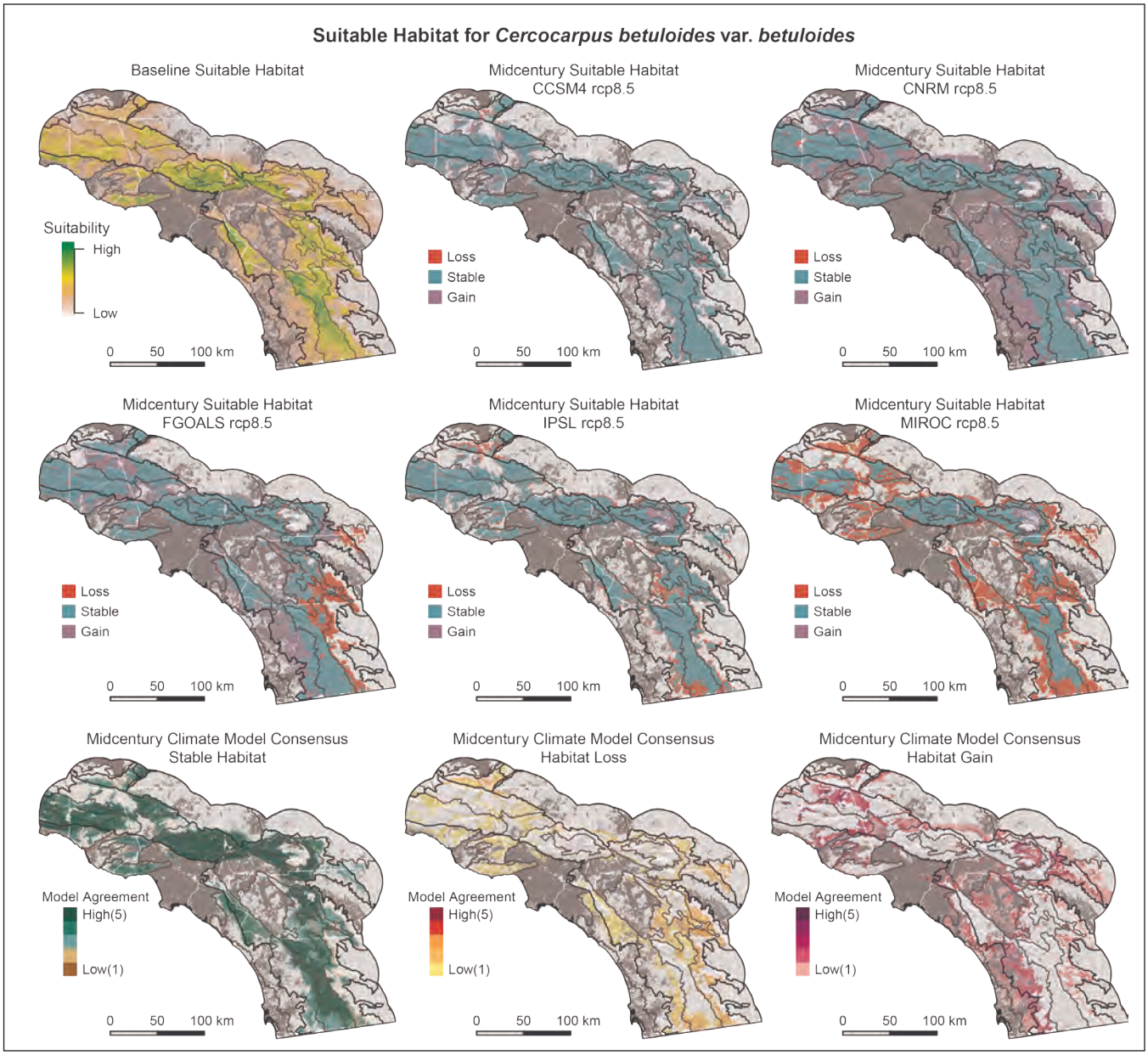

Figure 25—*Cercocarpus betuloides* var. *betuloides* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

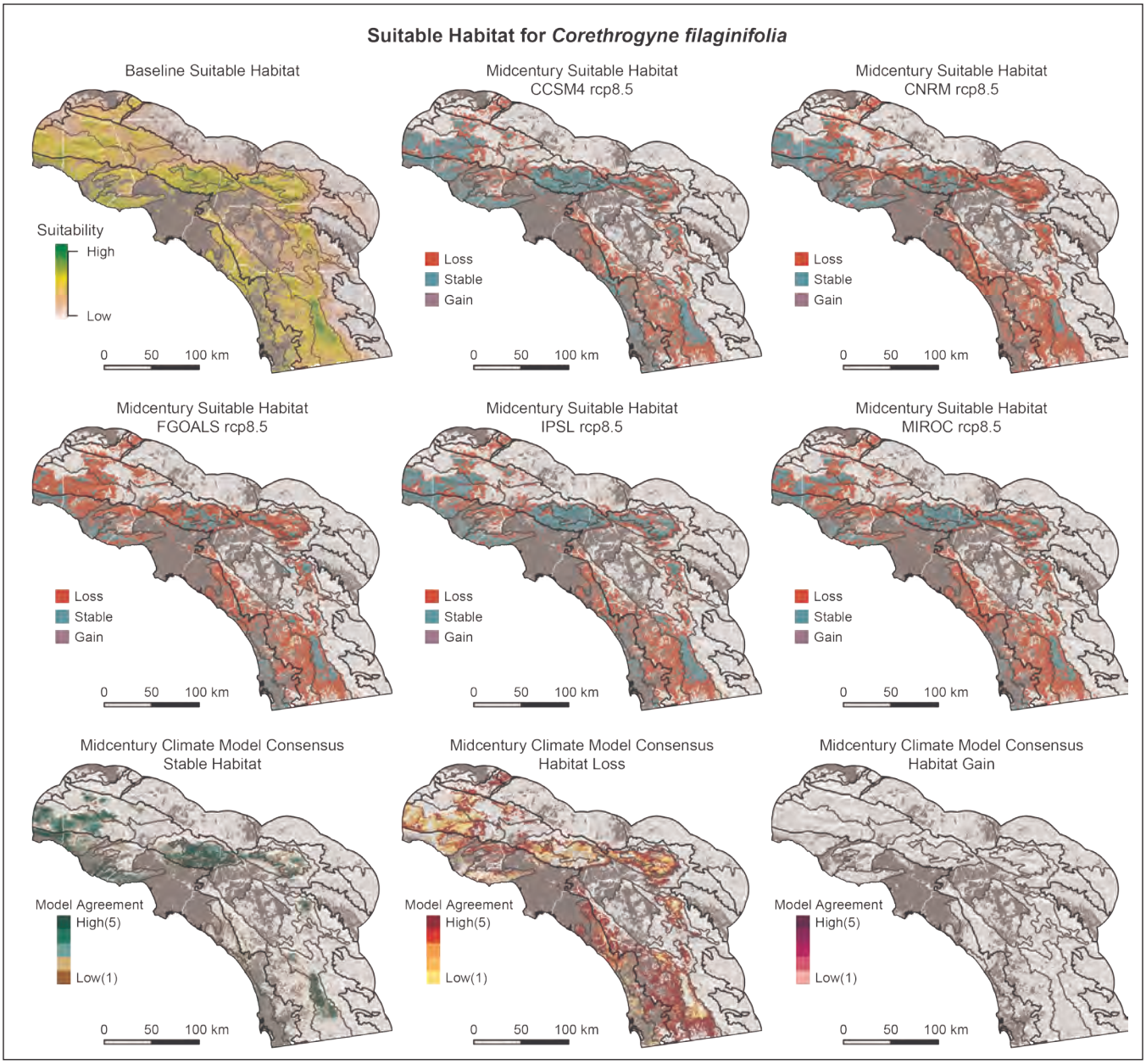

Figure 26—*Corethrogyne filaginifolia* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

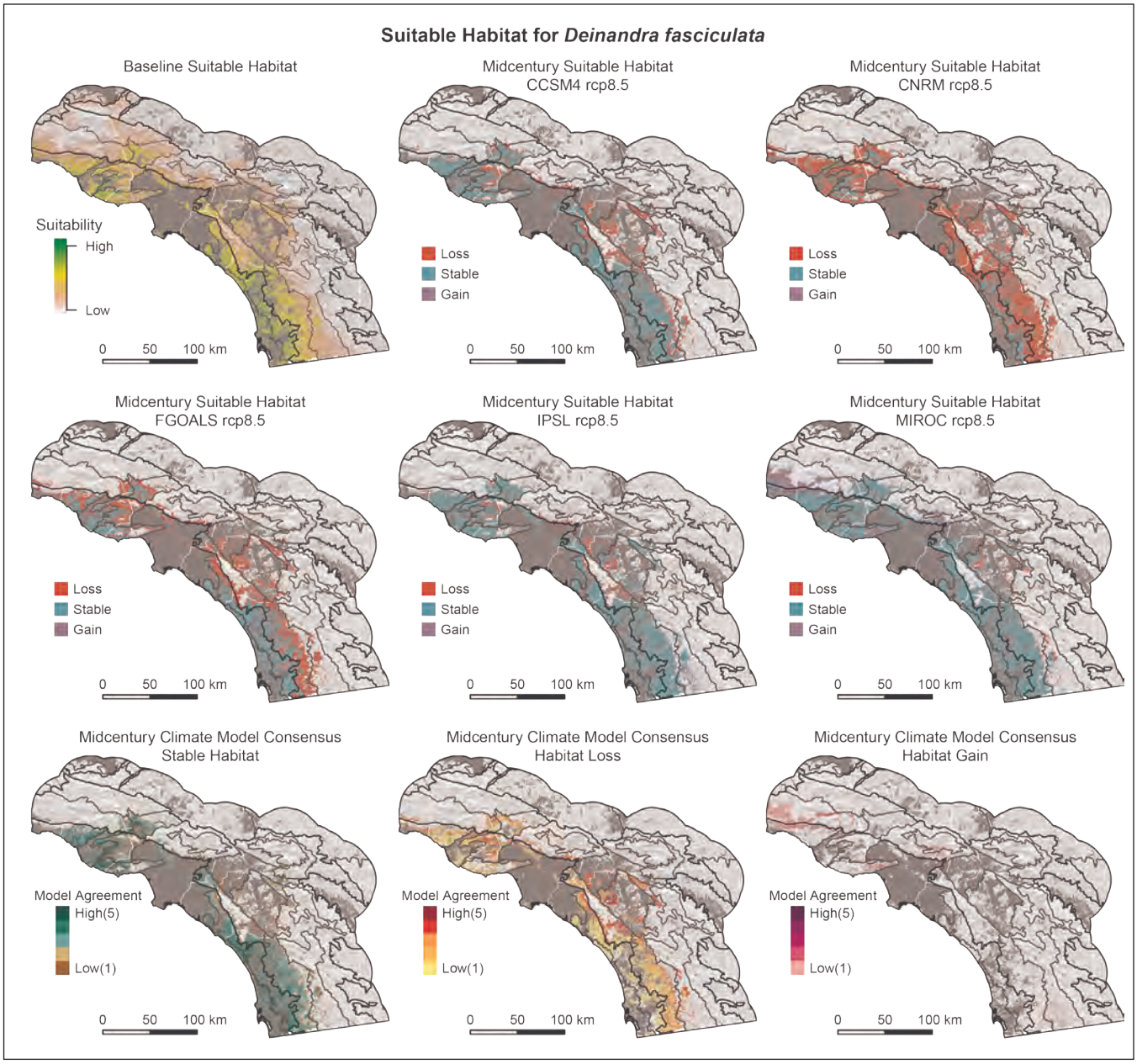

Figure 27—*Deinandra fasciculata* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

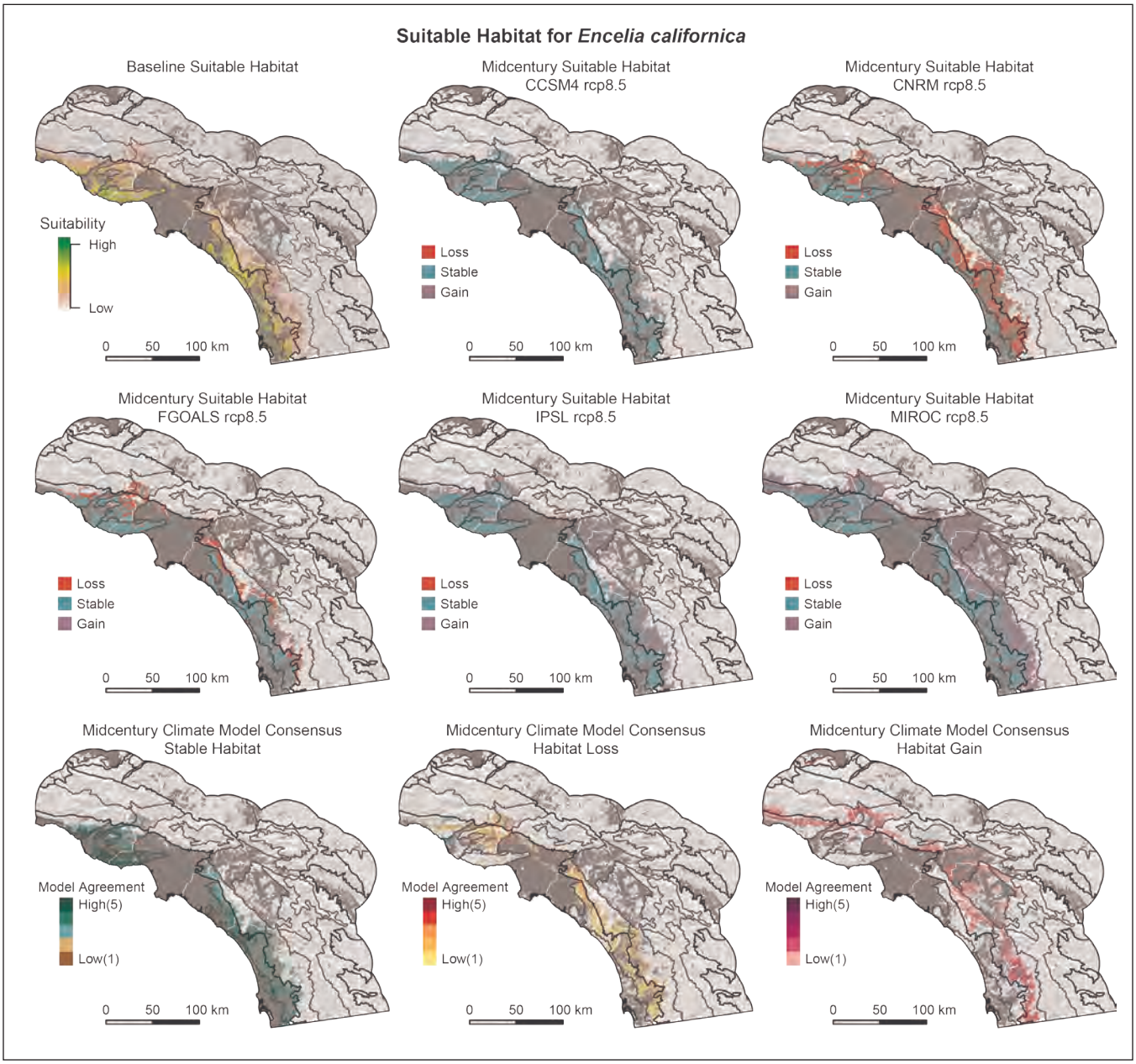

Figure 28—*Encelia californica* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

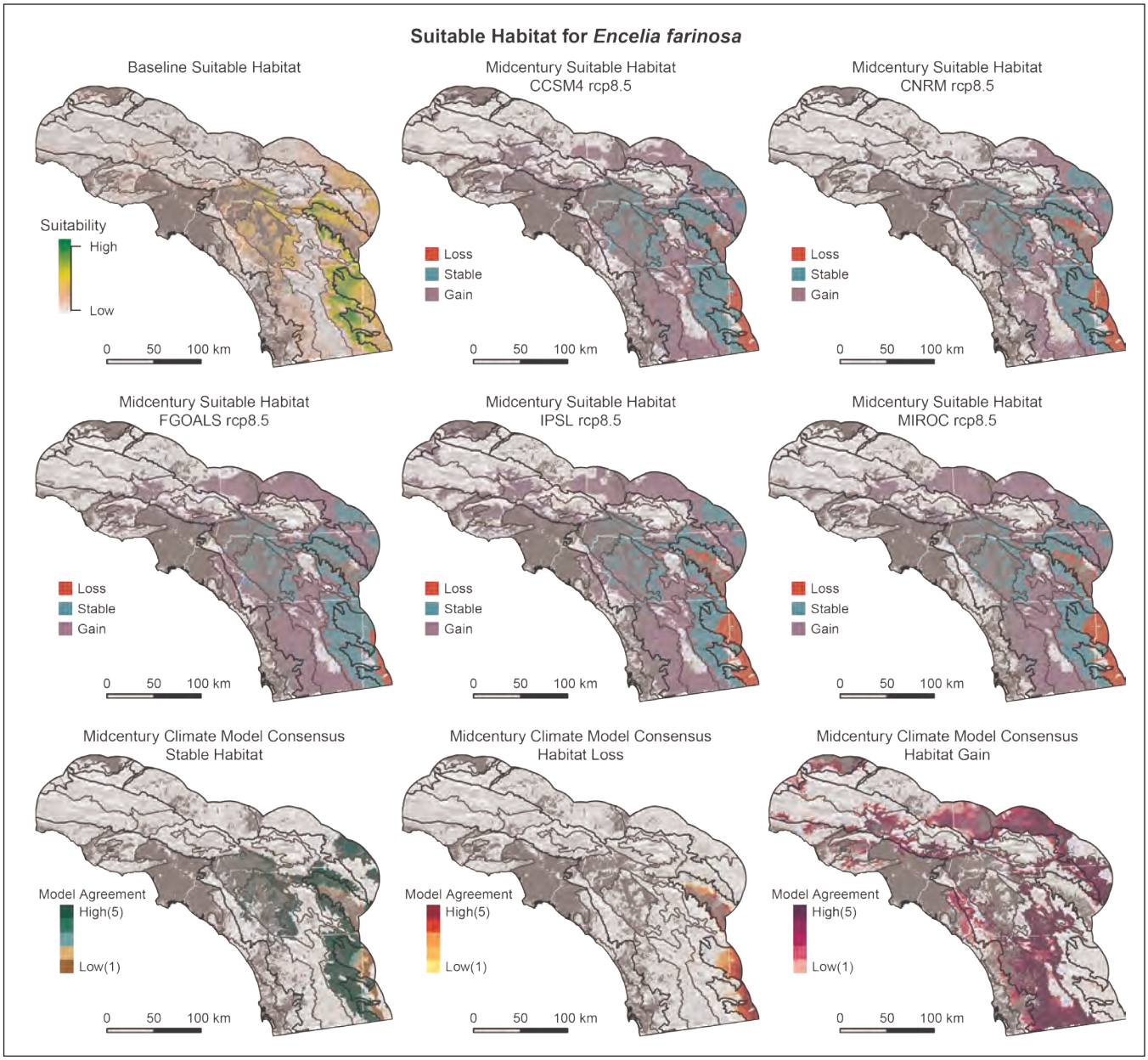

Figure 29— *Encelia farinosa* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

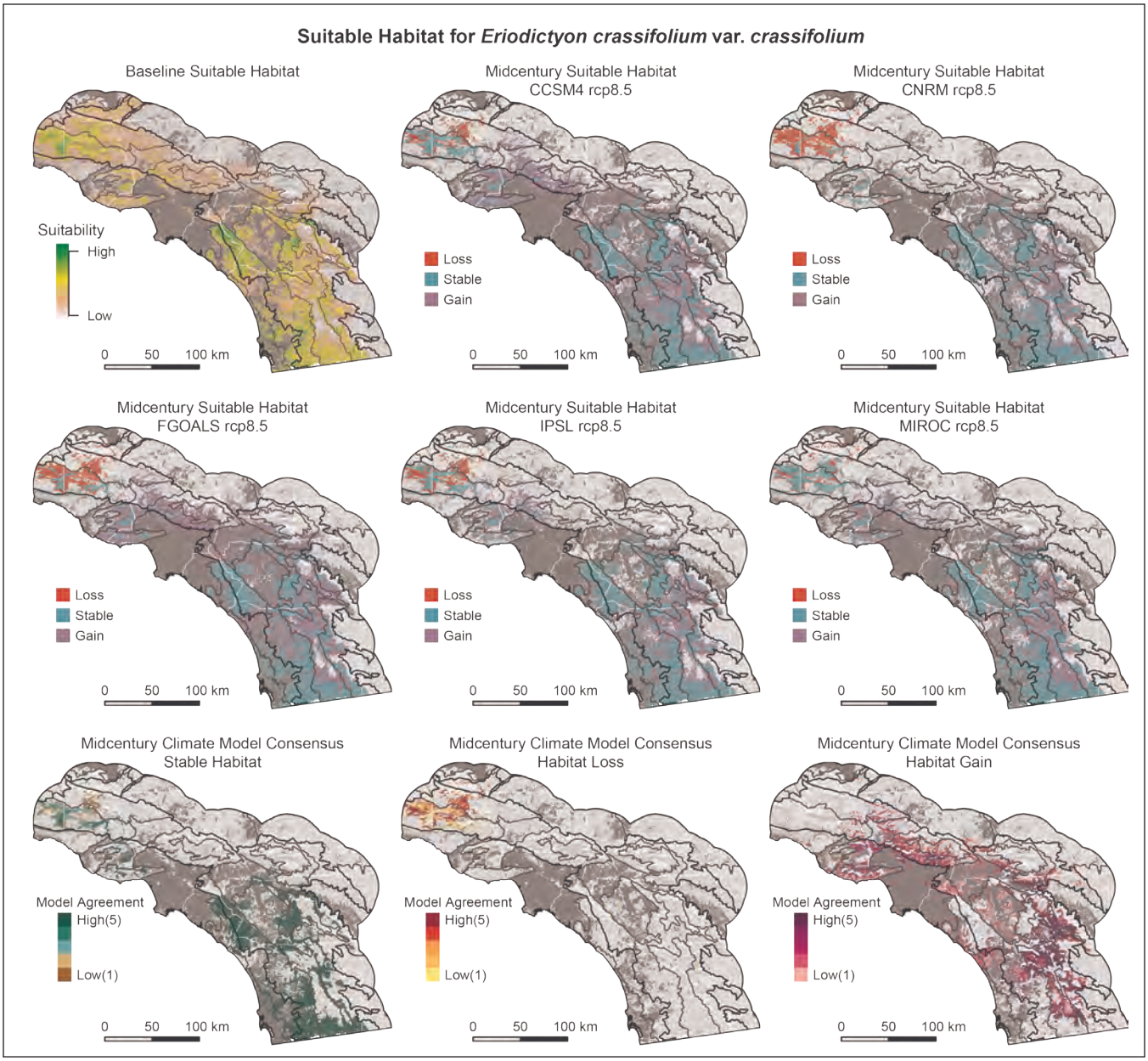

Figure 30—*Eriodictyon crassifolium* var. *crassifolium* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

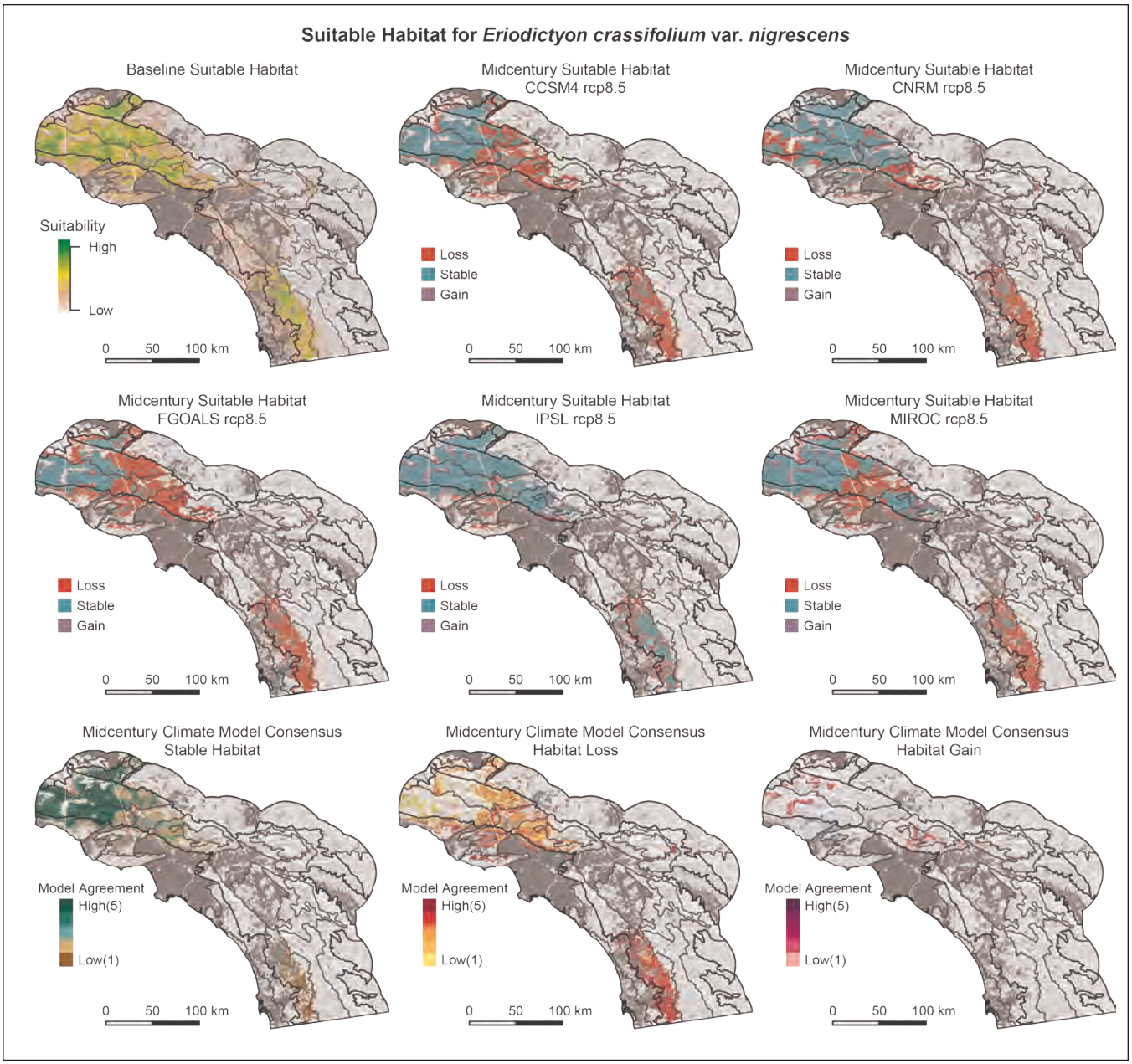

Figure 31—*Eriodictyon crassifolium* var. *nigrescens* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

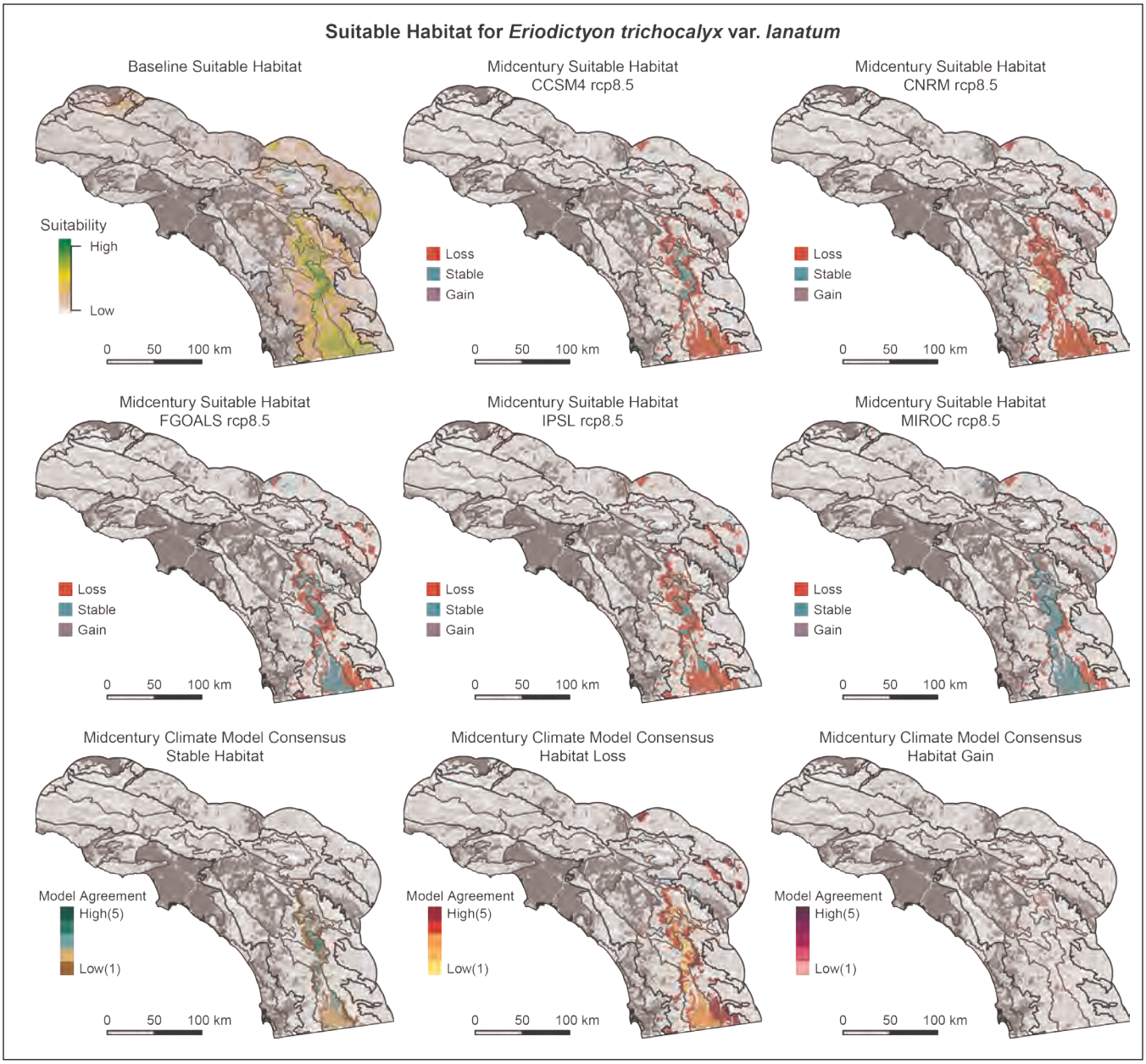

Figure 32—*Eriodictyon trichocalyx* var. *lanatum* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps

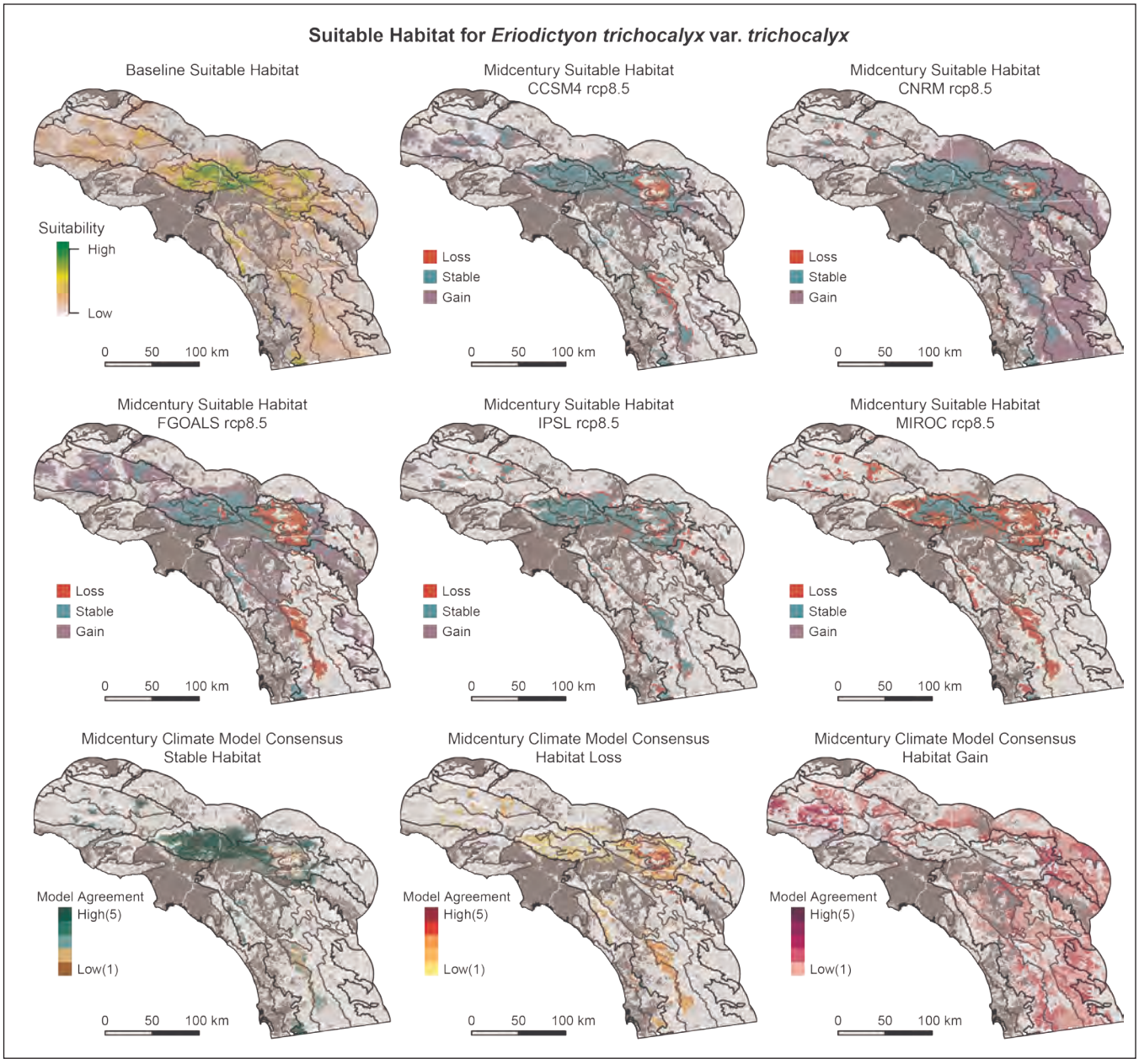

Figure 33—*Eriodictyon trichocalyx* var. *trichocalyx* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

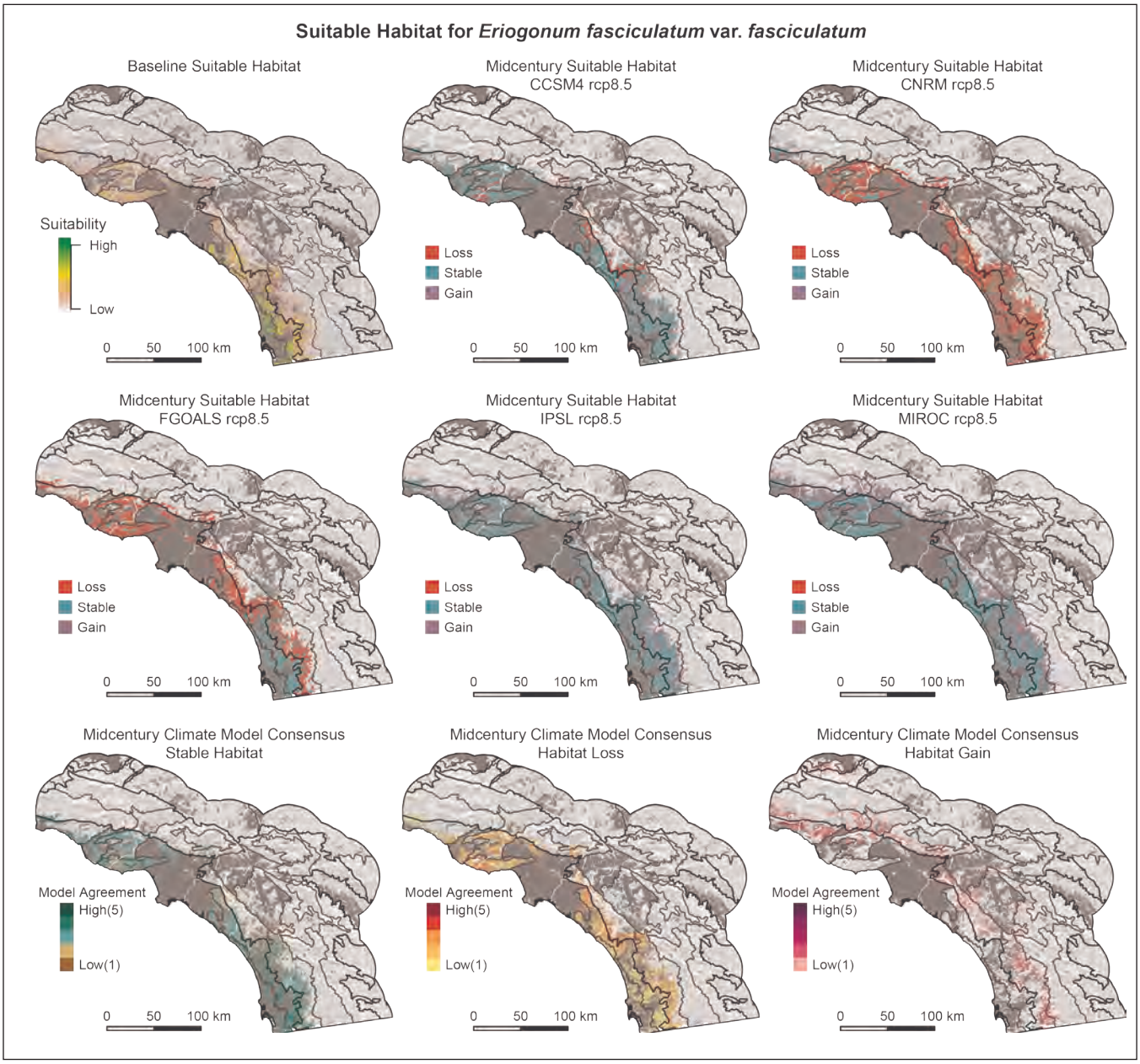

Figure 34—*Eriogonum fasciculatum* var. *fasciculatum* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

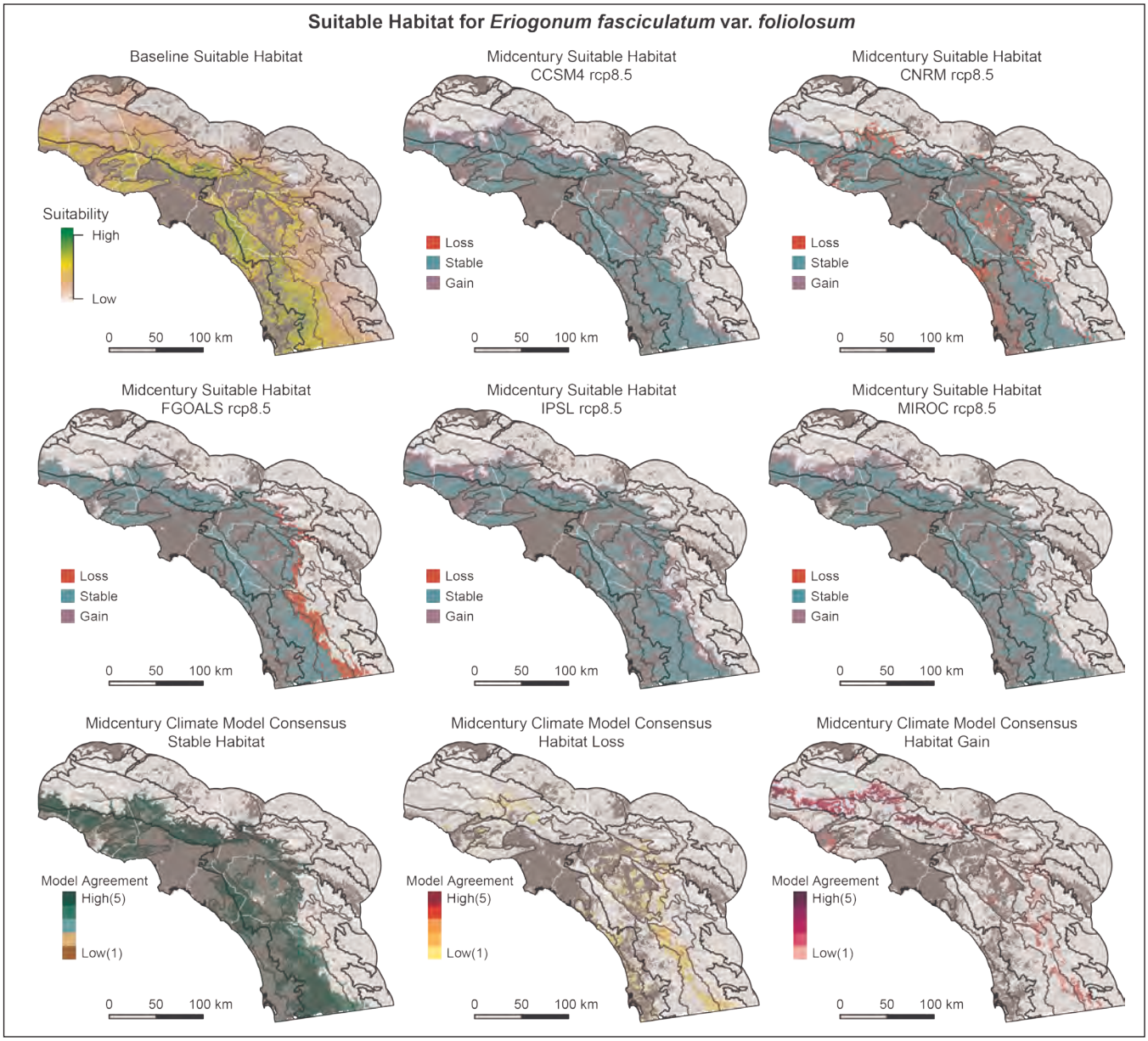

Figure 35—*Eriogonum fasciculatum* var. *foliolosum* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

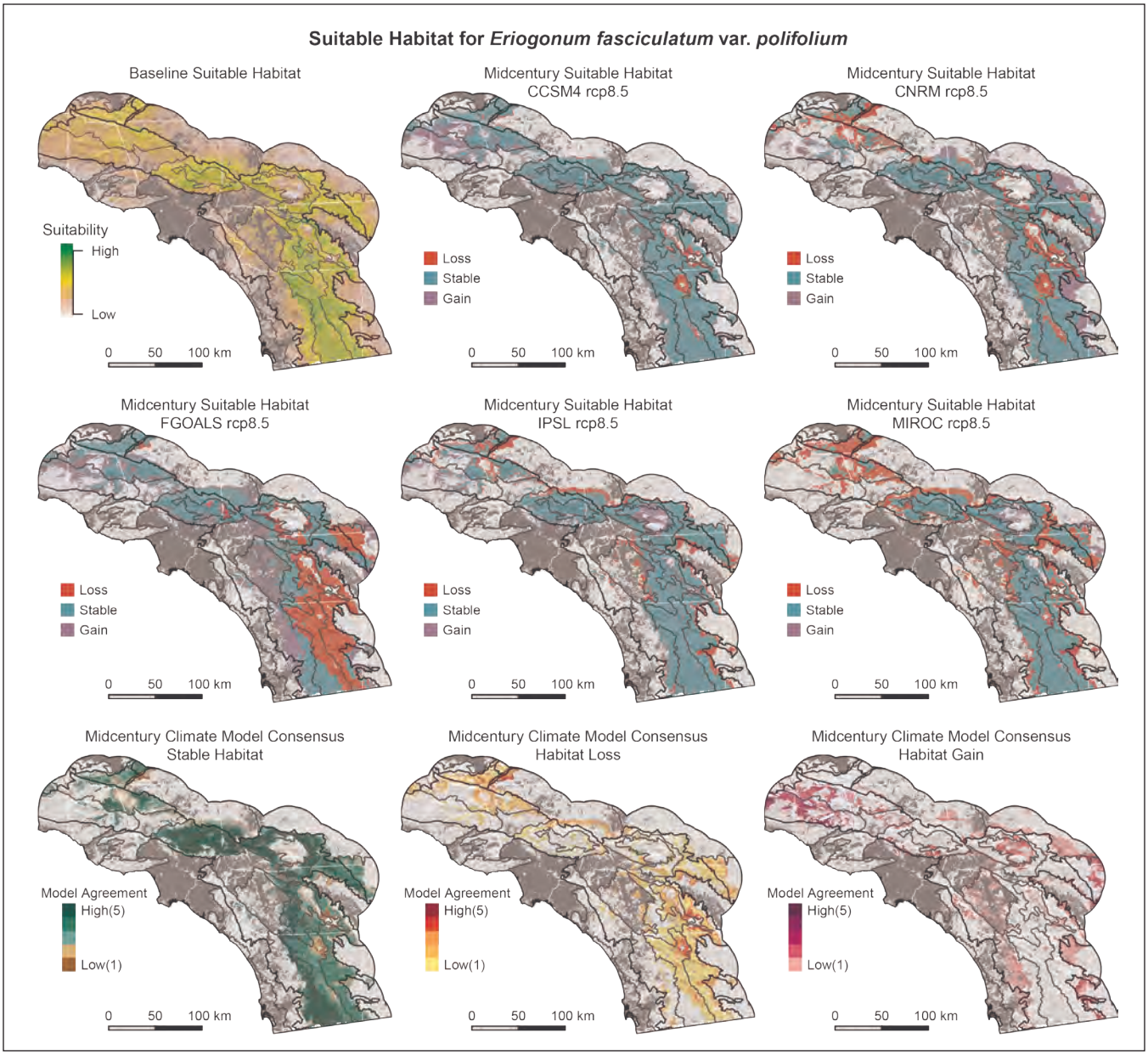

Figure 36—*Eriogonum fasciculatum* var. *polifolium* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

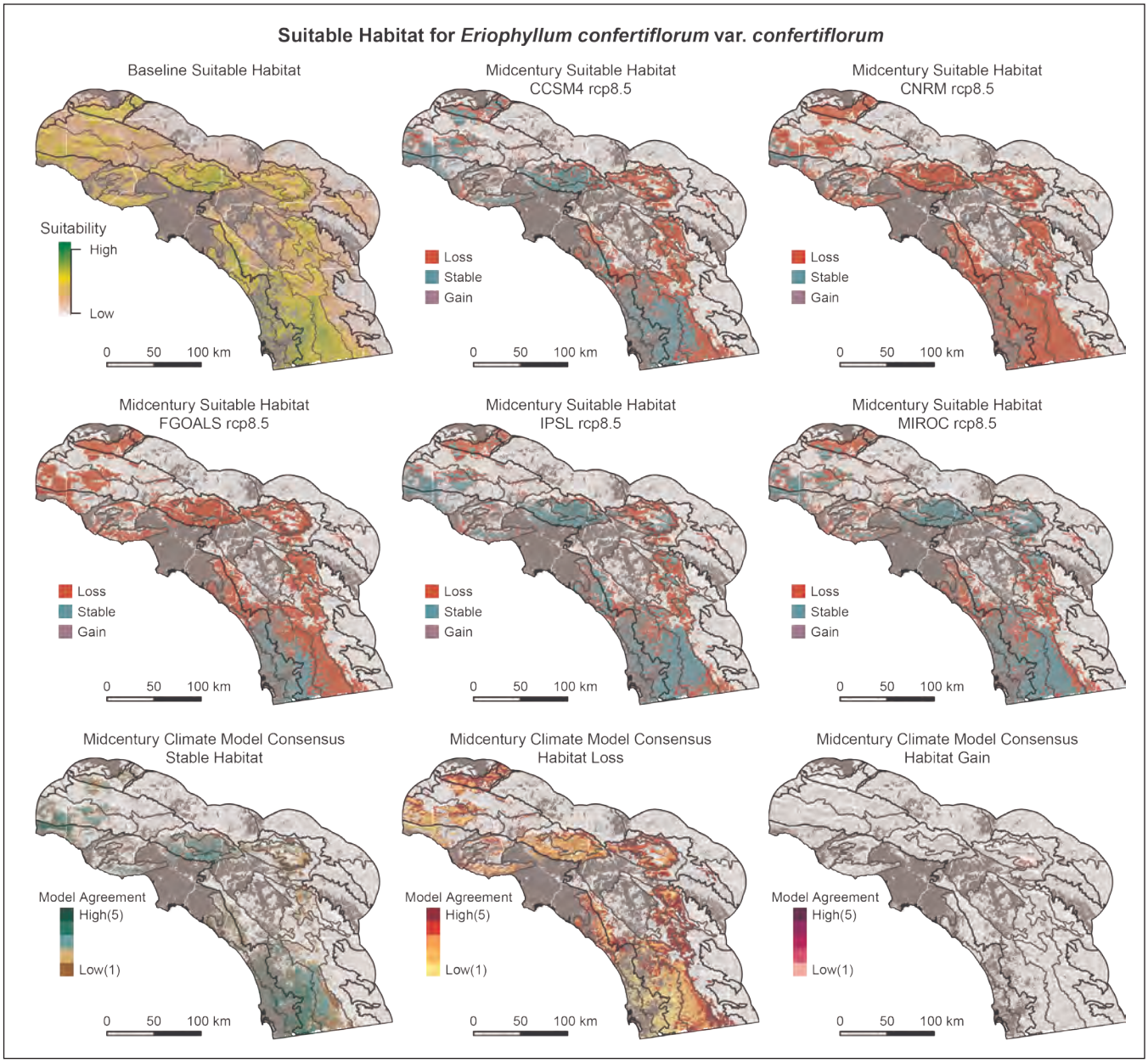

Figure 37—*Eriophyllum confertiflorum* var. *confertiflorum* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

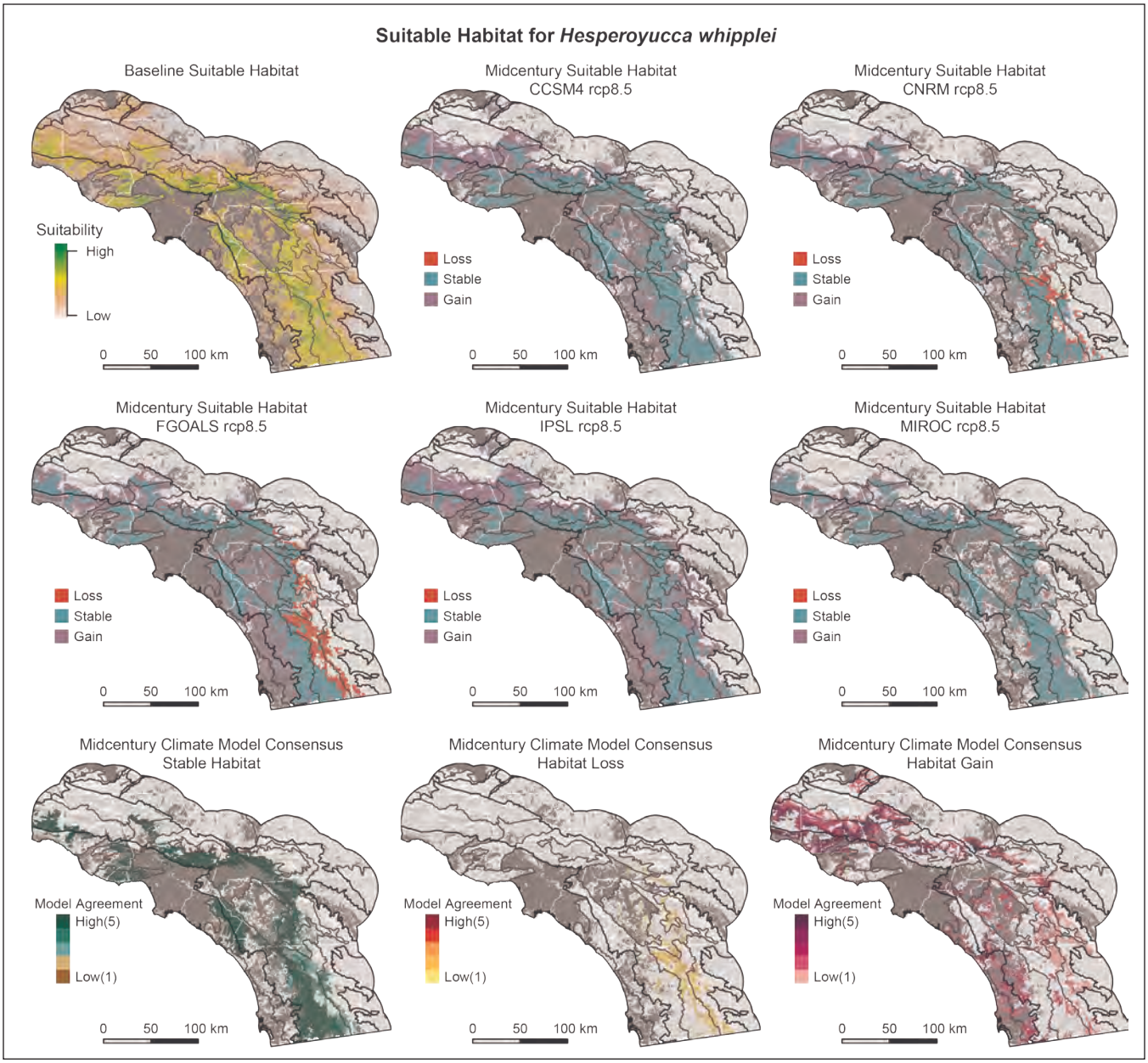

Figure 38—*Hesperoyucca whipplei* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

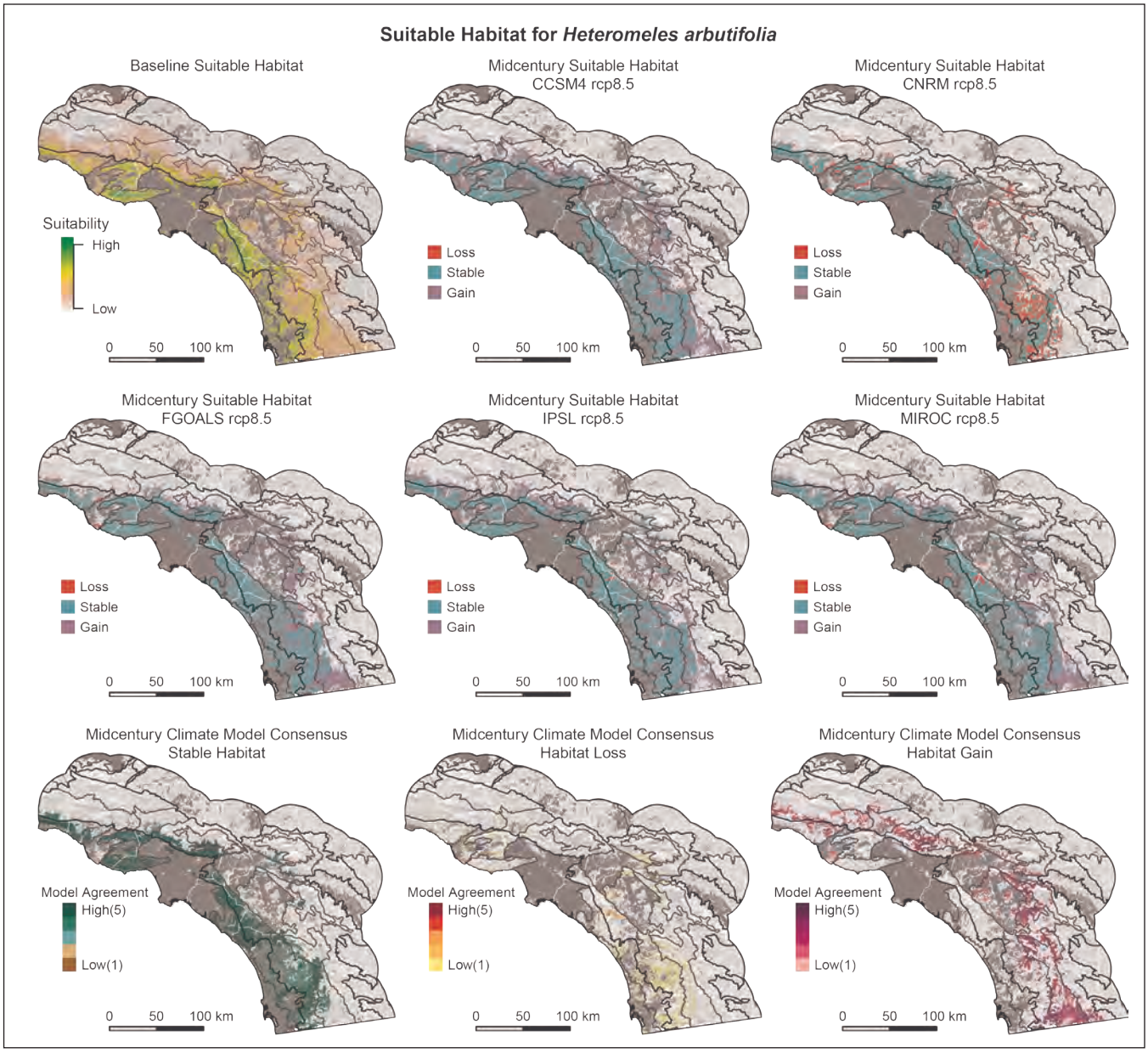

Figure 39—*Heteromeles arbutifolia* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

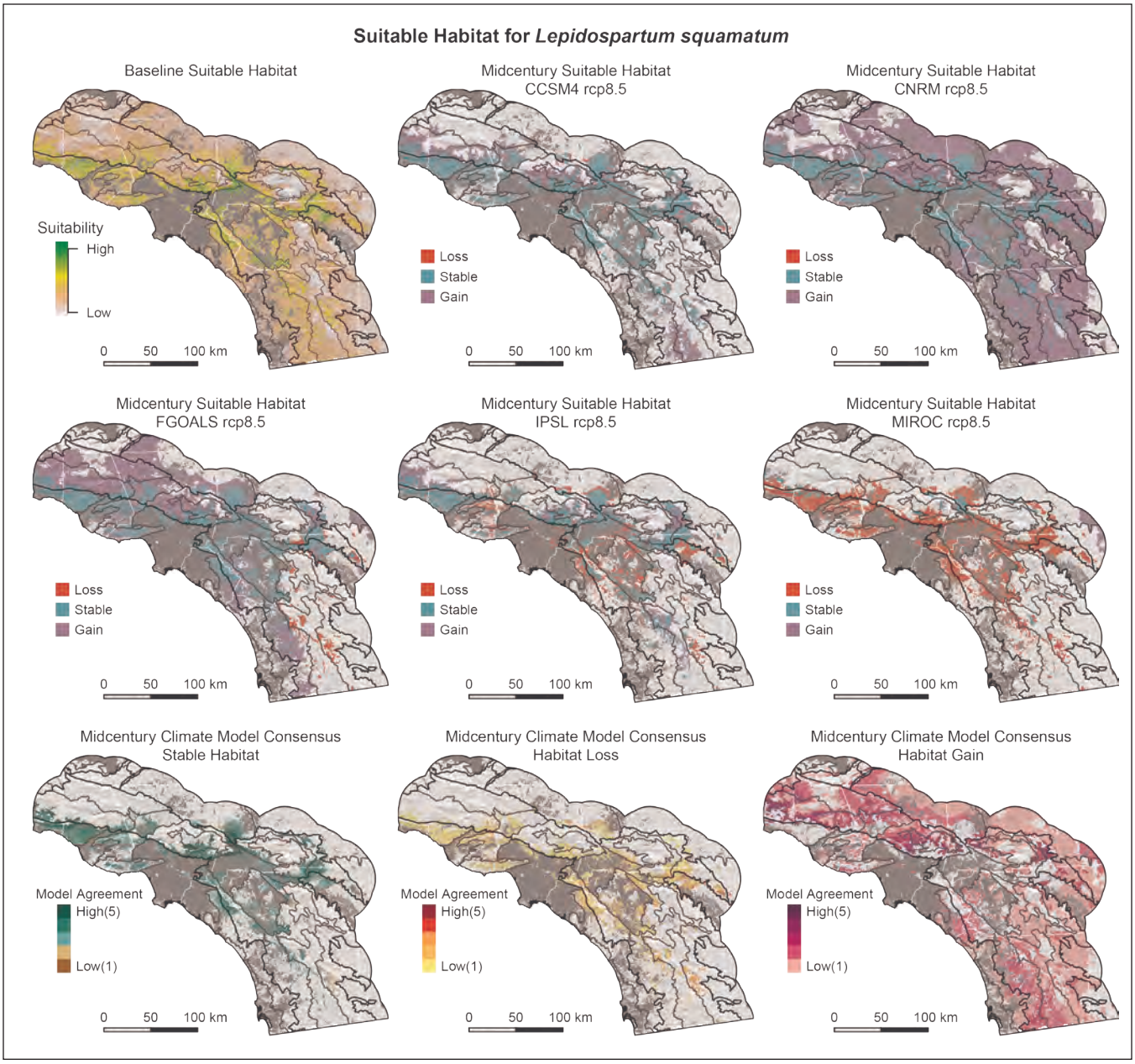

Figure 40—*Lepidospartum squamatum* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

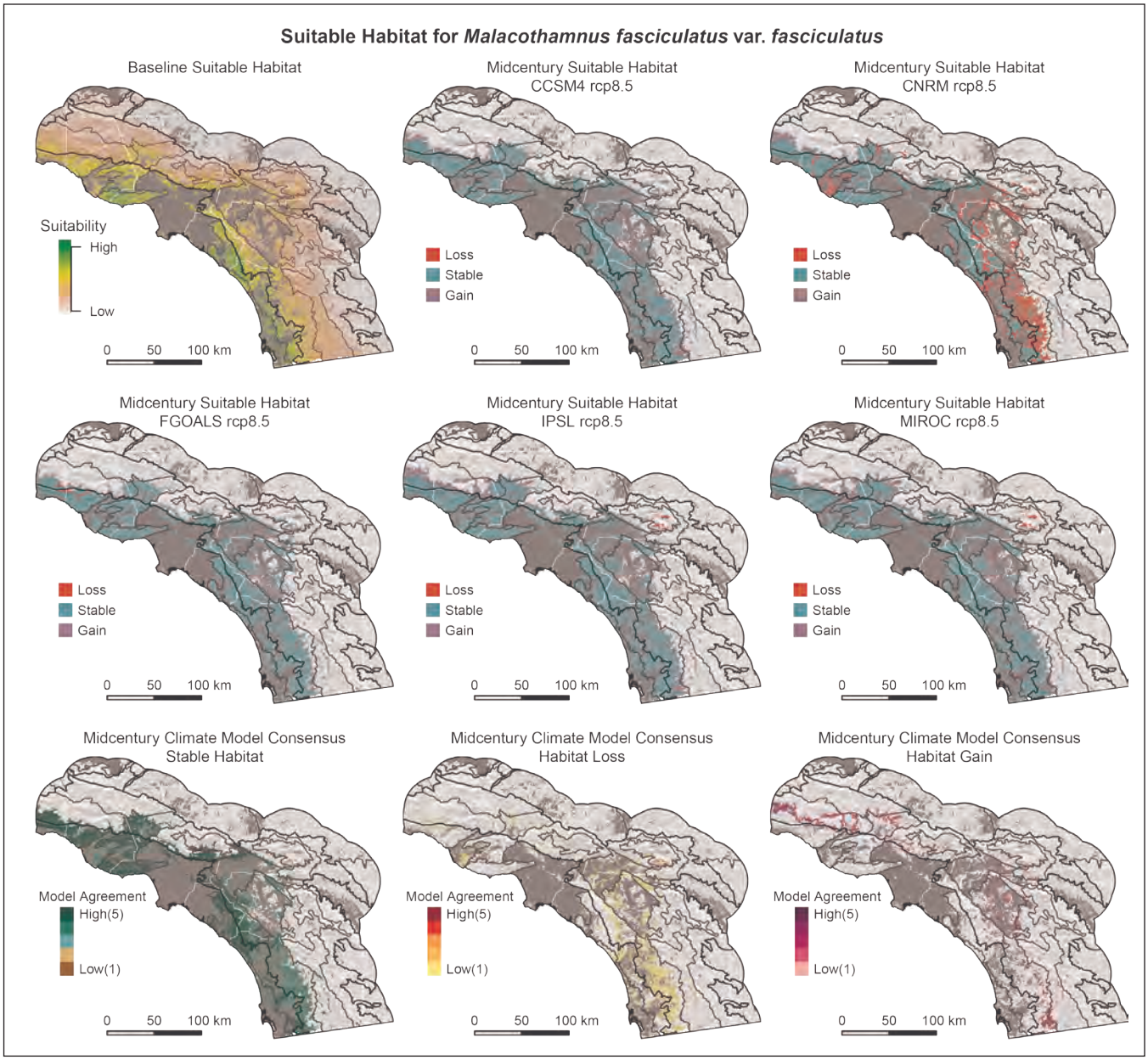

Figure 41—*Malacothamnus fasciculatus* var. *fasciculatus* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

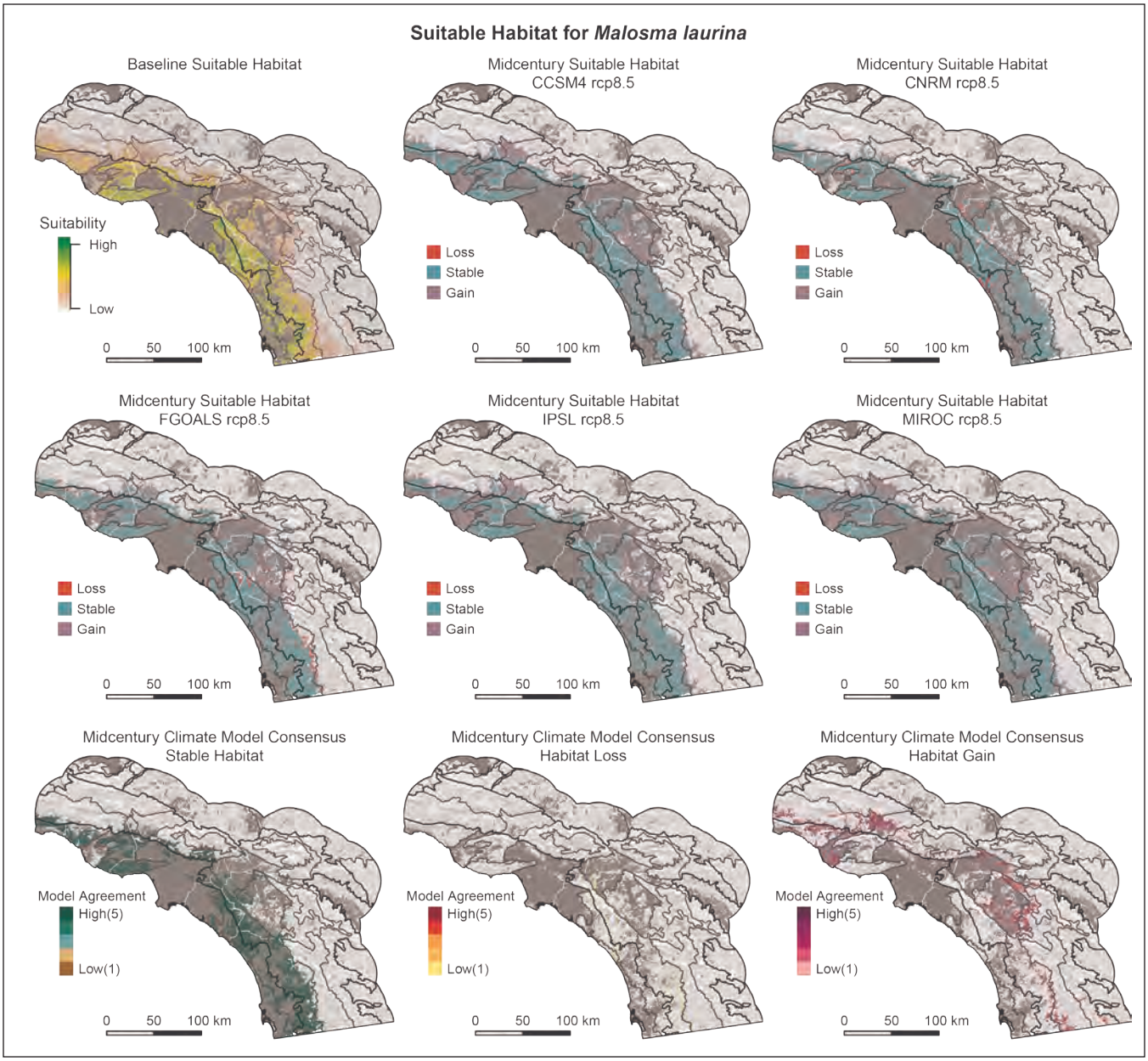

Figure 42— *Malosma laurina* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

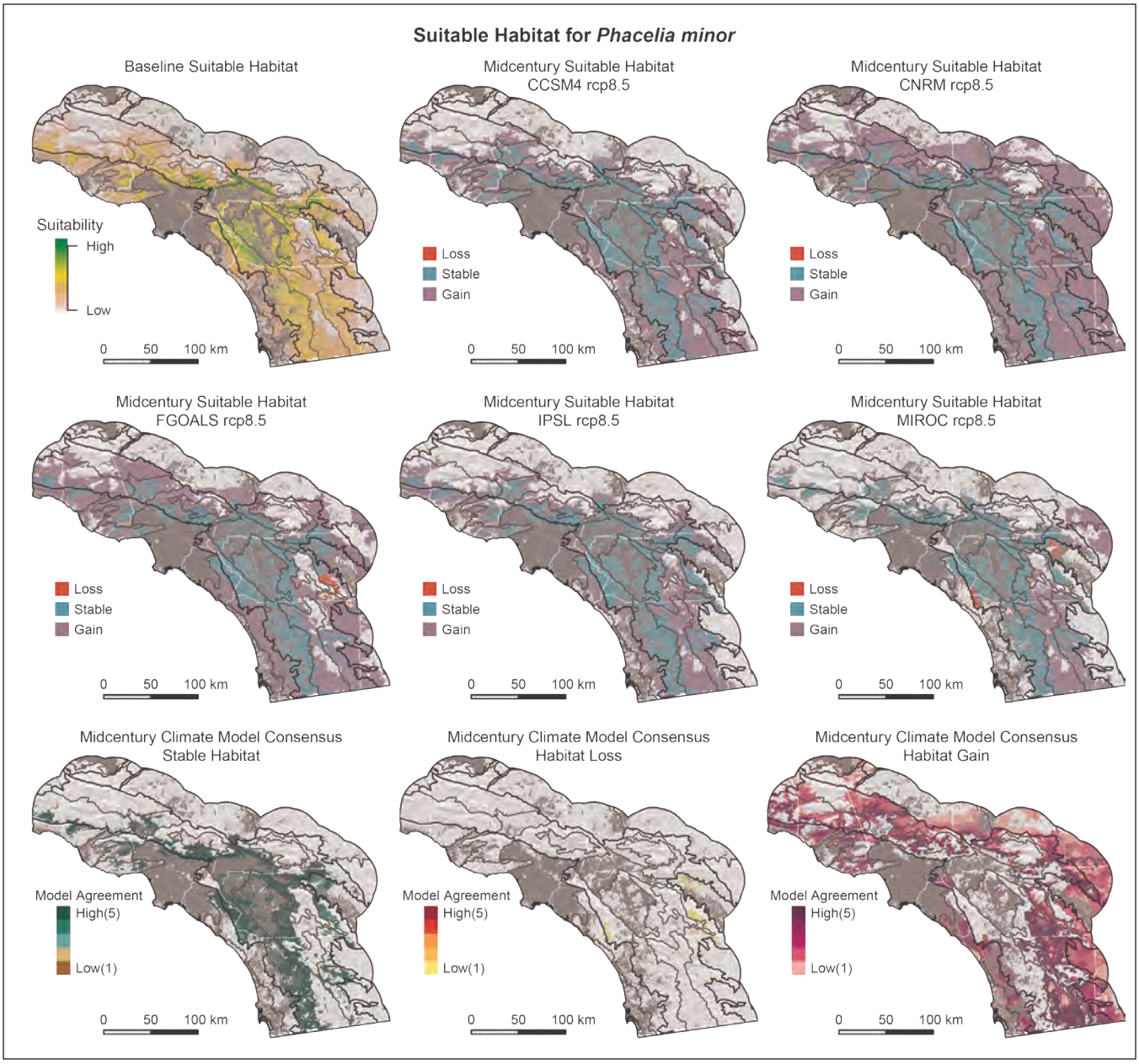

Figure 43—*Phacelia minor* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

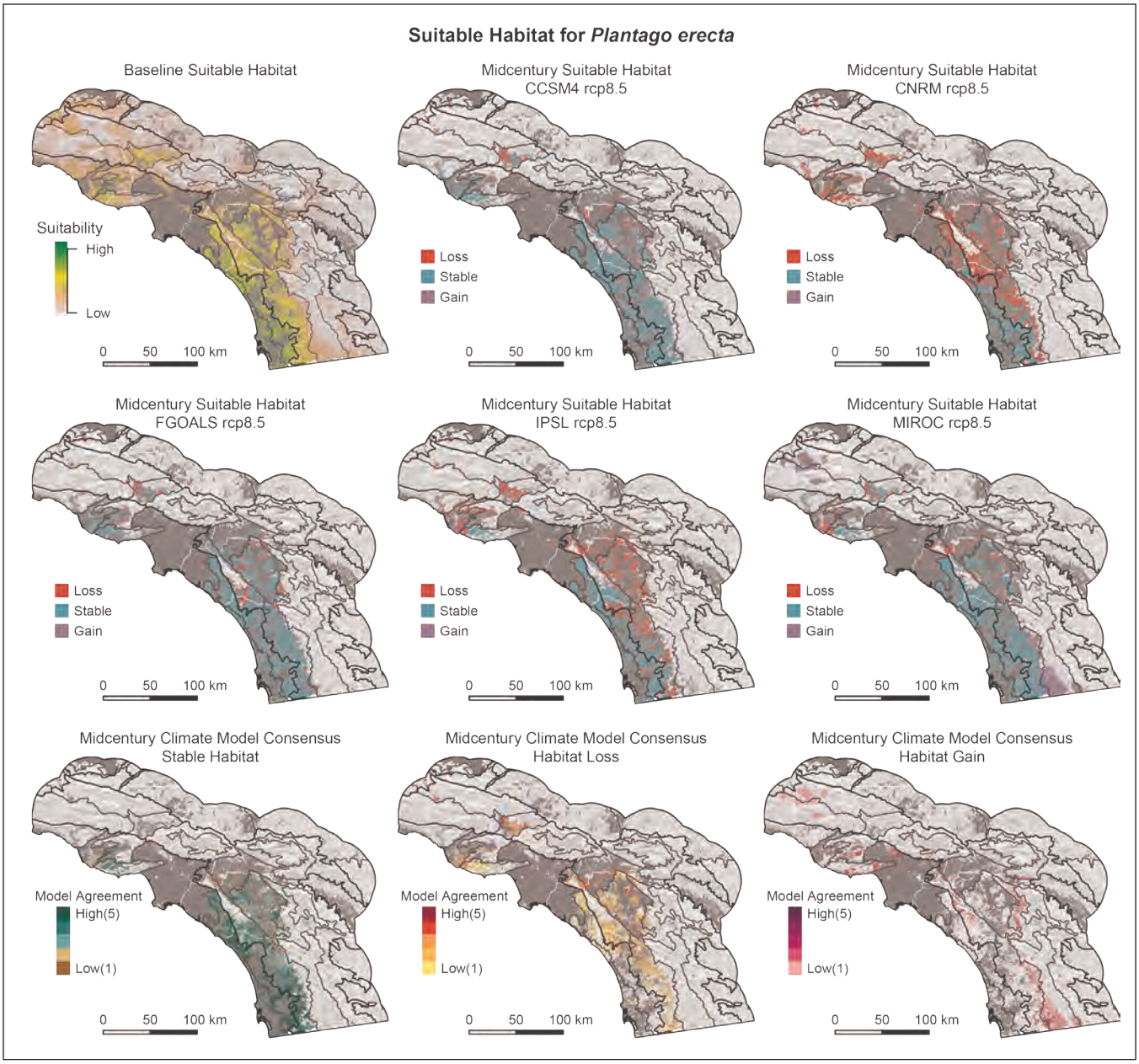

Figure 44—*Plantago erecta* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

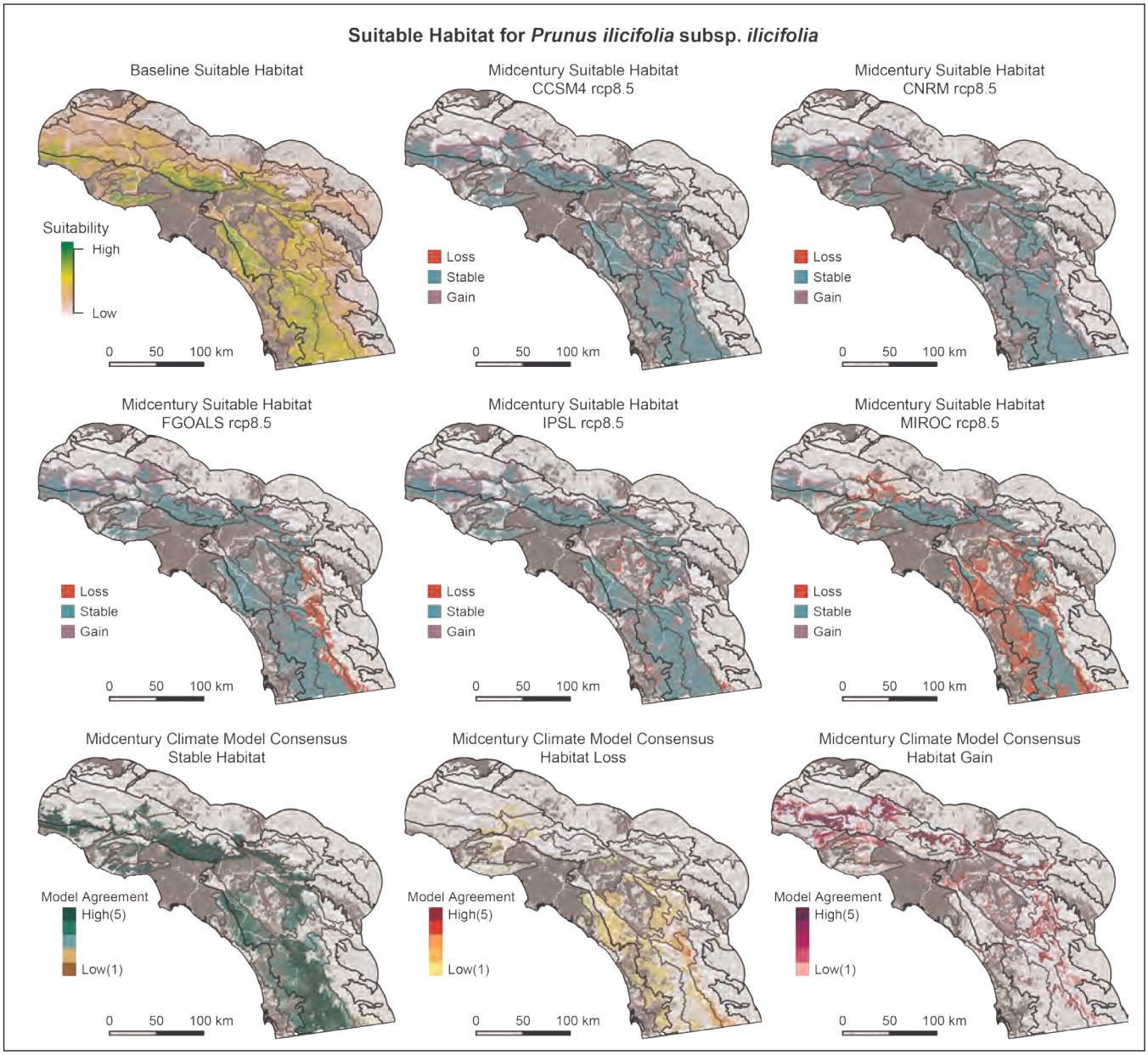

Figure 45—*Prunus ilicifolia* subsp. *ilicifolia* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

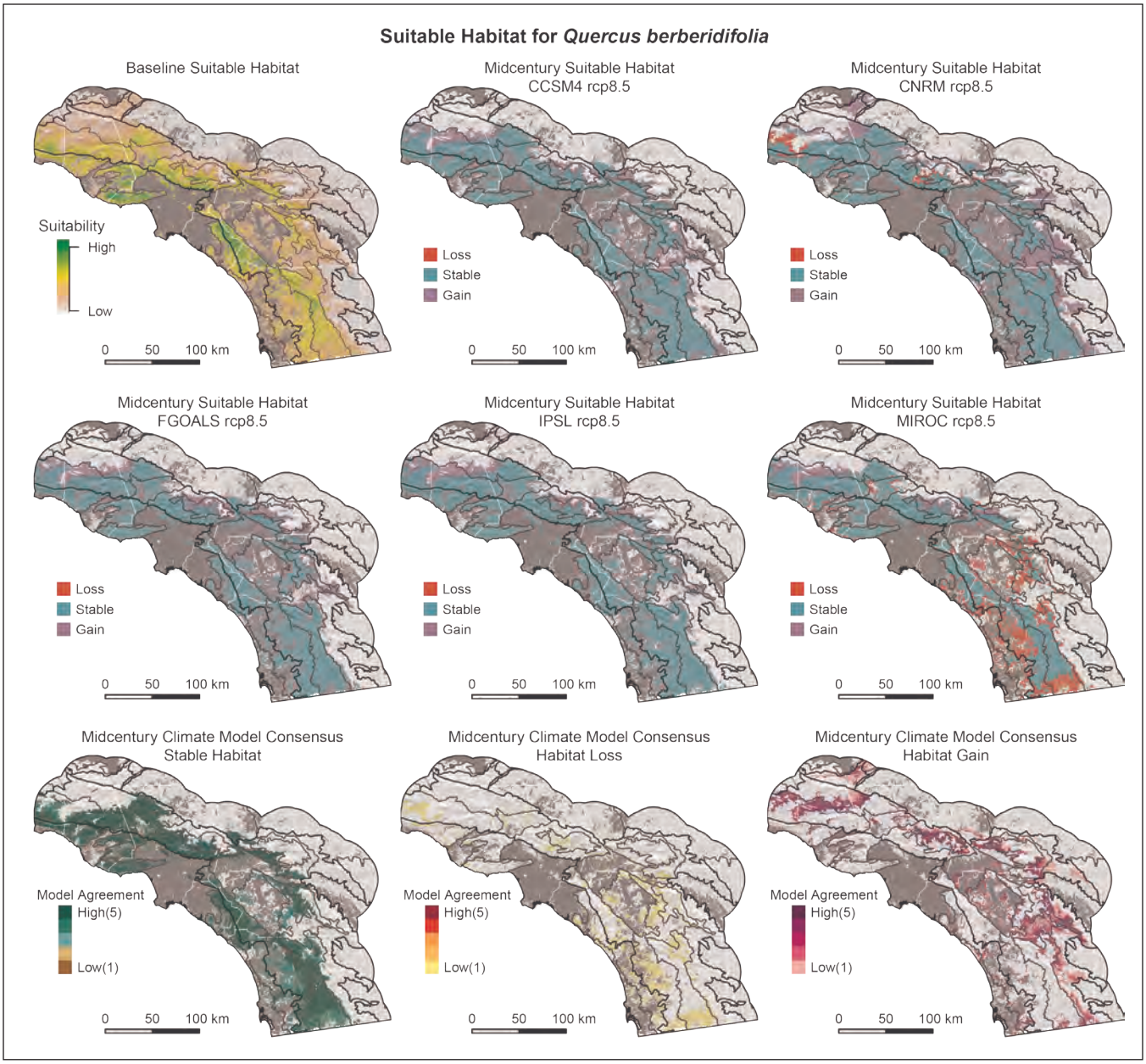

Figure 46—*Quercus berberidifolia* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

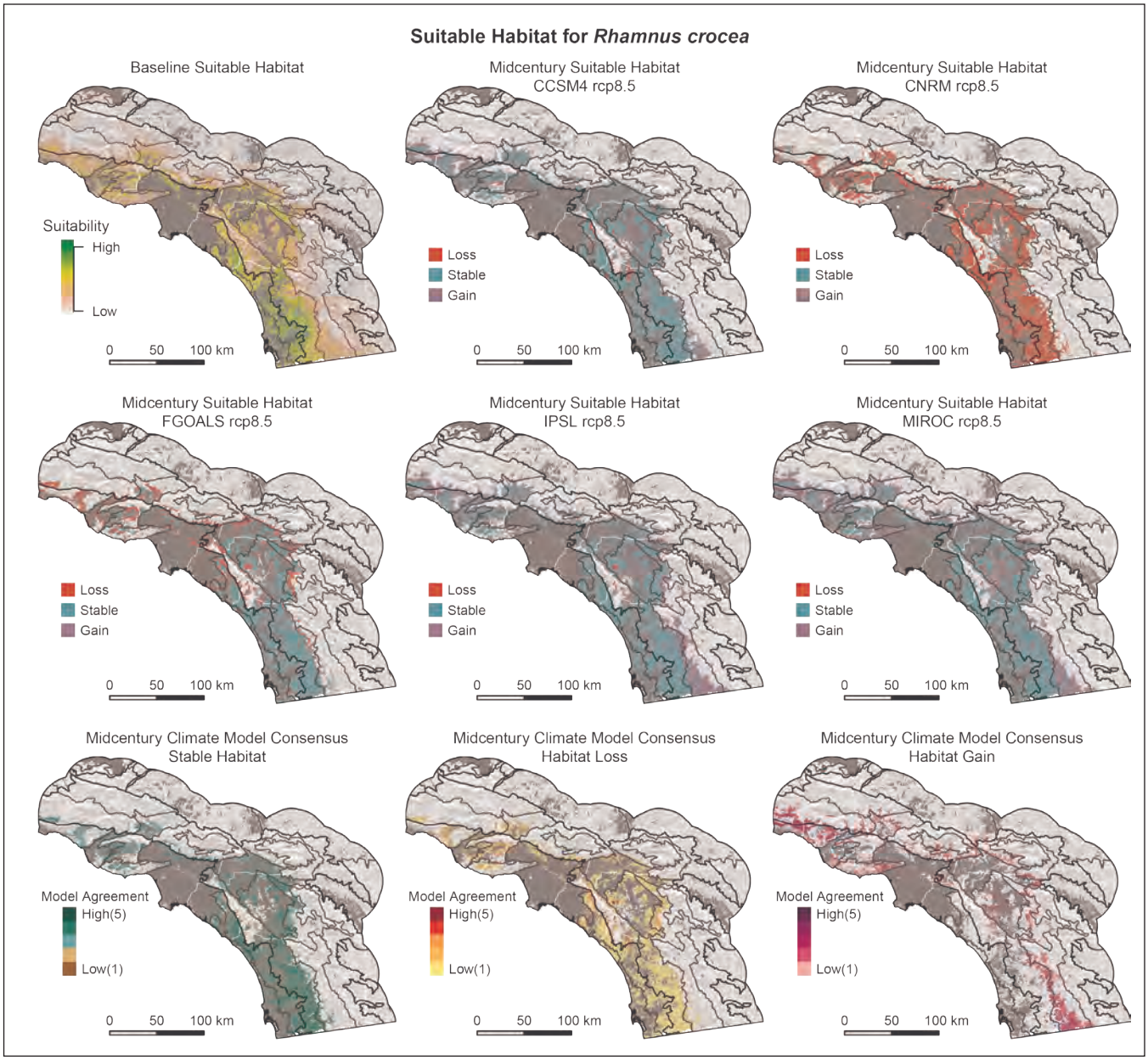

Figure 47—*Rhamnus crocea* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

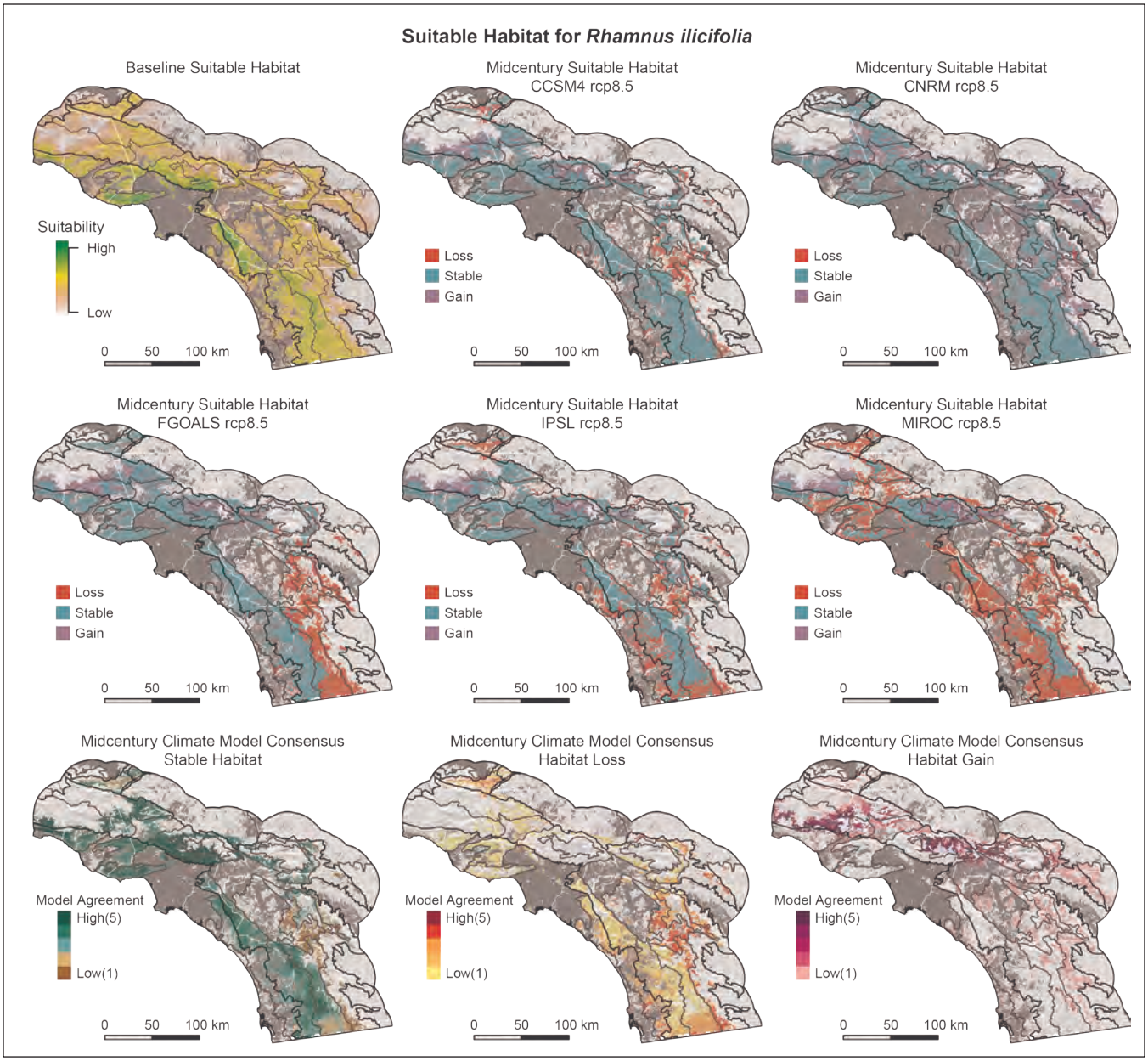

Figure 48—*Rhamnus ilicifolia* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

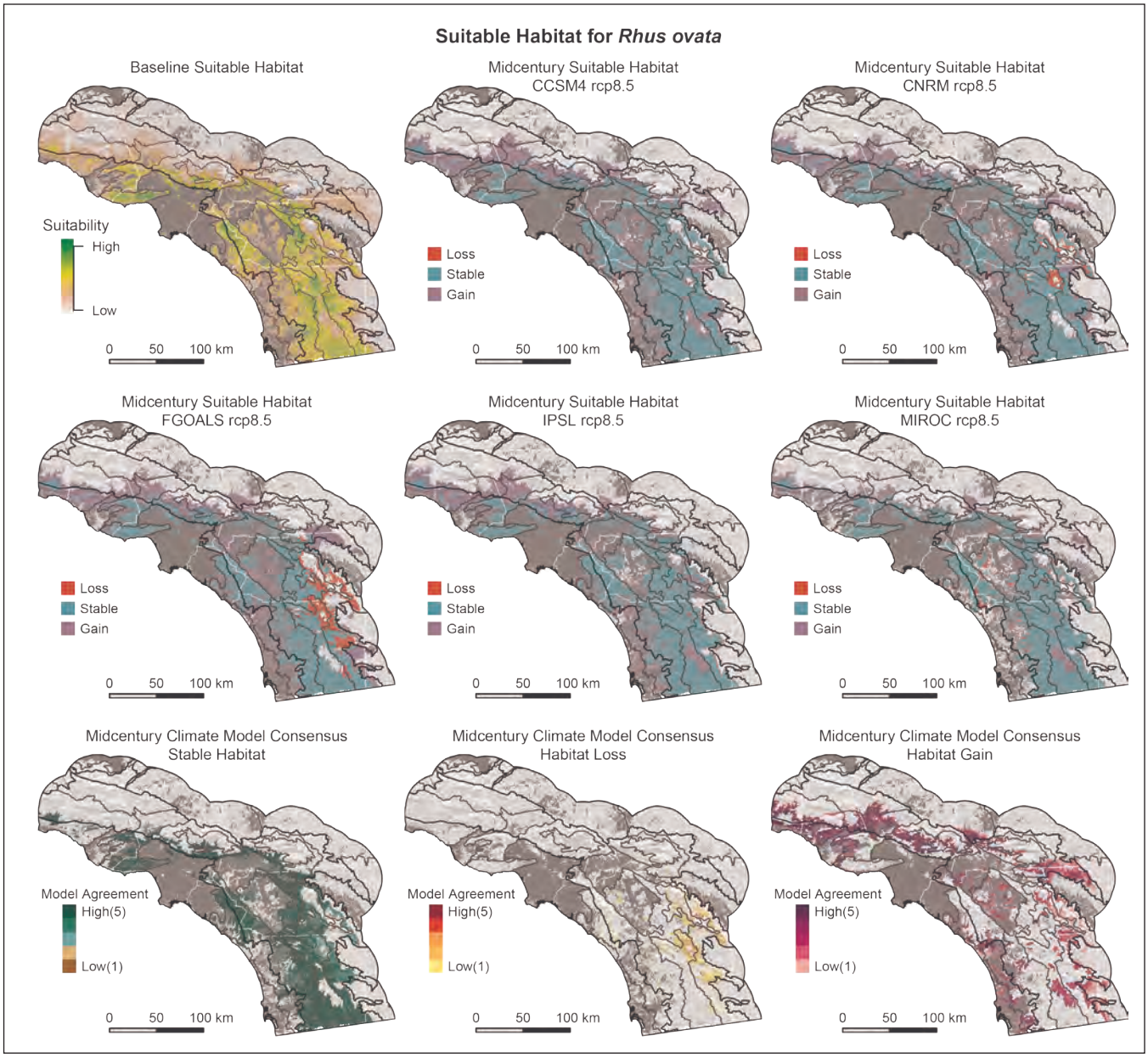

Figure 49—*Rhus ovata* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

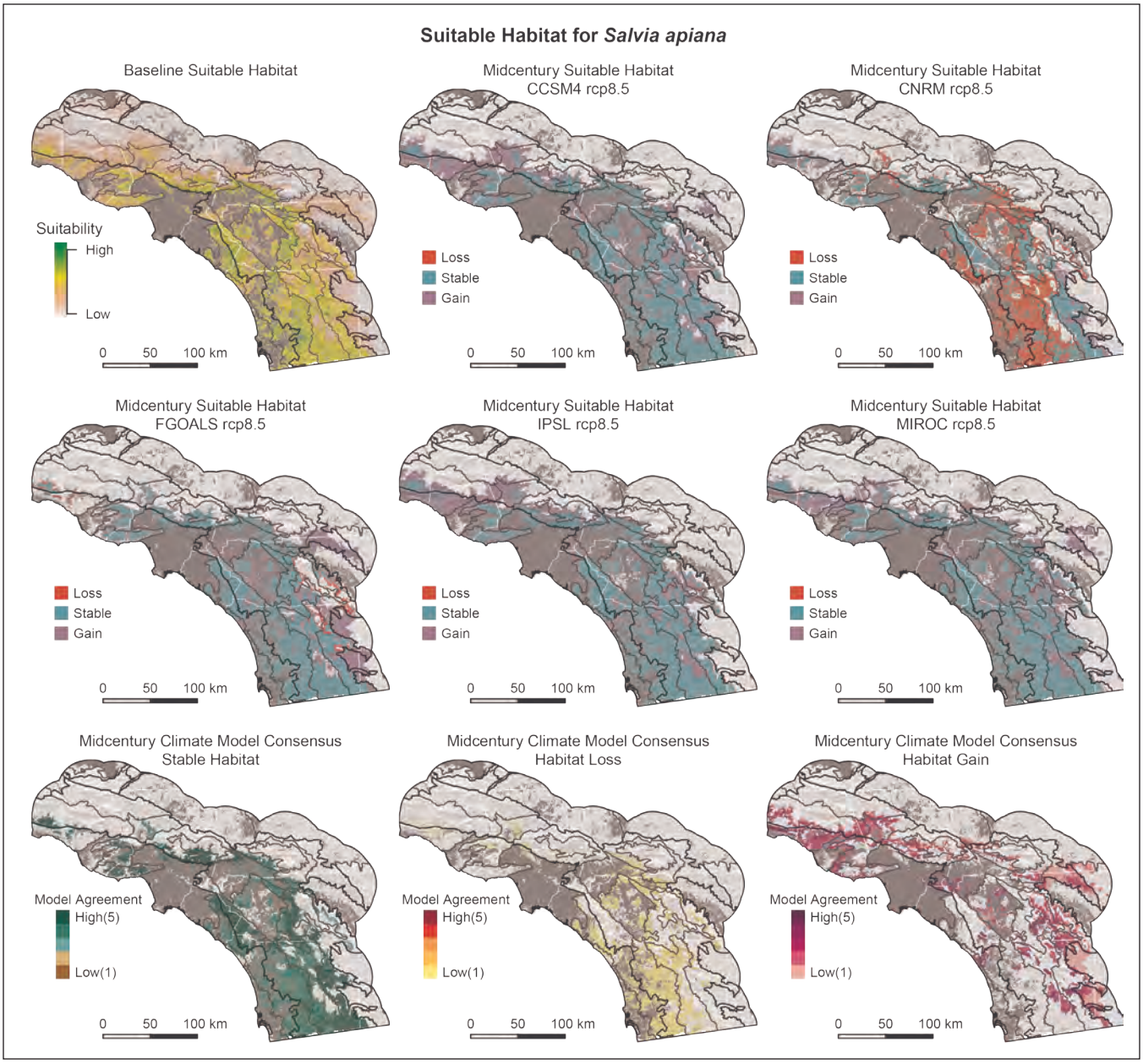

Figure 50—*Salvia apiana* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

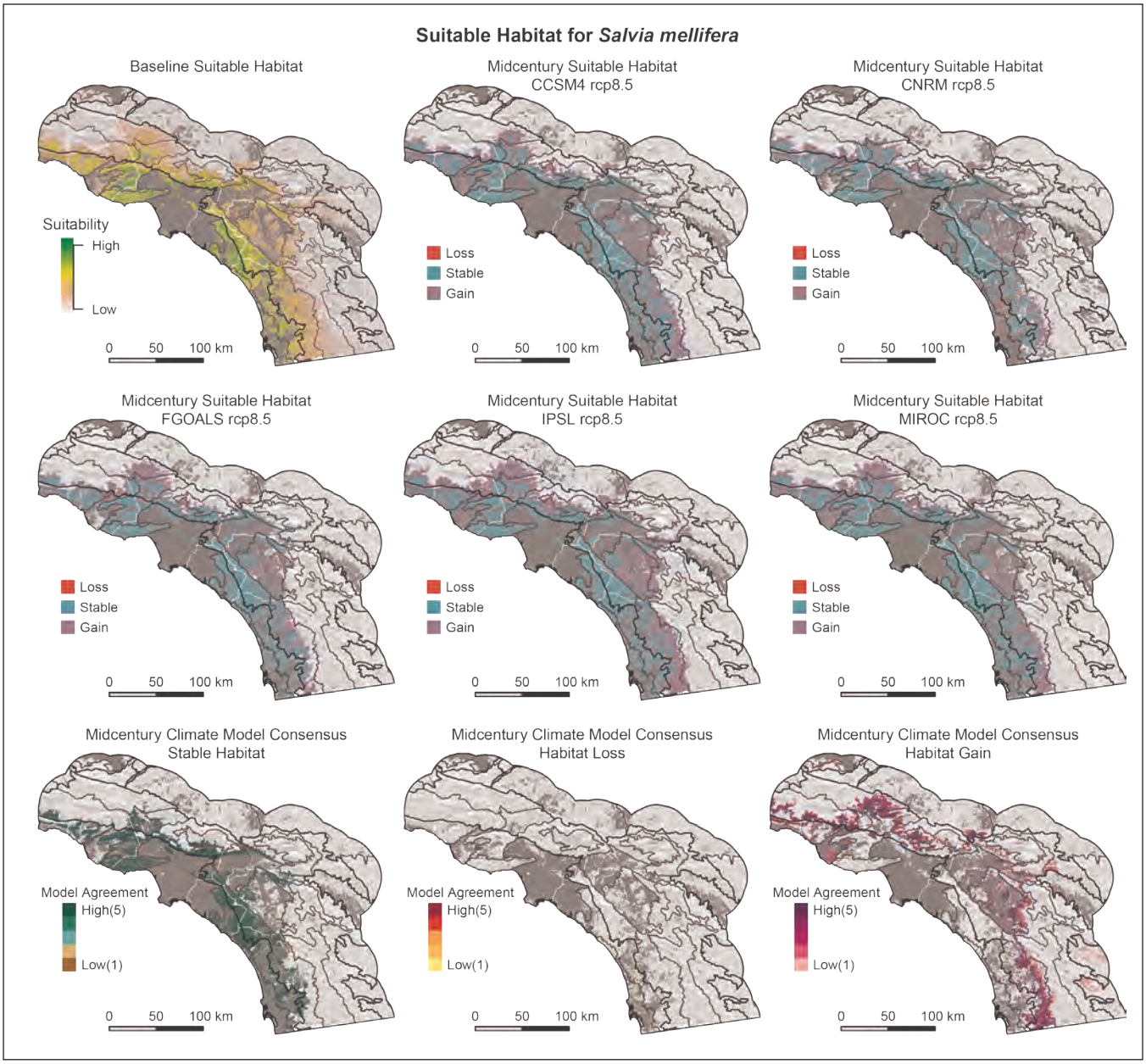

Figure 51—*Salvia mellifera* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

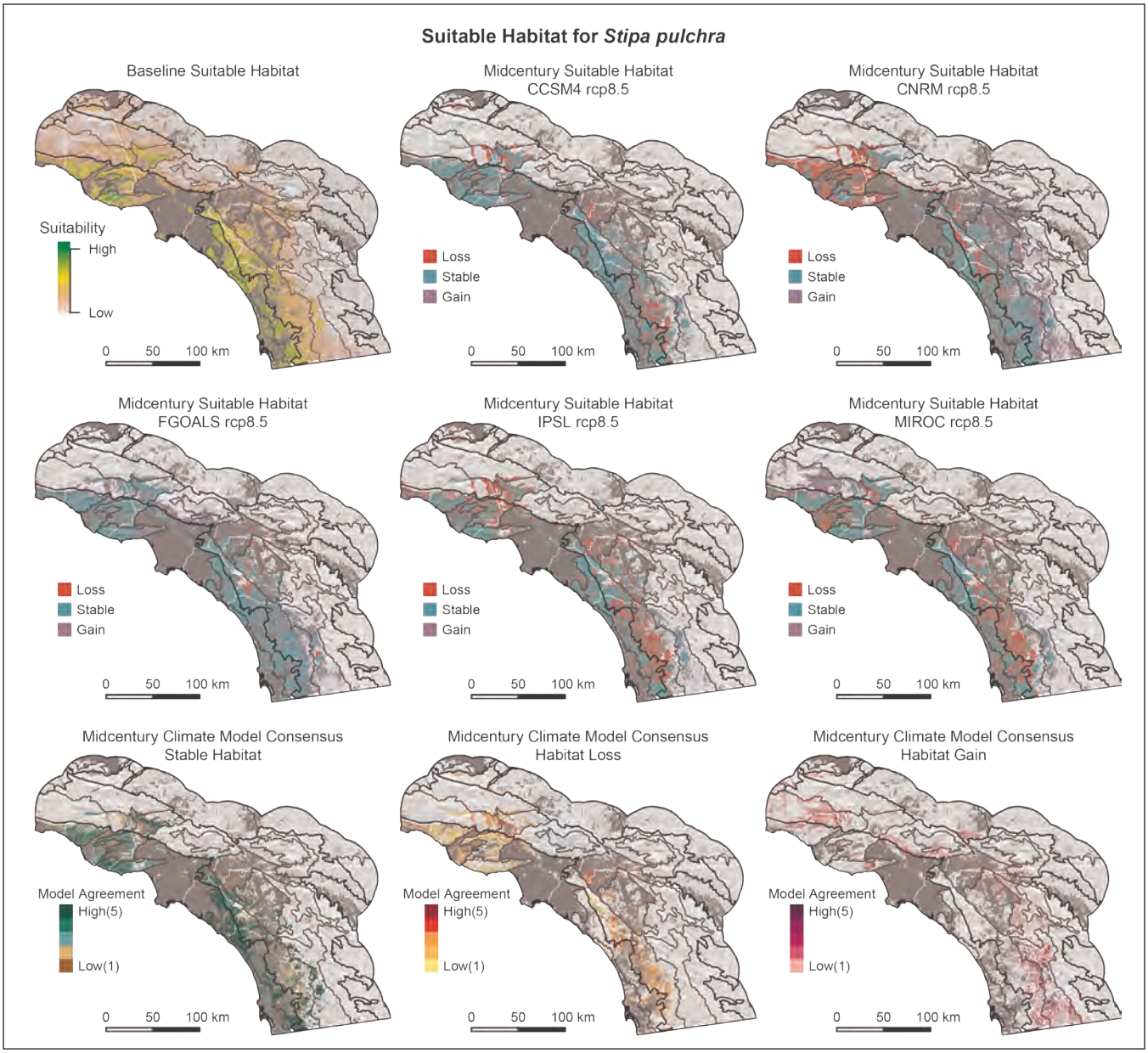

Figure 52—*Stipa pulchra* baseline (1951–1980) and midcentury (2040–2069) suitable habitat maps.

Appendix 5: Projected Midcentury Suitable Habitat for Scrub and Shrubland Vegetation Groups

Multiple-taxon overlay maps show the number of taxa with projected suitable habitat under midcentury (2040–2060) climate conditions for alluvial scrub, coastal sage scrub, low-elevation chaparral, and mixed chaparral-sage scrub vegetation groups (figs. 53 through 56). Projected change in suitable habitat is defined as: stable = suitable under baseline and future conditions; loss = suitable under baseline but unsuitable under future conditions; gain = unsuitable under baseline and becoming suitable under future conditions. Vegetation group assignments are not mutually exclusive (see table 2). For baseline suitability maps, see figure 6. In all maps, suitable habitat that has already been converted to urban and agriculture land uses is masked in dark gray (FRAP 2015).

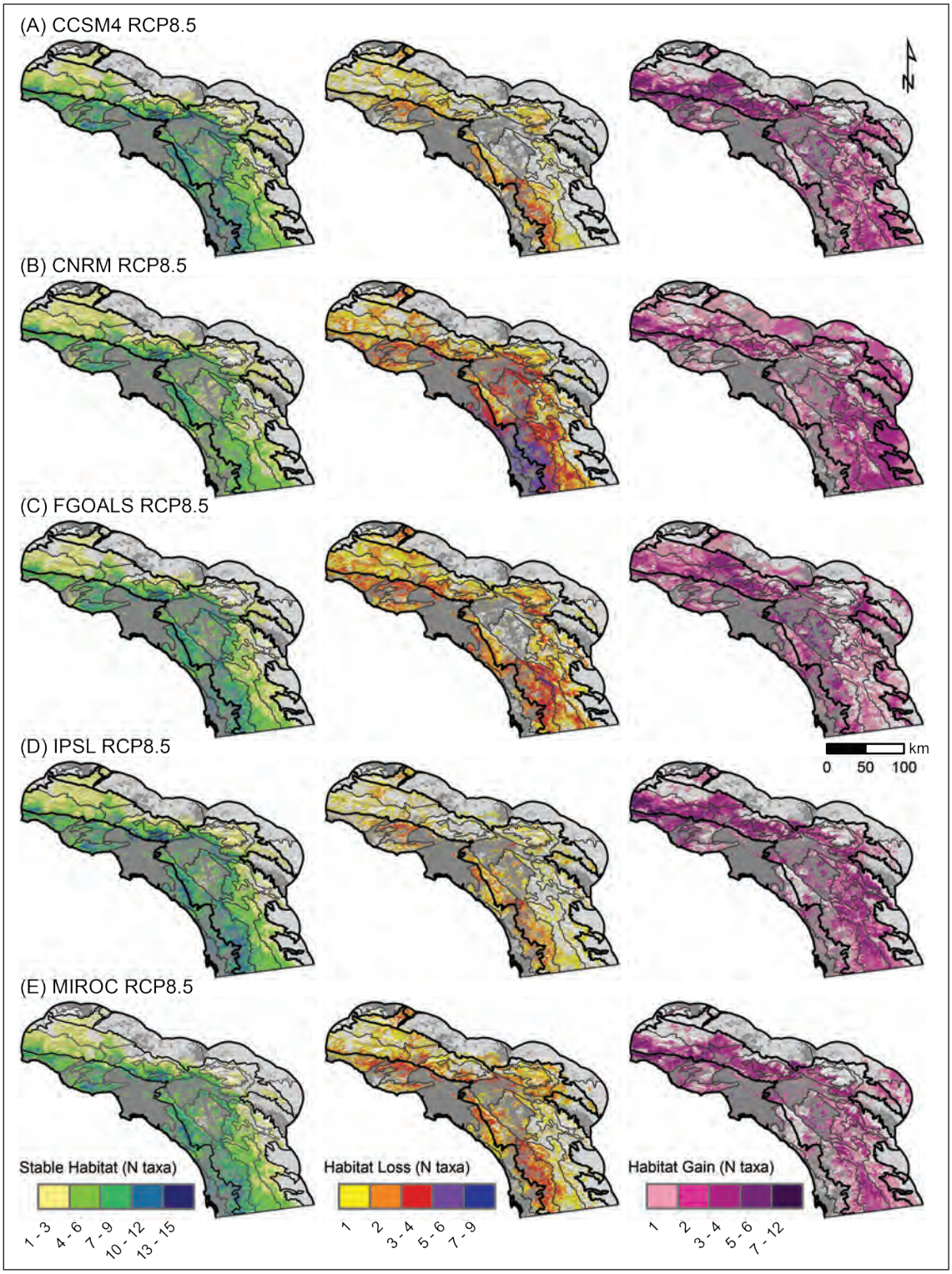

Figure 53—Projected habitat suitability for plant taxa associated with alluvial scrub under five future climate scenarios (A–E).

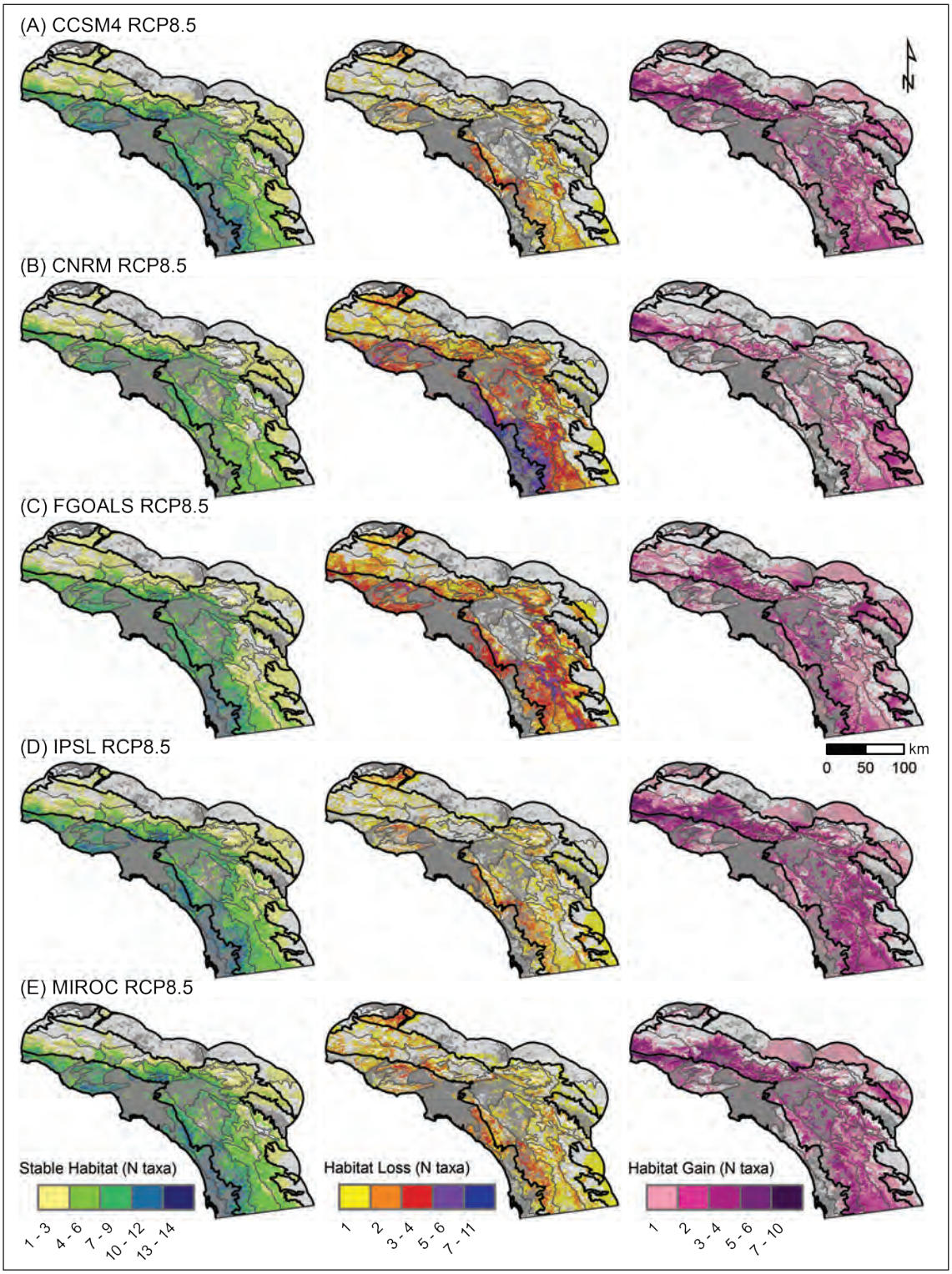

Figure 54—Projected habitat suitability for plant taxa associated with coastal sage scrub under five future climate scenarios (A–E).

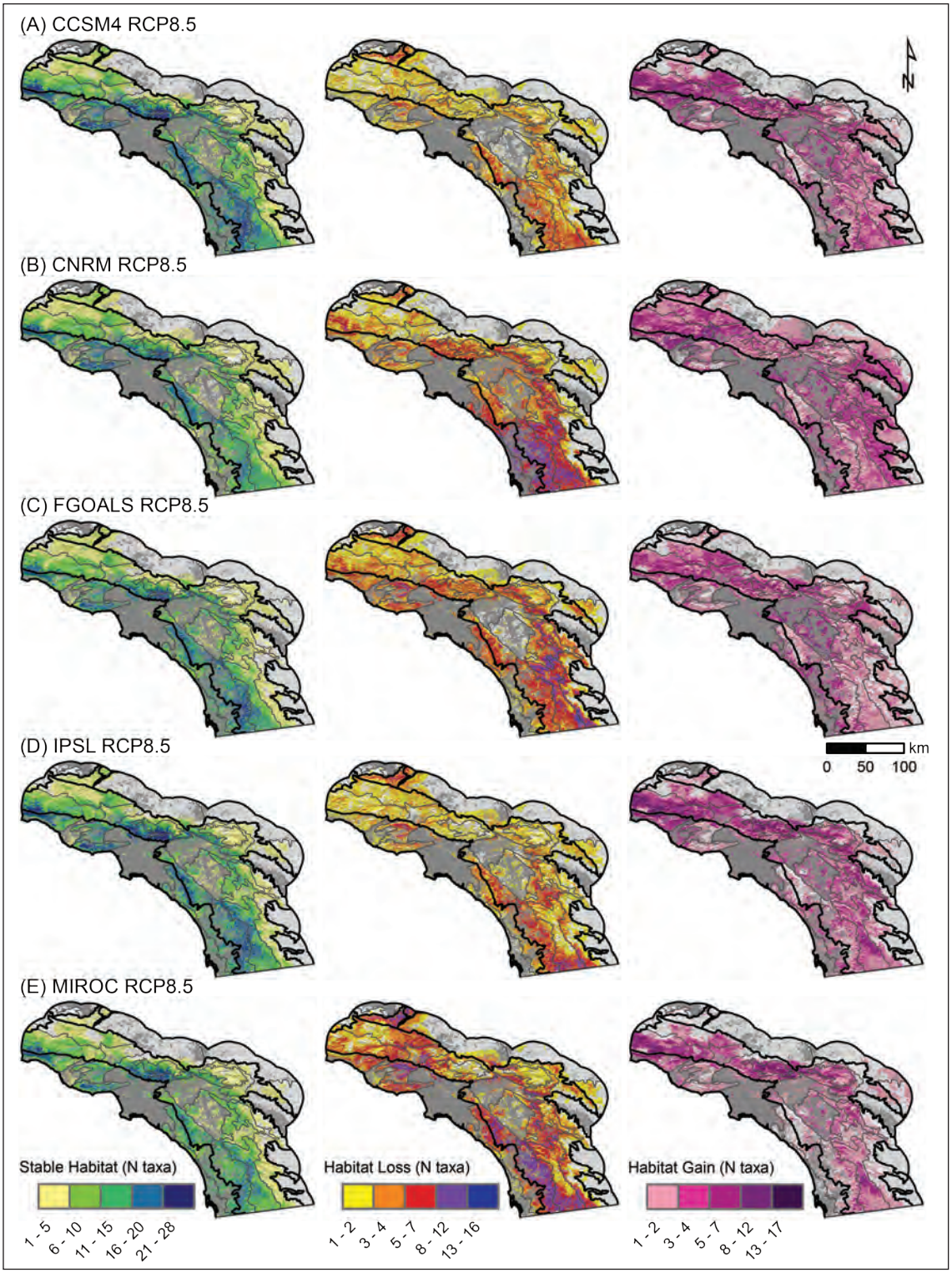

Figure 55—Projected habitat suitability for plant taxa associated with low-elevation chaparral under five future climate scenarios (A–E).

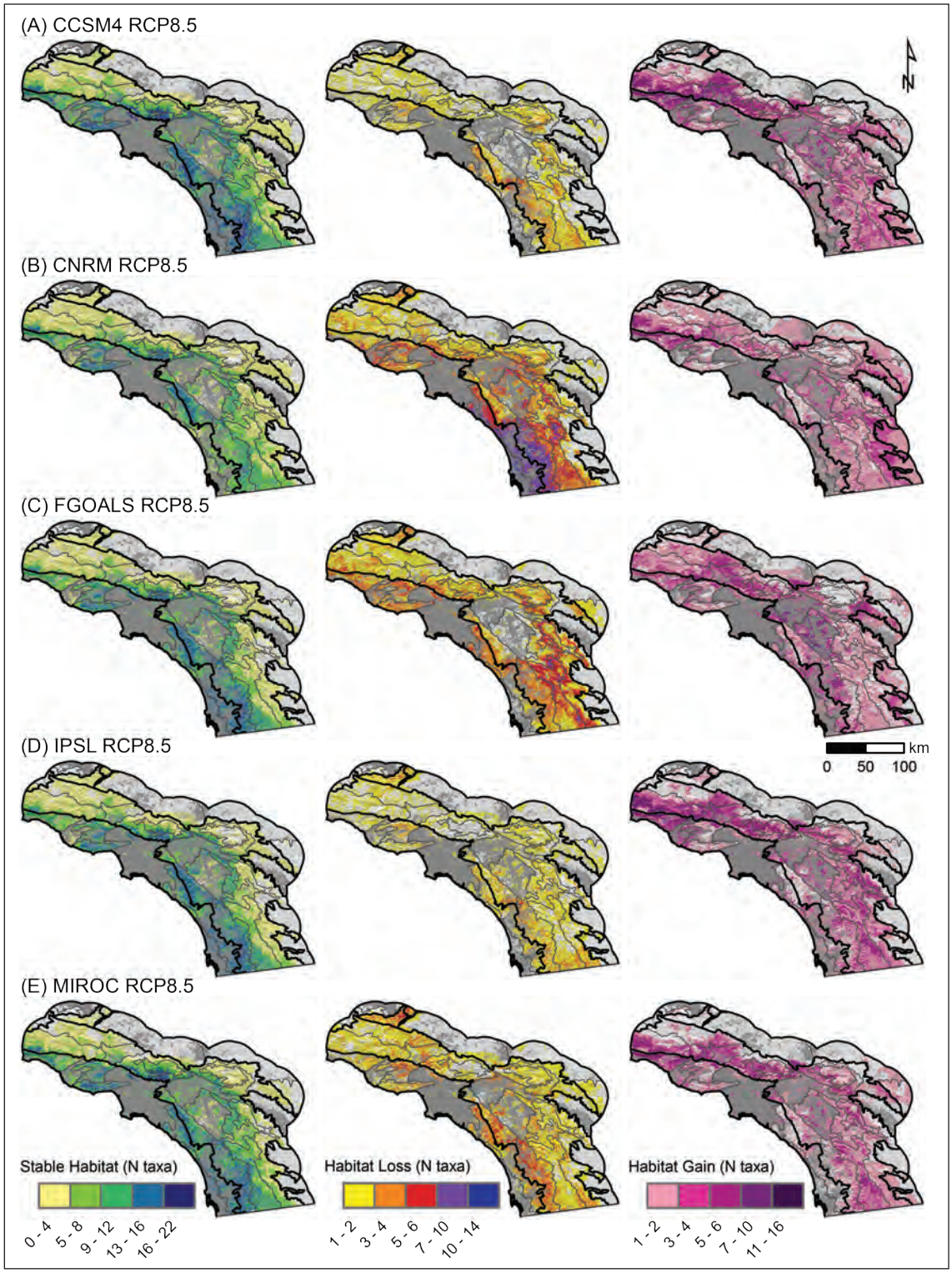

Figure 56—Projected habitat suitability for plant taxa associated with mixed chaparral-sage scrub under five future climate scenarios (A–E).

Appendix 6: Species Distribution Modeling Caveats

What Do SDM Habitat Suitability Maps Represent?

Predictions of baseline and future habitat suitability should be interpreted cautiously and are best applied in concert with expert knowledge about the biology, ecological relationships, population dynamics, and demographics of the species. Baseline maps identify the geographic distribution of suitable habitat meeting the abiotic (climate and parent geology) requirements of individual taxa under climate conditions averaged from 1951 to 1980. While not included in our models, biotic interactions, dispersal, human land use, and fire also influence plant distribution in southern California and affect the degree to which habitat suitability models match the known distribution, or realized niche, of the species modeled (Araújo and Peterson 2012). Future suitability maps show how spatial patterns in habitat suitability may change under midcentury climate conditions averaged from 2040 to 2069. We assumed unlimited dispersal ability within the study area for projections of suitability gain and assumed no dispersal (where species are unable to disperse to new areas of suitable habitat), for projections of suitability loss. Though biologically unrealistic, these dispersal assumptions are meant to cap the two extremes of potential habitat change under future climate. Suitable habitat projections are best interpreted as estimates of projected climate exposure rather than predictions of species persistence, which would require integrating species distribution models (SDMs) with models of population dynamics, physiological tolerances, and genetic variation (Dawson et al. 2011, Franklin et al. 2016, Richardson et al. 2014). For example, a prediction of suitability loss can identify high climate exposure and potentially stressful environmental conditions midcentury, but it does not indicate how the species may respond or if populations within the species range would respond differently.

Factors to Consider When Applying SDM in Decisionmaking

Spatial scale—

It is important to consider spatial scale (extent and resolution) when applying modeling results in decisionmaking. We modeled species-environment relationships at a regional extent and results are best used to inform decisionmaking within southern California. Our results are not transferable to other regions that may differ in the dynamics controlling habitat suitability and species distribution. When the underlying input data to the California Basin Characterization Model (CA-BCM) has high accuracy, spatial applications of the climatic and hydrologic data can be quite small, as fine as hillslope scale (Flint et al. 2013). However, uncertainties in the CA-BCM input variables, such as coarse resolution of soil data and difficulty incorporating

the impacts of human activities on hydrology for some areas in California (Flint et al. 2013) or measurement errors in the temperature and precipitation data (Oyler et al. 2015, Stoklosa et al. 2015), can limit the appropriate spatial resolution for applications. The occurrence data used in SDMs can introduce additional spatial uncertainties, such as spatial biases in collections and error in georeferencing accuracy (Barry and Elith 2006, Graham et al. 2008). Misidentifications (Costa et al. 2015) and even taxonomic ambiguities that arise as taxon concepts are refined (Romero et al. 2014) can affect model predictions and forecasts. Although our output habitat suitability maps have a high spatial resolution (270 m), patterns of suitability are best interpreted as summaries or trends at the ecological subsection to section level.

Uncertainty in future climate—

Uncertainty in future climate projections stems from a variety of sources. Climate change projections depend on general circulation models (GCMs)—mathematical representations of the Earth's climate system—that vary in their sensitivity of climate to greenhouse gases and radiative forcing (Daniels et al. 2012, Stott and Kettleborough 2002). Combined with scenarios for future greenhouse gas emissions, such as the representative concentration pathways (RCPs) used in the Intergovernmental Panel on Climate Change (IPCC) 5th assessment report (IPCC 2013), GCMs provide a range of possible future climate conditions for the 21st century. These projections tend to diverge dramatically across emission scenarios after the mid-21st century. Downscaling, which is necessary to convert the coarse scales of GCMs (250 km resolution) to finer regional-to-local scales relevant for land management, is another source of uncertainty in future climate projections. Precipitation, for example, is particularly challenging to forecast in southern California, as coarse-resolution GCMs are unable to represent the fine-scale variability introduced by the region's complex topography (Hughes et al. 2009). We use five GCMs under a 'business-as-usual' scenario that tracks our present high greenhouse gas emission trajectory (IPCC scenario RCP 8.5) to show how climate may change in southern California and highlight some of the uncertainty in these changes. It is possible that the five scenarios we selected may not encompass the actual climate conditions in southern California at midcentury. Temperature is projected to warm under continued greenhouse gas emissions, but to what degree and how quickly depends on a number of factors, including human actions to reduce those emissions (IPCC 2013). The magnitude and direction of precipitation change are also uncertain, with different GCMs projecting either increases or decreases in precipitation relative to the 20th century. Our selection of climate models spans both wetter (CNRM-CM5) and drier (MIROC-ESM) future conditions and can be used to explore sensitivity of habitat suitability to the direction in precipitation change.

Novel climates—

Climate change will likely result in novel future climate combinations that have no present-day analog, especially if greenhouse gas emissions continue to increase at current levels (Williams and Jackson 2007). Therefore, projecting SDM predictions under future climate often involves extrapolating models to novel environmental space outside the reference conditions used to train the models (Elith et al. 2010, Merow et al. 2013). In Maxent, the species-environment relationship can either be "clamped" to a constant probability when projected into novel space or simply extended, neither of which is likely to reflect a biologically realistic response (Merow et al. 2013). Consequently, suitability forecasts under novel conditions should be treated with extreme caution. Of the five future climate scenarios we considered, the CNRM-CM5 model had the greatest departure from the baseline 1951–1980 climate conditions. Novel climate conditions also introduce biotic uncertainty. Studies of past vegetation dynamics during the late Quaternary suggest that plant communities are unlikely to remain intact as species shift individualistically, with nonanalog conditions leading to nonanalog communities (Jackson and Overpeck 2000). Climate change, land use change, fire, and invasive species may all contribute to the rise of novel ecosystems, creating implications for conservation and restoration (Hobbs et al. 2009).

Uncertainty in SDM—

Uncertainty in correlative SDMs arises from a number of sources, some of which have already been discussed above. Model outputs depend on the quality of the input data, and errors in the species occurrences (e.g., Graham et al. 2008) and environmental predictors (e.g., Fernández et al. 2013, Stoklosa et al. 2015) introduce uncertainty into model predictions. Mismatches in the resolution between occurrence and environmental layers can compound these uncertainties (Wiens and Bachelet 2010); model resolution should ideally be matched to the scale of the conservation and management applications. For example, models built with coarse-scale environmental data may not be appropriate to inform decisionmaking at local or fine scales. Species geographical and ecological characteristics can also affect model performance and predictions (reviewed in Heikkinen et al. 2006). Methodological decisions and errors introduce uncertainty in SDMs, including choice of modeling algorithm, model misspecification, and missing covariates (Barry and Elith 2006, Beale and Lennon 2012). Methodological decisions in model parameterization affect the transferability of models in both space and time and are important to consider when projecting predictions under future climate change (García-Callejas and Araújo 2016). Comprehensive reviews on the sources of SDM uncertainty can be found

in Barry and Elith (2006), Beale and Lennon (2012), Heikkinen et al. (2006), and Wiens et al. (2009). Despite these challenges, SDMs can be a powerful tool to support decisionmaking. We emphasize the importance of close collaboration between modelers and data users to ensure that models are designed to address appropriate management questions and that uncertainties and limitations in application and interpretation are well-communicated.

Model assumptions—

Numerous papers have reviewed SDM assumptions and practical applications in conservation and management (Araújo and Peterson 2012, Guisan et al. 2013, Jarnevich et al. 2015, Schwartz 2012, Sinclair et al. 2010, Wiens et al. 2009). The degree to which a species violates certain SDM assumptions can lead to both overestimation and underestimation of risk under projected climate change (e.g., Early and Sax 2014, Schwartz 2012, Valladares et al. 2014). We highlight the fundamental assumptions underlying SDMs to better guide appropriate use of SDM results.

***Correlation*—**SDMs assume that a species' distribution is limited by the environmental variables included in the model; in our case climatic and geologic factors. For some species, the approach used to relate distributional data with environmental conditions may not correlate with the population-level processes driving species persistence. This is particularly relevant when extinction risk is sensitive to life history traits (e.g., recruitment response to fire) (Fordham et al. 2012, Lawson et al. 2010). Ultimately, SDMs linked to population dynamics are needed to address population persistence or extinction risk under projected climate change (Franklin et al. 2016).

***Equilibrium with climate*—**Species distribution models assume that the current distribution of a species is in equilibrium with the environment, meaning all suitable habitat is occupied by the species. However, dispersal, demographics, longevity, and biotic interactions (including humans) can affect the degree to which a species is in equilibrium with the current environment. For long-lived taxa, individuals and populations may continue to persist in areas where climate has become unfavorable for reproduction or seedling establishment. Projected climate change is expected to induce vegetation disequilibrium with climate at both leading and trailing edges of species ranges (Svenning and Sandel 2013). While unavoidable, this assumption should be acknowledged when interpreting SDM results.

***Niche conservatism*—**Species distribution models assume that the species-environment relationship remains fixed, or conserved, over space and time (niche conservatism) (Wiens and Graham 2005). That is, the model assumes that there is no local adaptation within a species range and that species will not have any adaptive response to changing conditions. Although an assumption of niche conservatism may be realistic for species with high dispersal ability and little population structure, or where the rate of climate change exceeds a species' adaptive capacity, it is likely to be violated for many species. For the widespread species we analyzed, our regional-scale modeling aims to capture relationships specific to southern California without including potentially confounding dynamics from other regions in the state. However, we are not able to address patterns of local adaptation and differential response to climate change without more detailed data on genetic variability of individual taxa across the landscape.

Glossary

actual evapotranspiration (AET)—Evaporative water loss (a function of temperature and radiation) from the ground surface and transpired by vegetation given prevailing water availability. Available water is defined as the amount of water held in the soil between wilting point and field capacity multiplied by soil depth (affected by precipitation over time) in the California Basin Characterization Model.

adaptive capacity—Ability of a system to adjust to climate change (including climate variability and extremes) to moderate potential damages, to take advantage of opportunities, or to cope with the consequences (IPCC 2007). At the population level, the ability of populations to adjust to climate change stimuli and maintain fitness through genetic change (evolutionary response), behavioral response, or plastic responses in physiology.

California Basin Characterization Model (CA-BCM)—A spatially explicit, regional water balance model that integrates physical watershed characteristics with historical or projected climate data to predict watershed-specific hydrologic responses for the California hydrologic region (Flint et al. 2013). It mechanistically models the pathway of precipitation into evapotranspiration, infiltration into soil, runoff, and the ability of water to percolate through the root zone and recharge groundwater, producing high-resolution surfaces (270 m) for the following variables: precipitation, air temperature, April 1st snowpack, recharge, runoff, potential evapotranspiration (PET), actual evapotranspiration (AET), and climatic water deficit (CWD).

climate scenario—Plausible and often simplified representation of the future climate based on a set of coherent and internally consistent assumptions about key driving forces and relationships (IPCC 2013).

climate exposure—Degree and nature to which a system is exposed to climate change. Exposure refers to extrinsic factors of climate change such as character, magnitude, and rate of change (Glick et al. 2011). Loss in climatic suitability predicted from correlative species distribution models based on climate variables can be interpreted in terms of climate exposure.

climate model—Numerical representation of the climate system based on the physical, chemical, and biological properties of its components, their interactions with feedback processes, and accounting for all or some of its known properties (IPCC 2013). See **general circulation model**.

climate projection—Simulated response of the climate system to a scenario of future emission or concentration of greenhouse gases and aerosols, or radiative forcing scenarios, often derived using climate models (IPCC 2013).

climatic water deficit (CWD)—Evaporative demand that exceeds water availability. Calculated as the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET) summed annually in the California Basin Characterization Model (Flint et al. 2013).

downscaling—A method that derives local- to regional-scale (10 to 100 km) information from larger scale models or data analyses (IPCC 2013).

emission scenario—Plausible representation of the future development of emissions of substances that are potentially radiatively active (e.g., greenhouse gases, aerosols) based on a set of coherent and internally consistent assumptions about driving forces and their relationships. Driving forces can include demographic and sociological development, technological change, etc. Concentration scenarios derived from emission scenarios are used as input to a climate model to compute climate projections (IPCC 2013). See **representative concentration pathways**.

general circulation model (GCM)—Comprehensive, three-dimensional global climate model that reflects the latest scientific understanding of complex physical, chemical, and biological properties of the climate system, as well as their interactions with feedback properties (IPCC 2013).

habitat suitability—Potential of a site to support a particular taxon. In species distribution modeling, the degree to which the environmental variables considered in the model (e.g., climate) are predicted to support the presence of a particular taxon in geographic space and time.

infraspecific—Refering to classification below the species level, as in subspecies and variety.

intraspecific—Refering to variation within a species, such as variation among populations or among individuals within populations.

Maxent—Species distribution modeling method tailored for presence-only data and based on a maximum entropy algorithm (Phillips et al. 2006).

potential evapotranspiration (PET)—Amount of water that could evaporate from the ground surface or transpire from vegetation given unlimited water, summed annually. In the California Basin Characterization Model, it is modeled from solar radiation and air temperature and partitioned to represent bare-soil evaporation and evapotranspiration owing to vegetation (Flint et al. 2013).

radiative forcing—Change in net radiative flux (expressed in W m^{-2}) at the top of the atmosphere owing to a change in a driver of the climate system, such as a change in the concentration of carbon dioxide or output of the Sun (IPCC 2013).

resilience—Degree to which a system rebounds, recoups, or recovers from a disturbance or hazard.

representative concentration pathway (RCP)—Scenarios of future emissions and concentrations of greenhouse gases, aerosols and chemically active gases, and land use/land cover. Each RCP provides just one of many possible future scenarios that could lead to the specific radiative forcing characteristics. Four RCPs were used to represent climate projections in the Intergovernmental Panel on Climate Change (IPPC) 5^{th} climate change assessment, RCP2.6, RCP4.5, RCP6.0, and RCP8.5 (IPCC 2013).

> **RCP8.5**—One possible high-concentration pathway in which radiative forcing reaches greater than 8.5 W m^{-2} by 2100.

sensitivity—Degree to which a species or system is affected, either adversely or beneficially, by climate variability or change (Glick et al. 2011, IPCC 2007). The effect may be direct (e.g., a change in crop yield in response to a change in the mean, range or variability of temperature) or indirect (e.g., damages caused by an increase in the frequency of coastal flooding owing to sea level rise) (IPCC 2007).

species distribution model (SDM)—Statistical model relating observations of species occurrence with environmental information to predict habitat suitability in space and time.

vulnerability—Degree to which a system is susceptible to, or unable to cope with, adverse effects of climate change, including climate variability and extremes. Vulnerability is a function of the climate exposure experienced by the system, its sensitivity, and its adaptive capacity (Glick et al. 2011).

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