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Effects of climate change and urban development on the distribution and conservation of vegetation in a Mediterranean type ecosystem

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Climate and land-use changes are projected to threaten biodiversity over this century. However, few studies have considered the spatial and temporal overlap of these threats to evaluate how ongoing land-use change could affect species ranges projected to shift outside conservation areas. We evaluated climate change and urban development effects on vegetation distribution in the Southwest ecoregion, California Floristic Province, USA. We also evaluated how well a conservation network protects suitable habitat for rare plant species under these change projections and identified primary sources of uncertainty. We used consensus-based maps from three species distribution models (SDMs) to project current and future suitable habitat for 19 species representing different functional types (defined by fire-response – obligate seeders, resprouting shrubs - and life forms – herbs, subshrubs), and range sizes (large/common, small/rare). We used one spatially explicit urban growth projection; two climate models, emission scenarios, and probability thresholds applied to SDMs; and high-resolution (90 m) environmental data. We projected that suitable habitat could disappear for 4 species and decrease for 15 by 2080. Averaged centroids of suitable habitat (all species) were projected to shift tens (up to hundreds) of kilometers. Herbs showed a small-projected response to climate change, while obligate seeders could suffer the greatest losses. Several rare species could lose suitable habitat inside conservation areas while increasing area outside. We concluded that (i) climate change is more important than urban development for vegetation habitat loss in this ecoregion through 2080 due to diminishing amounts of undeveloped private land in this region; (ii) the existing conservation plan, while extensive, may be inadequate to protect plant diversity under projected patterns of climate change and urban development, (iii) regional assessments of the dynamics of the drivers of biodiversity change based on high-resolution environmental data and consensus predictive mapping, such as this study, are necessary to identify the species expected to be the most vulnerable and to meaningfully inform regional-scale conservation.

Keywords: climate change; species distribution models; urban development; plant functional type; Mediterranean type ecosystem

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Introduction

Changes in land-use and climate, in order of relative contribution, are the two main drivers expected to greatly and negatively impact biodiversity in all terrestrial ecosystems in the coming century (Sala et al. 2000). Historically, conversion of wildlands to agricultural and urban land-use has caused considerable loss of biodiversity (Foley et al. 2005), a trend that is expected to continue into the future (Alcamo et al. 2006). Anthropogenic climate change during the past century has resulted in changes in phenology, species ranges, and community composition (Walther 2010). Conservation areas have been established worldwide, in part, to address land-use change. However, a number of studies project a loss of habitat, ranging from 6% to 48% (e.g. Araújo et al. 2004), from conservation areas due to climate change. Many studies have examined the effectiveness of conservation areas in meeting their conservation goals under projected climate change (e.g. Lemieux and Scott 2005) and others have done the same in the context of land-use change (e.g. Figueroa and Sanchez-Cordero 2008). Nevertheless, very few studies have considered the spatial cooccurrence of these threats in combination in order to evaluate how species projected to shift outside the bounds of conservation areas might be further affected by ongoing landuse change (Dirnböck et al. 2003, Hannah et al. 2005). Studies that include only climate or land-use change are likely to inadequately convey the impacts of both on biodiversity (de Chazal and Rounsevell 2009).

Understanding the role conservation areas play in providing safe haven for species whose distributions are projected to shift within reserves due to climate change, and expected to decline outside reserves due to land-use change, is of paramount importance in developing additional conservation strategies to address global change. Spatial ecology, focusing on the role of space and time in ecological processes (Skidmore *et al.* 2011), and geographic information science, with its deep roots in environmental modeling (Goodchild 2010), provide the framework, data, and analysis tools to support conservation planning. In this study, we used high-resolution geospatial data and predictive mapping methods (Franklin 1995) to examine the ability of a conservation network to protect the habitat of a suite of plant species in a biodiversity hot spot expected to be disproportionately affected by climate change and urban growth: the Southwest ecoregion of the California Floristic Province, USA (Figure 1).

Mediterranean Type Ecosystems (MTEs) are floral biodiversity hot spots (Myers *et al.* 2000) with some of the highest values of plant species richness and endemism globally (Cowling *et al.* 1996). MTEs are also among the biomes most threatened by global change (Sala *et al.* 2000). Urban and agricultural areas increased by 13% and 1%, respectively, from 1990 to 2000 in MTEs (Underwood *et al.* 2009). The range of some species in MTEs is expected to decrease even where the Mediterranean climate extent is projected to increase (Klausmeyer and Shaw 2009). Also, the generally small size of conservation areas in MTEs makes the time for current climate to cross a conservation area (climate residence time) one of the shortest of all biomes (Loarie *et al.* 2009). The high biodiversity and sensitivity to threats of MTEs makes it critical to understand the role of conservation areas for protecting MTE biodiversity under scenarios of future land-use and climate change.

The combined effects of land-use and climate change on biodiversity protection have seldom been addressed at the regional level in MTEs (e.g. Bomhard *et al.* 2005, Yates *et al.* 2010). We projected the impacts of land-use and climate change on the spatial distribution and protection of plant diversity within California's Southwest ecoregion (Figure 1) because (i) urban development is extensive and projected to expand (Syphard *et al.* 2011a), (ii) high-resolution downscaled climate data for several climate change scenarios exist for



Figure 1. Map showing the location of the California Floristic Province (thin black line) within the State of California (dotted black line on gray background), USA, the Natural Community Conservation Planning network (diagonal gray lines), and the modified Southwest ecoregion (solid gray) within the California Floristic Province. The combined effects of climate and land-use change analysis (analysis shown in Table 2 and Figure 2) were performed in the areas highlighted on the inset map.

this region, and, (iii) there is a well-developed conservation planning network (Natural Community Conservation Planning (NCCP)) whose effectiveness can be evaluated in light of future urban development and climate change. The NCCP program goal is to promote conservation of broad-based natural communities and species diversity by involving different stakeholders and key interests for addressing the cumulative impacts of development on biodiversity, while continuing to allow for appropriate development and growth in the region (California Fish and Game Code 2003).

Species distribution models (SDMs) extrapolate species occurrence data in space and time to provide projections of suitable habitat using statistical models (Franklin 2010a, Skidmore *et al.* 2011). Models calibrated for current climate conditions can be used to map potential future species distributions (habitat suitability) using climate models to project the effect of climate change on the spatial distribution of species (e.g. Thuiller *et al.* 2011, Franklin et al. 2013). SDMs are considered the most plausible means by which we can estimate species' exposure to climate change risk (Dawson et al. 2011). Yates et al. (2010) projected the impact of climate change on MTE plant distributions using SDMs in combination with current land-use patterns and found that the projected collapse for many Banksia species' ranges is worse when land-use is taken into account. However, that study only considered current land-use patterns and not future land-use changes. The most comprehensive study using SDMs to project the impacts of climate change on the California Floristic Province MTE concluded that up to 66% of all endemic plant species would experience a habitat reduction of up to 80% by the end of the twenty-first century (Loarie et al. 2008). However, Loarie et al. (2008) did not consider the effects of land-use change, or the role of conservation areas, in protecting plant species habitat under climate change. Moreover, that study was based on low-resolution (~ 12.5 km grid cells) environmental data, which can overestimate the area of suitable habitat projected by SDMs owing to spatial generalization (Seo et al. 2009, Franklin et al. 2013). Low-resolution climate data also do not characterize topoclimate, the strong effect of terrain, slope and aspect on the distribution of solar radiation (Dubayah and Rich 1995), and, consequently, the thermal environment (Sears et al. 2011) and soil-moisture availability experienced by organisms. Topoclimate varies at the scale of the average slope length of the terrain (Mark and Aronson 1984), typically on the order of tens of meters and, along with edaphic drivers, defines the physical template that organisms experience, and thus constrains habitat suitable for growth, survival, and reproduction (Dobrowski 2011).

We selected 19 species that span a range of life forms, fire responses, and range sizes representative of plant functional types (PFTs) found in MTE (Cowling and Campbell 1980) and fire-prone ecosystems globally. These species characterize the MTE shrub communities (chaparral and sage scrub) that dominate our study area. This selection allowed us to search for patterns of projected responses that varied with species attributes, thereby permitting generalization to other species that share these characteristics. The questions addressed in this study were as follows:

(1) What is the projected effect of climate change on the spatial distribution of the plant species studied, measured both by habitat area change and range centroid shift? How does the effect vary by species, plant functional type, and range size, i.e. small-range (rare) versus large-range (common) species?

Based on previous studies that projected plant habitat decreases, we expected our study species to lose suitable habitat under climate change, and species range centroids to shift proportionate to the shift in similar climate conditions (Iverson and Prasad 1998, Loarie

et al. 2008). We expected the resprouter shrub PFT (those species that resprout in response to fire) to be most affected by a drier future climate because establishment of resprouter seedlings has been shown to depend on rainfall the year after a fire (Esther *et al.* 2010). Further, we expected rare species to lose more suitable habitat under climate change scenarios than common species because rare species tend to occur in localized climatic conditions that have been projected to shrink more than areas with dominant climate types (Ohlemüller *et al.* 2008).

(2) What is the extent of suitable habitat for the study species supported by the current network of conservation planning areas, the individual planning areas versus the entire network, and how is that projected to change under climate change and urban growth scenarios?

We expected the current network might be insufficient to protect a significant fraction of species ranges as the climate in many of these areas could shift in such a way that there is no overlap between the coolest parts of the conservation area in the future and the warmest fraction today (Ackerly *et al.* 2010), and urban growth might take place in areas of future suitable habitat. Another possibility, however, is that suitable habitat might shift from one individual planning area to another within the network.

(3) What are the major sources of uncertainty for these projections? How much do different (a) thresholds applied to projected probabilities of species occurrence to define suitable habitat, (b) climate models, and (c) emission scenarios influence the projected distributions of suitable habitat?

We hypothesized that the use of different threshold criteria (Liu *et al.* 2005) and climate models, but not emission scenarios (Buisson *et al.* 2010), would contribute most to the variation observed in our results.

Methods

Study area, species, and geospatial data

We analyzed the effects of climate change on plant distributions for a slightly modified Southwest ecoregion (Syphard *et al.* 2011b) of the California Floristic Province that included the entire Transverse Ranges and the southern Coast Ranges extending into northern Santa Barbara and San Luis Obispo Counties (Figure 1). This ecoregion encompassed most of all of the ranges of the study species. The combined effects of urban growth and climate change were analyzed in the southern portion of the Southwest ecoregion, a subregion (1.61 million ha) where the NCCP areas are located and therefore where projections of urban growth were developed (Figure 1 inset). The total area under the conservation planning network in this subregion is approximately 1.39 million ha.

We compiled spatially explicit data on occurrences for 19 plant species (Table 1) from the Califora database (http://www.califora.org) and the California Department of Fish and Wildlife's Natural Diversity Database (http://www.dfg.ca.gov/biogeodata/cnddb/). We defined the PFTs by life form (herbs, shrubs, and subshrubs) (Cowling and Campbell 1980). Shrubs were further distinguished by fire response as obligate seeders or resprouters

					Current	area (ha)
Species	PFT class	Range size class	Number presences	Avg. AUC	Low threshold	High threshold
Acanthomintha ilicifolia	herb	small	104	0.970	810,754	15,614
Adenostoma sparsifolium	resprshr	large	374	0.954	365,445	178,618
Arctostaphylos glandulosa ssp. glandulosa	resprshr	large	393	0.894	696,704	13,415
Arctostaphylos rainbowensis	resprshr	small	73	0.960	758,556	8250
Ceanothus greggii var. perplexans	OS	large	289	0.957	454,809	107,202
Ceanothus tomentosus	OS	large	167	0.946	620,258	80,649
Ceanothus verrucosus	OS	small	126	0.987	312,163	30,750
Hesperocyparis (syn Cupressus) forbesii	OS	small	38	0.905	379,372	2137
Deinandra conjugans	resprshr	small	66	0.998	145,872	105,489
Delphinium hesperium	resprshr	small	45	0.979	120,783	10,509
Eryngium aristulatum var. parishii	resprshr	small	99	0.983	529,382	121,007
Galium angustifolium ssp. angustifolium	subshr	large	132	0.816	268,690	35,340
Hazardia squarrosa	subshr	large	637	0.870	275,525	47,948
Keckiella antirrhinoides	subshr	large	80	0.909	928,019	27,855
Quercus dumosa	resprshr	small	261	0.998	72,019	13,511
Quercus engelmannii	resprshr	large	181	0.901	742,076	90,020
Trichostema lanatum	resprshr	large	121	0.852	375,493	76,592
Viguiera laciniata	subshr	small	35	0.969	542,326	6772
Xylococcus bicolor	resprshr	large	190	0.951	352,846	77,215

Table 1. Study species and species distribution models (SDMs).

Notes: PFT, plant functional type; OS, obligate seeders; herb, herbs; resprshr, resprouting shrubs; subshr, subshrubs; Avg. AUC, area under the curve for three SDMs. Range size is defined in text.

(Keeley and Davis 2007). We designated small-range/rare species using the Calflora threatened index and a maximum range size of 10,000 km² (estimated from the total area of sub-ecoregions within which occurrences have been recorded).

We used the same set of six climate, two terrain, and three soil variables as mapped predictors to project both present and future suitable habitat distributions. They were selected based on their relationship to the distribution of plant species in Southern California (e.g. Syphard and Franklin 2010, Franklin *et al.* 2013). We used climate data (monthly precipitation, and temperature) that were statistically and spatially downscaled to 90 m (for details, see Flint and Flint 2012) and derived bioclimatic variables describing current climate, from monthly averages for the period 1970–1999. We selected 6 largely uncorrelated bioclimatic variables from 10 initial candidates using principal component analysis: maximum temperature of the warmest quarter, growing degree days above 5°C, mean annual precipitation, temperature seasonality, precipitation of the warmest quarter, and an aridity index (the ratio of annual precipitation and potential evapotranspiration).

Bioclimatic variables describing end of century climate were derived from monthly averages using downscaled future climate projections for the period 2070–2099 (attributed to the year 2080) simulated using the Geophysical Fluid Dynamics Laboratory (GFDL) model, and the Parallel Climate Model (PCM). These two models were used because they

realistically simulate the distribution of temperatures and the strong seasonal cycle of precipitation in California's recent historical climate (Cayan *et al.* 2008). Additionally, we used two contrasting emissions scenarios, A2 (medium-high) and B1 (low), developed by the Intergovernmental Panel on Climate Change based on demographic and socioeconomic development, and technological change (Nakićenović *et al.* 2000). The GFDL model is relatively sensitive to greenhouse gas forcing while the PCM is less sensitive. Therefore, the GFDL model projects higher end-of-century temperatures than the PCM in our southern California study region. Precipitation projections vary between the two models, with GFDL projecting 22% and 26% decreases in annual precipitation by the end of the century for the A2 and B1 emissions scenarios, respectively, while PCM projects an 8% and 7% increase for A2 and B1, respectively (Cayan *et al.* 2008). These contrasting scenarios have been widely used to project climate change impacts on California ecosystems because they encompass the range of conditions that would be projected by a larger ensemble of climate models (e.g. Lenihan *et al.* 2003).

We used slope gradient (steepness) and potential summer solstice solar insolation (Rich *et al.* 1995), both derived from a US Geological Survey 30-m resolution digital elevation model, to describe terrain effects on the biophysical environment. The soil variables used were soil depth, soil available water capacity, and soil pH. These variables were extracted from the California State Soil Geographic Database (STATSGO). Terrain and soil variables were assumed to remain unchanged over the modeling period. All climate, terrain, and soil variables were resampled to 100 m to match the resolution of the urban growth projections.

Current and future urban extent

We used projected urban development to represent future land-use change, as it is virtually the only type of land-use change taking place in southern California where population growth is anticipated, and little undeveloped land is suitable for agriculture. Syphard *et al.* (2011a) derived a map of current urban extent from a national data set, and urban development was simulated on an annual time step from 2000 to 2050 using SLEUTH, a spatially explicit, well-calibrated cellular automaton model (Clarke 2008). Federal and conservation lands were excluded from development, but NCCP lands (86% of the region) were allowed to develop. Although the urban growth and climate change simulations are asynchronous, overlaying urban growth projections for 2050 with 2080 climate change projections is reasonable because the projected urban development rate plateaued by 2050 owing to diminishing amounts of undeveloped private land (for details, see Syphard *et al.* 2011a).

Species distribution models

We created habitat suitability models with an ensemble of three SDM methods for each species using present climate conditions to estimate current habitat suitability. We then substituted future climate data in the models to create maps of climatically suitable habitat for the future based on the ensemble. We used generalized additive models (GAMs), decision trees (RandomForests (RFs)), and maximum entropy (MaxEnt) models because they are contrasting approaches (Franklin 2010a) that are among the best performing SDMs methods (Elith *et al.* 2006).

To fit the SDMs, we used 10,000 random points across the Southwest ecoregion for background (MaxEnt) or as pseudo-absences (GAM, RF). We down-weighted the absence data for GAM and RF so that the sum of the weighted absences was equal to the sum of the number of presences in order to achieve an optimal balance between omission and

commission errors (McPherson *et al.* 2004). All environmental variables were used in all models for all species. GAMs were estimated using a logit link for the binary response, and smoothing splines using up to four target degrees of freedom. We estimated RFs from 500 trees using three randomly selected variables for each tree. We created MaxEnt models using the default settings for features and regularization, and one sample without replacement, randomly dividing the sample 75/25% for training/testing (we also tested 10 replications with replacement but did not find any substantial difference between the resulting models). We evaluated the predictive performance of individual SDMs based on 500 bootstrapped estimates of the area under the receiver operator curve (AUC), a measure of a model's ability to discriminate occurrence from background/absence (Marmion *et al.* 2009). Although AUC must be interpreted in light of potential biases (Golicher *et al.* 2012, Hijmans 2012), it is a threshold-independent metric useful for comparison with other studies (Elith and Graham 2009). Models were fit using R (http://CRAN.R-project.org/) for GAM and RF and MaxEnt 3.3.3a software (Phillips *et al.* 2004, 2006).

We developed consensus maps for each species from the accuracy-weighted average of all models (Marmion *et al.* 2009). Consensus forecasting measures the central tendency for an ensemble of forecasts; in averaging several models, the 'signal' of interest emerges from the 'noise' associated with individual model errors and uncertainties (Araújo and New 2007).

From the continuous probability maps produced by the ensemble SDMs, we created binary maps using two thresholds (cut-off of occurrence probability value) to discriminate suitable versus unsuitable habitat. This allowed us to calculate habitat gained, lost, and stable under climate change and land-use scenarios and made our results comparable to other studies that also used thresholded projections (e.g. Loarie *et al.* 2008). We used two well-established threshold criteria based on model performance: Maximum (Sensitivity + Specificity), which minimizes probability of total false positives and negatives, as a low threshold, and MaxKappa, which maximizes the proportion of correctly classified locations after accounting for the probability of chance agreement, as a high threshold (Liu *et al.* 2005).

After creating the binary current (year 2000) and future suitability maps (year 2080), we overlaid these maps with current and future urban extents to estimate the separate and combined effects of climate and land-use change on the spatial distribution of suitable habitat. Additionally, we calculated the centroid of the current and future suitable habitat for each species and the distance between the two centroids as an indicator of the potential displacement of core suitable habitat (Iverson and Prasad 1998).

The suitable habitat projections were non-normal, and the sample sizes and variances were different among groups. Therefore, we used a non-parametric procedure for comparing multiple means in unbalanced designs developed by Herberich *et al.* (2010), to determine if projected habitat area changes resulting from different climate models, emission scenarios, and thresholds, or by grouping the plants into PFTs or range sizes (Table 1), were significantly different ($\alpha = 0.05$). Tests were implemented using the multicomp package in R.

Conservation planning network

We analyzed change in suitable habitat for all small-range/rare species (Table 1) because they comprise 'covered' (protected) species in the seven NCCP areas located within San Diego, Riverside, and Orange Counties. Although the conservation planning network encompasses the entire region, the individual planning areas are developed and implemented separately. We only included the part of the planning areas that lie within the Southwest ecoregion boundaries (Figure 1 inset). We compared projections for two of the planning areas (San Diego County Multiple Species Conservation Plan and San Diego County Multiple Habitat Conservation and Open Space Plan) versus all other NCCP areas aggregated, in order to investigate the ability of individual and combined conservation planning areas to protect suitable habitat for these rare species in the face of climate change and urban growth. All spatial data processing was done using ArcGIS 9.3.1 (ESRI, Redlands, CA, USA).

Results

Projected effects of climate change on habitat distribution

SDMs had high accuracy (bootstrapped AUC > 0.9) except for four large-range species (Table 1). Precipitation and maximum temperature of the warmest period were generally the variables that contributed the most to model fit. Soil variables and potential summer solar insolation were generally the least important variables, but were important for some species (Table A1).

We projected between 0 and 9 of the 19 species to undergo a net loss of suitable habitat under the PCM, and between 1 and 15 of these species to undergo a net loss of suitable habitat under the GFDL model (Table A2). Additionally, under climate change scenarios (A2 or B1), we projected up to five of the species to lose all suitable habitat within the Southwest ecoregion by 2080 (Table A2). Two of the species that were projected under climate change to maintain suitable habitat somewhere within the ecoregion lose their entire current suitable habitat (i.e. there is no overlap between projected current and future habitat), with six additional species losing 90–99% of their current habitat (Table A3). The variation in our estimates arises from the use of different climate models, emissions scenarios, and thresholds (see Uncertainty), and the range of species losing or gaining habitat is generally bracketed between the least-changed (PCM, low emission scenario and low threshold) and the most-changed scenario (GFDL, medium-high emission scenario and high threshold).

Species' habitat centroids were projected to shift an average distance of 78 km across all scenarios under the low threshold and 55 km under the high threshold (Figure A1). However, the average per-species suitable habitat shift with the low threshold was greater than that for the high threshold for only 11 of the 19 species. Larger centroid shifts were projected with the low threshold because the projected current and future habitat extents were generally greater than those projected using the high threshold. The largest average projected centroid shift (average of the two climate scenarios and two emission scenarios under each threshold for each species) was 185 km, but individual projections suggested suitable habitat centroids could shift up to 440 km.

The high threshold results suggested obligate seeders would be the PFT whose habitat distribution is most affected by climate change (Figure A2). The differences in projected area change between obligate seeders and the other PFTs were all significant using the high threshold (herbs P = 0.04, resprouting shrubs P < 0.01, and subshrubs P < 0.01). On the other hand, when using the low threshold, the average suitable area of all four PFTs was projected to increase, with herbs gaining the smallest area (143,000 ha). The increase in area for herbs (P = 0.02) and obligate seeders (P = 0.03) using the low threshold was significantly less than for subshrubs, but not significantly different from resprouters (Figure A2).

We projected suitable habitat area for small-range species to increase less (low threshold) or show little change (high threshold) compared to large-range species (Figure A3); the difference was significant (P = 0.006) only for the low threshold.

Climate and land-use change in conservation planning network

Current suitable habitat within the NCCP network for the nine rare species ranges from \sim 2000 to 77,000 ha (Table 2). Future suitable habitat for the same species in the NCCP network was projected to range from \sim 3 to 48,000 ha. We projected climatically suitable habitat inside the NCCP network to decrease for seven of the nine rare species and increase for two (Table 2). However, three of the species projected to lose suitable habitat within the NCCP network were projected to gain habitat overall (in the ecoregion), one species was projected to lose a proportional amount of overall and protected habitat, and the three others to lose most of their habitat.

Current urban extent in the subregion (266,000 ha) was projected to increase by 48% to approximately 395,000 ha in 2050 (Syphard *et al.* 2011a). The projected rate of development is high at the beginning but slows considerably by about 2020 (Syphard *et al.* 2011a). The relative effects of climate and urban development differed among species. We projected all nine small-range species to lose habitat in response to urban development; however, four species were projected to lose only a small amount (<200 ha; Table 2). We projected climate change to have a negative impact on suitable habitat for seven of these species, and a positive impact on two (Table 2). Climate change was the dominant driver of suitable area loss for five of the seven species negatively impacted by urban growth and climate change. We also projected climate change to be the dominant driver of suitable area change for the two species negatively impacted by urban growth but positively impacted by climate change (Table 2). The combined effect of climate change and urban development was not simply additive. The combined effect was smaller than the sum of both effects for five of the rare species, while it was larger for the remaining four species (Table 2).

We projected an increase in the extent of suitable habitat for two species in the San Diego County Multiple Species Conservation Plan area (Figure 2a). Additionally, we projected a considerable increase for two species and a slight increase for another one in the San Diego County Multiple Habitat Conservation and Open Space Plan area (Figure 2b). The other NCCP areas, collectively, were projected to become a refuge for two of the rare species (Figure 2c). However, some of these species overlap, and the whole NCCP network was projected to remain a refuge for only four of the nine rare species. All four of these species were projected to gain a substantial amount of total suitable habitat in the ecoregion; however, two of them lose on average 30% and 78% of their protected habitat (Table 2). These results were based on suitable habitat areas calculated using the high threshold cut-off but the same pattern was observed using the low threshold (Figure A4).

Uncertainty

On average, we projected a slight (high threshold) to moderate (low threshold) increase in species' suitable habitat, but this was mainly driven by a few species projected to gain a large amount of habitat while most were projected to lose habitat. The difference between the average habitat change projected by the high and the low thresholds was statistically significant for all species (P < 0.001). When we separated the results from the climate models by threshold, the difference between the projected changes in suitable area under

Table 2. Projected current and future suitable habitat and average suitable habitat gained or lost due to urban growth (UG) and/or climate change (CC) for nine small-range species in the Southwest ecoregion of the California Floristic Province. Protected is the portion of the suitable habitat, either present or future, inside the Natural Community Conservation Planning network. Total includes suitable habitat that is outside of the subregion that contains the conservation network. Protected habitat percentage change is the projected change inside the conservation network between 2000 and 2080. Average area gained or lost from current protected area was calculated from two climate change models (PCM and GFDL) and emissions scenarios (A2 and B1), applying the high threshold to projected probabilities of species occurrence.

	Current	area (ha)	Future	area (ha)	Protected habitat	Averag	ge area (ha) gained/	'lost
Species	Total	Protected	Total	Protected	percentage change	Urban growth	Climate change	UG + CC
Acanthomintha ilicifolia	15,614	13,480	20,898	10,385	-23	-1709	-684	-3095
Arctostaphylos rainbowensis	8250	8225	25	3	-100	-182	-8222	-8222
Ceanothus verrucosus	30,750	24,487	3022	42	-100	-3821	-24,297	-24,445
Hesperocyparis (syn Cupressus) forbesii	2137	2124	1403	1369	-36	-4	-752	-756
Deinandra conjugans	105,489	69,440	157,814	48,324	-30	-30,549	-2661	-21,117
Delphinium hesperium	10,509	10,453	31,755	30,699	194	-91	20,479	20,246
Eryngium aristulatum var. parishii	121,007	77,237	132,707	16,872	-78	-13,862	-57,743	-60,366
Quercus dumosa	13,511	8227	150	67	-99	-5176	-8115	-8160
Viguiera laciniata	6772	6500	44,796	37,812	482	-223	34,033	31,312



Figure 2. Current and projected area of suitable habitat for small-range/rare species in (a) San Diego County Multiple Species Conservation Plan Area, (b) San Diego County Multiple Habitat Conservation Open Space Plan Area, and (c) all other Natural Community Conservation Planning areas in the Southwest ecoregion, in response to projected climate change by 2080. The average and standard deviation were calculated from two different climate change models (PCM and GFDL) and emission scenarios (A2 and B1), using the high threshold to projected probabilities of species occurrence to define suitable habitat. ACIL, *Acanthomintha illicifolia*; ARRA, *Arctostaphylos rainbowensis*; CEVE, *Ceanothus verrucosus*; CUFO, *Hesperocyparis* (syn *Cupressus*) forbesii; DECO, *Deinandra conjugens*; DEHE, *Delphinium hesperium*; ERAR, *Eryngium aristulatum* var. *parishii*; QUDU, *Quercus dumosa*; VILA, *Viguiera laciniata*.

the two models was not significant (Figure A5). But when we separated the emissions scenarios by threshold, the difference between the suitable area change in each emissions scenario was significant (P = 0.05 for high and low threshold), with the medium-high emissions scenario projecting more modest average gains (~ 2800 ha, A2 high threshold) than the low emissions scenario ($\sim 60,000$ ha, B1 high threshold) (Figure A5).

Discussion

Projected effects of climate change on species habitat distribution

Our results coincide with other studies in MTEs (Bomhard et al. 2005, Loarie et al. 2008, Yates et al. 2010) that project suitable habitat reduction in response to climate change. However, the magnitude of habitat loss projected for the same 19 species by the study that modeled habitat for all endemic plant species in the California Floristic Province using low-resolution geospatial data (Loarie et al. 2008) ranged from 3 to 468 times larger than ours (depending on the threshold we used). This difference was not related to differences in prevalence (species frequency in the training data) between the two studies, nor was there a relationship between suitable area and prevalence in our study. The pixel area for the geospatial data we used was four orders of magnitude finer grained $(0.01 \text{ km}^2 \text{ vs.} \sim 156 \text{ km}^2)$ than those used by Loarie *et al.* (2008) and the differences in our results were consistent with previous findings that coarser scale climate data projects larger species ranges area owing to spatial generalization (Franklin et al. 2013). Further, finer scale models more accurately project current species distributions (Seo et al. 2009). SDMs using fine-scale climate data that capture topoclimate effects show markedly different range loss and extinction estimates under climate change scenarios than coarse-scale models (see Trivedi et al. 2008). Because topoclimate and soil conditions control the local conditions that organisms experience (Dubayah and Rich 1995, Dobrowski 2011, Sears et al. 2011), the resulting projections are appropriately scaled for spatially explicit analysis of the NCCP network, although still affected by the uncertainties evaluated in this study.

We found the average magnitude of projected centroid shift to be similar to that of coarser resolution studies (e.g. Iverson and Prasad 1998, Loarie *et al.* 2008), suggesting that data resolution does not strongly influence centroid shift estimates. We projected shifts in the location of core habitat on the order of tens of kilometers or more by the end of the century. The need to disperse long distances and across urbanized landscapes might be problematic for species in several of the genera considered, e.g. *Arctostaphylos, Ceanothus,* and *Xylococcus*, that tend to disperse close to the parent plant most of the time, or rarely recruit from seeds (Keeley and Davis 2007).

Effects of climate change on different PFTs and range sizes

The PFT most affected by projected climate change impacts was obligate seeders rather than resprouters. This contrasted with our prediction that resprouters would be most susceptible, which we based on a published model (Esther *et al.* 2010) that explicitly incorporated fecundity (seed production), survivorship, dispersal, and establishment, especially as a function of rainfall. Our approach, in contrast, identified the range of climate conditions defined by our bioclimatic variables that are correlated with current distributions (of adult plants) and then projected the future location of similar conditions. While resprouters may be sensitive to dry conditions at the seedling stage, they can persist by resprouting, and therefore, they may occur as adults over a broader range of current climatic conditions than would be suitable for seedling establishment. The obligate seeders considered in this study are dominated by *Ceanothus* species (Table 1); habitat specialization may be related to niche partitioning in this genus (Ackerly *et al.* 2006) and SDMs more accurately project the distributions of habitat specialists (vs. generalists) and of obligate seeders (Syphard and Franklin 2010). Half of the obligate seeders also had small ranges so the effects of functional type could be confounded by the effect of small range size. Nonetheless, if the projected reduction in climatically suitable habitat for obligate seeders is a general result, then this, compounded with slow recruitment due to altered fire regimes (Regan *et al.* 2012) and short dispersal distances, makes conservation planning for obligate seeders a priority. While about half of the small-range species were projected to lose suitable habitat, the dominant climate types associated with large-range species were projected to become more common, possibly facilitating the expansion of the common species at the expense of the rare species.

Climate and land-use change in conservation planning network

In its current configuration, the NCCP network is ineffective in protecting climatically suitable habitat for all the covered species under the future climate and land-use scenarios we examined. We had anticipated habitat for a covered species might decrease in one planning area and increase in another, suggesting the need for greater coordination among planning areas. That was only the case for one species in our study (Figure A4). If we consider the six rare species for which some suitable protected habitat may persist, three of them were projected to lose protected habitat while their habitat increased overall in the ecoregion but outside the conservation network (Table 2). To effectively protect at least as much habitat as is currently protected under these future scenarios, current conservation areas could be replaced by new ones that are more likely to achieve conservation goals (Fuller et al. 2010) and/or additional conservation areas could be created in areas that are robust to uncertainty. Consensus projections like ours can inform these decisions as they identify areas that are selected consistently in different models and offer the least investment risk (Carvalho et al. 2011). An additional way to protect species' suitable habitat area at a future time would be to create conservation easements, manage land-use activities in the landscape matrix (Franklin 1993), and coordinate conservation management regionally to allow for the protection of species outside of conservation areas (Griffith et al. 2009).

For our study species and region, projected habitat loss due to climate change was far larger than the loss due to projected patterns of land-use change. Our results are in contrast with the results of Sala *et al.* (2000), who found that projected land-use change was a larger threat than climate change to habitat at the global scale and in MTEs. Even though the land-use change modeling did not encompass the same temporal domain as the climate change modeling, the rate of land-use change projected by the year 2050 was negligible due to diminishing amounts of undeveloped private land in this region. Even if the area of habitat loss due to projected urban growth were doubled, land-use change would become the dominant factor for only one additional species (Table 2). However, while SDMs based on climate simulations project species' exposure to risk, urban development leads to direct loss of habitat and has other indirect impacts on species, such as altering fire regimes and hydrology. These results highlight the need to explicitly consider scale in order to better understand the relative importance of the regional drivers of biodiversity change in support of conservation policy (Skidmore *et al.* 2011).

Uncertainty

SDMs take advantage of the well-established relationship between climate and plant distributions (reviewed in Franklin 2010a). However, SDMs are correlative models built on current distributions that do not account for physiological tolerances (the fundamental niche), dispersal limitations, or demographic processes affecting species' migration (Franklin 2010b). SDMs may overestimate climate-driven range contraction because species may be able to persist in currently occupied habitat better than expected; therefore, for conservation planners SDM projections might be more reliably used to identify where climatically suitable habitat may expand (Schwartz 2012). And while predictive performance of future ('out of sample') projections from SDMs is likely to be lower than performance estimated from current distributions (Dobrowski *et al.* 2011), SDMs can provide information on species' exposure risk to declines in climatically suitable habitat (Dawson *et al.* 2011).

We addressed the uncertainty that is introduced by using different modeling techniques (Pearson *et al.* 2006) with consensus forecasting, which reflects the central tendency of selected forecasts and increases the agreement between projected and observed range shifts. Uncertainty due to thresholds (cut-off of occurrence probability value) (Thuiller 2004), climate change models (Beaumont *et al.* 2008), and emission scenarios (Thuiller 2004) was characterized by using a range of values or scenarios for each. Our results were consistent with previous studies in the California Floristic Province (Loarie *et al.* 2008) and other MTEs (e.g. Fitzpatrick *et al.* 2008, Yates *et al.* 2010), which found that the projected variation in suitable area differed according to emissions scenarios and climate models. We also evaluated a best (low threshold) and a worst (high threshold) case scenario. Although both threshold criteria are widely used, the criterion we used for low threshold (Maximum (Sensitivity + Specificity)) can substantially overestimate the range of low prevalence species, while the high-threshold criterion (MaxKappa) yields unbiased estimates of species prevalence (Freeman and Moisen 2008).

The difference between the high and low emission scenario was the greatest source of uncertainty, meaning that, depending on the trend of greenhouse gas emissions by the end of the century, we could see two very different outcomes for the distribution of climatically suitable habitat for plant species in the Southwest ecoregion. However, atmospheric measurements (Canadell *et al.* 2007) indicate that we are on track to surpass even the medium-high emission scenario (A2) we used in this study. If this is the case, the projections from the A2 scenario are more likely than those from the low emissions (B1) scenario. The combination of the more plausible high threshold criterion with a more likely A2 scenario by the end of the century suggests that the most severe results (high threshold/medium-high emission scenario) from this study portray the more likely picture of climatic habitat suitability.

In conclusion, of the plant functional types we examined, obligate seeders are expected to lose the most habitat. Protecting climatically suitable habitat for the covered species may require expansion of the current conservation network or coordinated conservation strategies outside these areas. Regional assessments of the dynamics of the drivers of biodiversity change based on high-resolution geospatial data and consensus forecasting, such as this study, are necessary to understand the drivers' relative importance at the regional scale and to identify the species expected to be the most vulnerable in order to meaningfully inform regional-scale conservation.

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models to a chi-square distribution with degrees of freedom equal to the degrees of freedom between the two models. In RandomForest (RF), variable importance is calculated as the reduction of predictive performance after a random permutation of the values assumed by each environmental variable. In MaxEnt, variable Area under the curve (AUC) for the models used to create consensus maps of suitable habitat. The variable importance (by rank) is shown for the variables used to create the models. In generalized additive models (GAMs), variable importance is calculated by comparing the change in deviance between two importance is a heuristic estimate of relative contributions of the environmental variables to the model. TMX, maximum temperature of warmest period; GRW, growing days above 5° C; PPT, annual precipitation; TSE, temperature seasonality; PWQ, precipitation warmest quarter; ARI, aridity index; DEPL, soil depth; AWCL, soil available water capacity; PHL, soil pH; SLOPE, slope gradient (steepness) derived from digital elevation model; SUMRAD, potential summer solstice solar insolation. Table A1.

				Variable	importar	nce (rank)	_						
Species	Model	AUC	TMX	GRW	ΡΡΤ	TSE	PWQ	ARI	DEPL	AWCL	PHL	SLOPE	SUMRAD
Acanthomintha illicifolia	GAM	0.966	ę	9	~	-	4	6	5	7	S	11	10
2	RF	0.973	4	L		5	7	6	С	8	10	11	9
	MAXENT	0.971	4	5	8		9	7	10	e	6	7	11
Adenostoma sparsifolium	GAM	0.956	7	1	6	4	2	8	5	9	ŝ	11	10
4	RF	0.956	ς	7	2	9	1	4	10	S	11	8	6
	MAXENT	0.949	4	9	8	б	1	11	7	5	7	6	10
Arctostaphylos glandulosa	GAM	0.883	2	1	10	4	б	8	5	9	7	11	6
ssp. glandulosa	RF	0.871	10	1	5	ς	7	6	8	9	7	4	11
1	MAXENT	0.929	7	m	1	9	4	9	5	10	8	11	6
Arctostaphylos	GAM	0.941	1	7	8	ŝ	4	10	5	9	7	11	6
rainbowensis	RF	0.988	1	9	ŝ	4	2	8	7	5	10	11	6
	MAXENT	0.950	7	1	2	4	8	6	9	ŝ	10	5	10
Ceanothus greggii var.	GAM	0.961	2	4	m	7	1	5	8	9	6	11	10
perplexans	RF	0.956	7	7	1	6	S	ŝ	8	4	11	9	10
4	MAXENT	0.954	2	m	4	9	1	7	6	8	10	5	11
Ceanothus tomentosus	GAM	0.948	4	L	5	-	7	11	9	8	ę	6	10
	RF	0.961	2	7		9	8	ω	6	11	5	10	4
	MAXENT	0.928	4	-	9	5	б	10	٢	10	7	8	6

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Connections warrantee	GAM	0.081	۲	Ŧ	v	-	9	×	-	L	ç	10	0
	RF	0.990) 	- 10	0 4	7 7	5 00	. 9	. ~	6	1	11	6
	MAXENT	0.990	8		9	2	0	2	-	7	5	6	4
Hesperocyparis (syn	GAM	1.000	б	7	7	-	4	~	0	5	9	9	11
Cupressus) forbesii	RF	0.983	4	6	2	11	4	4	8	0	e	1	7
	MAXENT	0.734	2	L	10	9	e	6	4	8	5	1	11
Deinandra conjugens	GAM	0.998	1	11	Э	4	6	7	9	5	7	10	×
	RF	0.998	m	7	9	5 1	-	8	1	7	4	6	10
	MAXENT	0.998	7	4	5	3 1	1	1	5	8	6	7	10
Delphinium hesperium	GAM	0.951	4	10	e	8	1	2	7	6	11	5	9
	RF	0.998	7	5	4	10	e	7	9	9	8	1	11
	MAXENT	0.987	9	6	2	10	1	4	7	5	8	e	10
Eryngium aristulatum var.	GAM	0.983	7	ŝ	2	1	9	4	1	5	10	8	6
parishii	RF	0.994	2	4	1	9	3	2	0	6	11	8	5
I	MAXENT	0.972	4	9	5	1	1	7	6	Э	8	9	10
Galium angustifolium ssp.	GAM	0.772	7	1	2	4	0	9	6	Э	5	11	8
angustifolium	RF	0.824	m	7	1	5	8	6	0	9	11	7	4
	MAXENT	0.852	6	1	5	с П	0	1	7	2	9	4	8
Hazardia squarrosa	GAM	0.848	5	1	7	6	- 7	0	8	9	б	4	11
	RF	0.839	7	7	1	8	9	4	9	0	11	ŝ	5
	MAXENT	0.922	6	-	8	2	-	0	4	9	5	ŝ	10
Keckiella antirrhinoides	GAM	0.896	1	10	2	6	7	1	8	9	4	5	m
	RF	0.942	ε	9	4	7	1	8	9	-	10	7	5
	MAXENT	0.889	1	5	2	8	6	0	4	7	6	e	11
Quercus dumosa	GAM	1.000	1	-	-	-	-	1	-	1	1	-	1
	RF	1.000	1	4	2	Э	7	5	1	6	9	10	8
	MAXENT	0.996	6	4	1	2	5	1	0	Э	7	8	9
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Table A1. (Continued).

				Variable	importan	ce (rank)							
Species	Model	AUC	TMX	GRW	PPT	TSE	PWQ	ARI	DEPL	AWCL	PHL	SLOPE	SUMRAD
Quercus engelmannii	GAM	0.905		91	<i>ი</i> , ი	S r	00	~ ~	r (4 ;	11 :	10	6
	KF MAXENT	0.920 0.877			6 5	v 4	ოო	8 11 8	e a	5	0 7 7	0 %	9 10
Trichostema lanatum	GAM	0.794	7	5	1	9	7	10	6	4	8	11	n
	RF	0.874		4	e	7	8	11	9	6	10	9	4
	MAXENT	0.890	4	7	1	10	6	11	m	5	8	9	7
Viguiera laciniata	GAM	0.927	4		9	7	10	6	5	7	ς	8	11
	RF	0.995	4	ς	9	7	6	11	5	10	9	1	×
	MAXENT	0.984	9		11	4	8	7	7	5	6	б	10
Xylococcus bicolor	GAM	0.942	7	5	8	7	с	6	4	9	-	10	11
	RF	0.962	7	8		7	5	б	11	6	4	10	9
	MAXENT	0.951	10		5	ς	7	6	8	9	7	4	11
Average variable importance			3.68	4.47	4.25	4.60	5.16	7.23	6.98	6.56	6.53	6.95	8.35

		Perc	entage are	a change	between	2000 and	2080	
		High tł	nreshold			Low th	reshold	
	GF	DL	РС	CM	GF	DL	PC	CM
Species	A2	B1	A2	B1	A2	B1	A2	B1
Acanthomintha ilicifolia	-68	6	119	222	-65	-21	60	136
Adenostoma sparsifolium	-63	27	64	149	13	47	47	118
Arctostaphylos glandulosa ssp. glandulosa	-43	-55	663	389	21	62	152	148
Arctostaphylos rainbowensis	-100	-100	-100	-99	31	175	17	173
Ceanothus greggii var. perplexans	-98	-62	-48	-98	45	97	102	174
Ceanothus tomentosus	-100	-71	-86	81	-76	23	-4	87
Ceanothus verrucosus	-99	-70	-9	-93	15	39	-37	54
Hesperocyparis (syn Cupressus) forbesii	-83	-40	-68	60	7	97	44	63
Deinandra conjugans	-13	278	47	-20	116	299	82	80
Delphinium hesperium	28	175	731	122	61	94	170	98
Eryngium aristulatum var. parishii	-24	46	-32	72	-35	37	-43	53
Galium angustifolium ssp. angustifolium	-60	161	33	257	-5	78	27	160
Hazardia sauarrosa	-71	44	-21	155	-49	38	29	205
Keckiella antirrhinoides	-100	-79	-94	127	108	160	104	169
Ouercus dumosa	-100	-100	-97	-94	-94	2	-48	3
Quercus engelmannii	150	467	147	442	96	173	64	179
Trichostema lanatum	71	30	162	197	27	30	178	158
Viguiera laciniata	418	739	543	920	328	328	345	370
Xylococcus bicolor	-100	115	69	160	-58	66	65	128

Table A2. Projected percentage area change for 19 species in the Southwest ecoregion of the California Floristic Province under two different climate change models (GFDL and PCM), emissions scenarios (A2 and B1), and thresholds (high and low) applied to projected probabilities of species occurrence to define suitable habitat.

Table A3. Projected percentage current area of suitable habitat that is also projected to be suitable by the end of the century (stable area) for 19 species in the Southwest ecoregion of the California Floristic Province under two different climate change models (PCM and GFDL), emission scenarios (A2 and B1), and thresholds (high and low) applied to projected probabilities of species occurrence to define suitable habitat.

		Perc	entage st	able area	between 2	2000 and	2080	
		High th	nreshold			Low th	reshold	
	GF	DL	РС	CM	GF	DL	РС	CM
Species	A2	B1	A2	B1	A2	B1	A2	B1
Acanthomintha ilicifolia	0	9	42	92	12	32	60	81
Adenostoma sparsifolium	17	59	72	90	55	72	71	91
Arctostaphylos glandulosa ssp. glandulosa	6	18	83	74	55	75	90	93
Arctostaphylos rainbowensis	0	0	0	0	39	53	26	64
Ceanothus greggii var. perplexans	1	10	23	0	66	89	94	67
Ceanothus tomentosus	0	12	6	71	11	48	43	68
Ceanothus verrucosus	0	0	0	0	20	29	24	49
Hesperocyparis (syn Cupressus) forbesii	1	1	3	3	37	77	62	62
Deinandra conjugans	8	46	21	18	20	56	37	41
Delphinium hesperium	50	48	96	52	74	77	96	81
Eryngium aristulatum var. parishii	3	4	4	11	6	14	14	42
Galium angustifolium ssp. angustifolium	8	73	43	90	41	69	56	85
Hazardia sauarrosa	14	53	34	89	21	45	39	83
Keckiella antirrhinoides	0	4	1	36	86	93	93	97
Ouercus dumosa	0	0	1	3	3	29	25	44
Ouercus engelmannii	37	84	57	94	64	87	71	95
Trichostema lanatum	40	45	63	87	39	51	92	90
Viguiera laciniata	83	97	95	99	98	98	98	100
Xylococcus bicolor	0	74	64	85	18	74	73	89



Figure A1. Boxplots showing the projected species centroid shift (km) for 19 species in the Southwest ecoregion of the California Floristic Province under two climate change models (GFDL and PCM), emission scenarios (A2 and B1), and thresholds (high and Low) applied to projected probabilities of species occurrence to define suitable habitat. Each boxplot shows the smallest observation (minimum distance the species centroid was projected to shift), lower quartile (Q1), median (Q2), upper quartile (Q3), and the largest observation (maximum distance the species centroid was projected to shift). Hollow circles above or below the boxplots are outliers. Note that the *y*-axes have different ranges.



Figure A2. Boxplots showing the projected species centroid shift (km) for 19 species in the Southwest ecoregion of the California Floristic Province under two climate change models (GFDL and PCM), emission scenarios (A2 and B1), and thresholds (high and Low) applied to projected probabilities of species occurrence to define suitable habitat. For description of boxplots, see FigureA1 caption. Note that the *y*-axes have different ranges.



Figure A3. Boxplots for projected change in climatically suitable habitat area for 19 species in the Southwest ecoregion of the California Floristic Province showing the differences in response for species grouped by range size class (large/common and small/rare). For description of boxplots, see FigureA1 caption. Note that the *y*-axes have different ranges.



Figure A4. Current and projected area of suitable habitat for rare species in (a) San Diego County Multiple Species Conservation Plan Area, (b) San Diego County Multiple Habitat Conservation Open Space Plan Area, and (c) all other Natural Community Conservation Planning network in the Southwest, in response to projected climate change by 2080. The mean and standard deviation were calculated from two different climate change models (PCM and GFDL) and emission scenarios (A2 and B1), using the low threshold to projected probabilities of species occurrence to define suitable habitat. ACIL, *Acanthomintha illicifolia*; ARRA, *Arctostaphylos rainbowensis*; CEVE, *Ceanothus verrucosus*; CUFO, *Hesperocyparis* (syn *Cupressus*) forbesii; DECO, *Deinandra conjugens*; DEHE, *Delphinium hesperium*; ERAR, *Eryngium aristulatum* var. *parishii*; QUDU, *Quercus dumosa*; VILA, *Viguiera laciniata*.



Figure A5. Boxplots for projected change in climatically suitable habitat area for 19 species in the Southwest ecoregion of the California Floristic Province: (a) differences projected under GFDL versus PCM climate models and (b) differences projected using A2 and B1 emission scenarios. High and low threshold results are shown (cut-off of occurrence probability value) in both figures. For description of boxplots, see FigureA1 caption. Note that the *y*-axes have different ranges.