



Does functional type vulnerability to multiple threats depend on spatial context in Mediterranean-climate regions?

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ABSTRACT

Aim Conservation efforts in Mediterranean-climate regions are complicated by species' variability in response to multiple threats. Functional type classifications incorporating life history traits with disturbance response strategies provide a framework for predicting groups of species' response to fire, but it is unclear whether these classifications will be useful when species are exposed to multiple threats or differ in spatial context. We evaluate whether species of the same fire-response functional type exhibit similar responses to disturbance relative to, and in combination with, climate and land-use change and whether the dominant threat depends on spatial context.

Location Mediterranean southern California.

Methods We developed species distribution models under current and future climate conditions for two fire-obligate seeding native shrub species that differ in geographical location and area of occupancy. Dynamic habitat maps representing alternative scenarios of climate change and urban growth were coupled with population models and simulated stochastic fire regimes.

Results The disturbance that defines their classification, fire, is projected to be the most serious threat to both species when fire frequency is high. At longer fire return intervals, however, the projected ranking of threats differed between the species, and spatial context played an important role in defining vulnerability.

Main conclusions Considering ongoing increases in fire frequency in Mediterranean-climate regions worldwide, functional type classification based on disturbance response may continue to provide a useful framework for biodiversity conservation efforts, but spatial context should also be accounted for. It may be most useful to consider the distribution of vulnerable species with regard to urban development patterns, areas of 'high-velocity' climate shifts, and places where altered fire regimes are likely to interact with other threats.

Keywords

Altered fire regimes, biodiversity, climate change, global change, land-use change, obligate seeder, population model, southern California, species distribution model.

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INTRODUCTION

Mediterranean-climate ecosystems are consistently identified as regions of high global conservation concern (Klausmeyer & Shaw, 2009). Their unique climatic and edaphic conditions

support exceptional species richness and endemism, especially of plants, but biodiversity in Mediterranean ecosystems is threatened by multiple global change factors, particularly altered fire regimes, climate change and land-use change (Médail & Quézel, 1999). The urgent need to implement

conservation measures in Mediterranean ecosystems is complicated due to large uncertainties about how species will respond to multiple stressors and their interactions.

Because species vary in their sensitivity to different stressors, conservation management approaches may be differentially effective, depending on the species. If species traits pre-dispose them to extinction by certain stressors, then grouping species that share attributes can facilitate the prediction and management of global change impacts. Functional type classifications typically incorporate life history and demographic traits with disturbance response strategies. These groups of species, particularly plants, show predictable changes along environmental and disturbance gradients (Noble & Gitay, 1996; Rusch *et al.*, 2003). Thus, functional types are employed in conservation and management assessments (e.g. Bradstock & Kenny, 2003; Gondard *et al.*, 2003); are used to predict vegetation change at the landscape scale (e.g. Pausas & Lloret, 2007; Millington *et al.*, 2009); and form the foundation for global change impact assessments in Dynamic Global Vegetation Models (DGVMs, Bachelet *et al.*, 2001). Despite demonstrated success in simplifying impact assessments under specific drivers of change, what remains unclear is whether functional type classifications will still be useful under simultaneous changes from multiple threats (Lavorel *et al.*, 2007). Also, unclear is the role of spatial context and whether species with similar traits but different locations, extents of occurrence and areas of occupancy will exhibit predictable responses to multiple threats.

In Mediterranean-climate ecosystems, most functional type classifications involve species' post-fire-response strategies (Bradstock & Kenny, 2003; Pausas, 2003) because fire is a key process that shapes ecosystem structure and function. These classifications have been useful for understanding how species vary in response to altered fire regimes (e.g. Syphard *et al.*, 2006; Pausas & Lloret, 2007), which is a primary threat to biodiversity in these regions (Syphard *et al.*, 2009). For example, serotinous or obligate seeder species that produce fire-refractory seeds may be disproportionately vulnerable to unnaturally high fire frequency compared with species that vigorously resprout in response to fire (Keeley *et al.*, 2012).

It is reasonable to hypothesize that species grouped by fire response may exhibit similar responses to climate change because fire-adaptive traits are correlated with other life history characteristics that affect vulnerability to climate change, such as tolerance to water stress or dispersal mode (Keeley *et al.*, 2012). Climate also controls the distribution of wild-fire (Syphard *et al.*, 2008). Prediction accuracy for species distribution models (SDMs) of plants in southern California, based largely on climate, was significantly related to fire response (Syphard & Franklin, 2009), suggesting a relationship between disturbance and functional type distribution. Obligate seeders may also be disproportionately sensitive to changing climate, as drought and warming in the Mediterranean Basin reduced the competitive ability of an obligate seeder relative to an obligate resprouter (Prieto *et al.*, 2009).

Even if fire-response functional types are useful for predicting species' responses to climate change, additional uncertainties arise when considering land-use change, which has been the primary threat to biodiversity in Mediterranean ecosystems (Underwood *et al.*, 2009) and may override the effects of climate, at least in the short term (Lavorel *et al.*, 1998). This is because, even if groups occupy similar portions of environmental (niche) space, they may occur in distinct areas of geographical (range) space. Land-use change does not occur randomly across a landscape, and housing development can preferentially occupy particular habitat types (Underwood *et al.*, 2009). Species preferences in relation to temperature and soil acidity have been correlated with urban land use (Knapp *et al.*, 2009). Therefore, certain functional types may be disproportionately vulnerable to habitat loss from urban development if their distributions in environmental space correlate with patterns of land use.

Projecting the relative vulnerability of species or functional types to multiple stressors, particularly under future scenarios, invariably requires some form of modelling. Assessing impacts of altered fire regimes on plant functional types often involves simulation modelling of successional dynamics under alternative scenarios (e.g. Pausas, 2003; Syphard *et al.*, 2006); and the primary tool used to predict impacts of climate change on biodiversity is SDMs (Franklin, 2010). The use of SDMs alone in predicting impacts of climate change has been criticized because SDMs do not typically account for demographic or other factors that control how species may adapt to change, nor do they account for processes driving distribution dynamics (Akçakaya *et al.*, 2006). Therefore, the use of SDMs in concert with other modelling approaches, such as process-based or phylogeographical models, has been recommended (Keith *et al.*, 2008; Keppel *et al.*, 2012).

Here, we follow these recent advances and integrate species distribution and population models to compare relative impacts of altered fire regimes, climate change and urban development on two obligate seeding native shrub species in Mediterranean southern California. Although the species are in the same genus with similar fire-response strategies, demographic characteristics and life history traits, they differ in geographical location and area of occupancy. Therefore, we tested the assumption that functional types are a useful framework for predicting vulnerability to global change in the face of multiple threats and different spatial contexts.

We asked the following questions:

1. Do two species within the same fire-response functional type exhibit similar responses to disturbance relative to, and in combination with, climate and land-use change?
2. Does the dominant threat to the functional type depend on the spatial context of the threat or distribution of the species?

METHODS

We developed SDMs under current and future climate conditions for two congeneric species and overlaid the maps of

predicted habitat suitability with projections of urban development. Dynamic habitat maps representing climate change and urban growth scenarios were coupled with population models and simulated stochastic fire regimes (additional details in Appendix S1 in Supporting Information).

Study area and species

The study area includes 16,076 km² of land located within the Natural Communities Conservation Planning area, a subarea of California's Southwest Ecoregion (as defined in Hickman, 1993), where the most extensive vegetation type is chaparral shrublands. The obligate seeding species we compared are from the genus *Ceanothus* and the *Cerastes* subgenus, with species particularly tolerant of drought (Davis *et al.*, 1999). *Ceanothus greggii* var. *perplexans* (*C. greggii* henceforth) is located farther inland, in higher elevation, chaparral-dominated areas that are partly protected as national forests. *Ceanothus verrucosus* is located in some of the last remaining open-habitat areas distributed in fragments along the southern coastal portion of the study area. *Ceanothus verrucosus* is much rarer than *C. greggii*, although both are endemic. The species also occupy distinct areas in environmental space, as the higher elevation and further inland distribution of *C. greggii* brings higher summer and lower winter temperatures, a shorter period of summer drought and higher average precipitation (Davis *et al.*, 1999).

Species distribution and urban growth modelling

To create habitat maps to integrate with population models, we used MaxEnt (Phillips & Dudík, 2008) because of its high performance with presence-only data (Elith *et al.*, 2006). MaxEnt assigns a probability of species presence in each cell in a map by iteratively evaluating contrasts between values of environmental predictor variables at species occurrence locations, and for a large background sample of the predictor variables across the entire study area (Elith *et al.*, 2011). Although we present only the results from MaxEnt in this study, we created SDMs using other modelling methods (Generalized Additive Models and Random Forests), which produced similar predictions at the landscape scale. We obtained 104 presence records for *C. verrucosus* and 172 records for *C. greggii* from the San Diego Natural History Museum and a database of vegetation plots.

To estimate models of habitat suitability under recent climate conditions (i.e. averaged from 1970 to 1999), we used climate data from the Parameter-Elevation Regressions on Independent Slopes Model, available in a gridded map format at 800 m, but that were downscaled to 90 m to account for finer-scale topographic effects using spatial and statistical interpolation methods (Flint & Flint, 2012). The climate variables included mean January minimum temperature, mean July maximum temperature and mean annual precipitation (Syphard & Franklin, 2009). Environmental predictors also included soil and terrain variables known to

be important in predicting plant species distributions in the study area (Syphard & Franklin, 2009). See Appendix S1.

To project potential habitat suitability under future climate conditions, we acquired projected future climatologies based on two general circulation models (GCMs) for the IPCC Fourth Assessment A2 emissions scenario: the National Center for Atmospheric Research and the Department of Energy's Parallel Climate Model (PCM) that projects a slightly wetter and hotter climate; and the National Oceanic and Atmospheric Administration Geophysical Fluid Dynamics Laboratory CM2.1 model (GFDL) that predicts a substantially hotter and drier climate. Because predictions vary among GCMs, it is common in species distribution modelling to acquire output from several models to bracket the range of projections that are likely to occur (e.g. Heikkinen *et al.*, 2006; Beaumont *et al.*, 2008). Although a model consensus approach (averaging predictions across many GCMs) is sometimes used (e.g. Brook *et al.*, 2009), the GCMs used here provide contrasting scenarios that most realistically simulate California's climate (Cayan *et al.*, 2008) and have been used in other environmental projections for the region (Sork *et al.*, 2010; Flint & Flint, 2012). Projected temperature and precipitation variables for 2070–2099 were averaged and downscaled as before to represent projected climate ca. 2099. To create habitat suitability maps under potential future climate conditions, we reprojected the MaxEnt model onto the predictor variables while substituting the future climate data for the current climate data.

Because the population model operates on discrete patches of species habitat, it was necessary to select a threshold to convert our map of continuously distributed probabilities of species occurrence into a map representing a series of suitable habitat patches. We used 'equal training sensitivity and specificity' as a threshold criterion (Freeman & Moisen, 2008) based on 'availability' data of MaxEnt. All areas with probabilities of occurrence lower than the threshold value were assigned a habitat suitability value of 0.

After applying the thresholds to the habitat maps, we used maps of the current distribution of each species to distinguish between patches that were initially occupied for the population models and patches that represented suitable but unoccupied habitat. We assigned an initial habitat suitability of 1.0 to all occupied habitat patches and maintained a continuous distribution of predicted probabilities (i.e. between the threshold value and 1.0) for unoccupied suitable patches to serve as indicators of relative habitat quality, which is related to carrying capacity in the population models. To create dynamic habitat maps across 100 years, we applied a linear interpolation between the gridded habitat maps representing current and future climate on a cell-by-cell basis. This resulted in 100 maps representing annual time steps from 2000 to 2099 for the two climate models.

After creating the interpolated time series of habitat maps for the climate models, we overlaid them with dynamic projections of urban growth. Spatially explicit, binary projections of urban development were developed for the study area

(Syphard *et al.*, 2011) using SLEUTH, a cellular automaton model that predicts future development as a function of past drivers of development unique to each study area (Clarke, 2008). Publicly owned land and conservation reserves were excluded from development in the simulations. Only 50 years of urban growth were simulated because the predicted rate of growth asymptotes in about 2020, and further development beyond 2050 would be negligible according to the assumptions and development trends in the model (Syphard *et al.*, 2011).

For all scenarios, we converted urban areas in 2000 to habitat suitability of 0 where patches overlapped urban areas. The habitat scenarios to input to the population model included (1) current climate and no urban growth (status quo); (2) GFDL or PCM climate change scenarios with no urban growth (climate change only); (3) current climate with 50 years of urban growth (urban growth only); and (4) climate change scenarios with 50 years of urban growth (combined climate change and urban growth).

Population models

We based construction of the population models for *C. greggii* and *C. verrucosus* on models established in the literature (Lawson *et al.*, 2010; Regan *et al.*, 2010), which we updated with recent data. As our aim was to gain insights into the impacts of threats to a plant functional type, we used composite data from obligate seeding species occurring in southern California within the genus *Ceanothus* when data were lacking.

Survival rates

The population models for both species were structured as age-based matrix models because most data were reported in terms of stand age. Table 1 shows the rates used for both species with relevant sources. Explanations of the population model parameterization are detailed in Appendix S1. Environmental variation in survival rates was represented via a lognormal distribution with the means and standard deviations described in Appendix S1 and presented in Table 1. Demographic stochasticity was represented in all survival parameters.

Fecundity and seed survival

A polynomial function was fitted to 5-year time series of annual average seed production per plant for ages 6–10, 13–17, 32–36, 57–61, 82–86 years for north- and south-facing slopes from Zammit & Zedler (1993) to estimate annual seed production per plant for *C. greggii* (Appendix S1). Fifty per cent of seeds produced by *C. greggii* shrubs in each year are viable (Keeley, 1977), and seed predation was estimated as 74.8%. The average number of seeds entering the seed bank per year (fecundity) was then calculated as the product of the seed production function, first-year seed viability and predation rate (Table 1). Due to evidence of high seed

turnover in the seed bank (Keeley, 1977) and high uncertainty in seed bank viability, fecundities were further reduced by a factor of 10; this ensured a stable average population trajectory under the historic optimal fire regime (Lawson *et al.*, 2010; Regan *et al.*, 2010). The fecundity per year was drawn from a lognormal distribution with these calculated means and a coefficient of variation of 200%.

As seed production rates were unavailable for *C. verrucosus*, we used relative seed sizes to scale the fecundity of *C. greggii* to a function more appropriate for *C. verrucosus*. We made the following assumptions: average size of plants for both species was approximately the same for each age class (verified in Baldwin *et al.*, 2012; Zammit & Zedler 1993), *C. greggii* produces 50,700 seeds per kg and *C. verrucosus* produces 141,100 seeds per kg (S & S Seeds, 2011), and plants with smaller seeds produce more of them at a rate directly proportional to relative seed weight. This results in scaling the *C. greggii* fecundity equation by a factor of 2.78 to produce estimated fecundities for *C. verrucosus* (Table 1). Annual viability of seeds in the soil-stored seed bank is highly uncertain, but it is speculated that seed longevity is at least 100 years (Keeley *et al.*, 2006). The annual seed viability of soil-stored seeds was back-calculated assuming a longevity of 100 years for 95% of plants in the age class, with 5% reaching older ages. Inter-patch seed dispersal is negligible for both *Ceanothus* species.

Fires and post-fire recruitment

We used hazard functions based on the Weibull distribution to specify the probability of an unplanned fire, $\lambda(t) = ((ct^{c-1}) \setminus b^c)$, where $\lambda(t)$ is the probability of a fire, t is the time since last fire, c is a shape parameter describing the change in fire probability through time and b is a scale parameter that defines the fire recurrence interval (Moritz, 2003). The parameter $c = 1.42$ is the Maximum Likelihood Estimate for mixed chaparral (Moritz, 2003) and the scale parameter, b , was assigned such that the desired average fire frequency coincided with the mode of the probability density function for the fire interval distribution (Moritz, 2003). We investigated the impacts of eight different average fire return intervals (10, 20, ..., 80 years) on abundances of *C. greggii* and *C. verrucosus*. Each time a fire occurs, all standing plants die, seeds germinate and the fire function is reset to $\lambda(0)$. When seed fire mortality (90%; Quinn, 1994), predation of exposed seeds (33%; Quinn, 1994), seedling emergence (44/45; Quinn, 1994) and first-year survival (Table 1) are accounted for, germination of the seed bank occurs at a rate of 0.018 for *C. greggii* and 0.015 for *C. verrucosus*. In the absence of fire, incidental germination from the seed bank occurred at a rate of 10^{-7} .

Carrying capacity and self-thinning

To ensure that simulated population densities remained within biologically realistic bounds, ceiling carrying capacities, K ,

Table 1 Parameters and data sources used in the construction of the population models.

Parameter	<i>Ceanothus greggii</i>		<i>Ceanothus verrucosus</i>	
	Mean values (SD or CV)	Reference	Mean values (SD or CV)	Reference
Fecundity (incl. seed predation and 1st year seed viability)	$-0.0431x^2 + 4.2696x + 129.79$ $x = \text{age of plant}$ (CV = 200%)	Zammit & Zedler (1993); Keeley (1977); Davey (1982)	$-0.2044x^2 + 20.6527x + 255.31$ $x = \text{age of plant}$ (CV = 200%)	Zammit & Zedler (1993); S & S Seeds (2011); Keeley (1977); Davey (1982)
Annual seed bank viability	0.9705	Assume 5% of seed bank survives for > 100 years (Keeley <i>et al.</i> , 2006)	0.9705	Assume 5% of seed bank survives for > 100 years (Keeley <i>et al.</i> , 2006)
Post-fire germination rate (including 1st year survival)	0.01807	Schmalbach (2005); Keeley <i>et al.</i> (2006); Regan <i>et al.</i> (2010)	0.01504	Tyler & D'Antonio (1995); Thomas & Davis (1989); Frazer & Davis (1988); Keeley <i>et al.</i> (2006); Regan <i>et al.</i> (2010)
Age 1 survival	0.95 (SD = 0.19)	Keeley <i>et al.</i> (2006)	0.707 (SD = 0.253)	Thomas & Davis (1989); Keeley <i>et al.</i> (2006)
Age 2 survival	0.99 (SD = 0.0017)	Keeley <i>et al.</i> (2006)	0.707 (SD = 0.253)	Thomas & Davis (1989); Keeley <i>et al.</i> (2006)
Age 3 – 5 survival	0.99 (SD = 0.0017)	Keeley <i>et al.</i> (2006)	0.718 (SD = 0.016)	Tyler & D'Antonio (1995); Thomas & Davis (1989); Frazer & Davis (1988); Odion and Davis (2000); Keeley <i>et al.</i> (2006)
Age 6 – 12 survival	0.9925 (SD = 0.0017)	Zammit & Zedler (1993)	0.9925 (SD = 0.0017)	Zammit & Zedler (1993)
Age 13 – 31 survival	0.9971 (SD = 0.0033)	Zammit & Zedler (1993)	0.9971 (SD = 0.0033)	Zammit & Zedler (1993)
Age 32 – 56 survival	0.9776 (SD = 0.0102)	Zammit & Zedler (1993)	0.9776 (SD = 0.0102)	Zammit & Zedler (1993)
Age 57 – 81 survival	0.9694 (SD = 0.0096)	Zammit & Zedler (1993)	0.9694 (SD = 0.0096)	Zammit & Zedler (1993)
Age 82 – 97 + survival	0.8384 (SD = 0.0023)	Assume 5% of age class survive to > 100 years old (Keeley 2006)	0.8384 (SD = 0.0023)	Assume 5% of age class survive to > 100 years old (Keeley 2006)
<i>K/ha</i> for age 60+	150	Zammit & Zedler (1993); J. Franklin, unpublished data	1173	Zammit & Zedler (1993); unpublished data

based on stand age were estimated using maximum recorded densities in Zammit & Zedler (1993). Two sets of parameters are required to calculate *K* across the landscape: the per hectare maximum density of plants in the largest-sized age class and the relative differences in *K* across age classes. A carrying capacity of 150 plants per ha was estimated for 60+ year old stands of *C. greggii*. For *C. verrucosus*, a carrying capacity of 1173 per ha for age 60+ shrubs was estimated (refer to Appendix S1). The large difference in *K* for the two species is due to differences in spatial heterogeneity of suitable habitat throughout the species ranges: very large patches of suitable habitat, that are unlikely to comprise a monoculture of *Ceanothus* across the entire patch, are predicted for *C. greggii*, whereas very small patches of suitable habitat, that could conceivably comprise *Ceanothus* plants across the entire patch, are predicted for *C. verrucosus*. The relative weights, or multiplication factors, used for scaling

K by age class were estimated using age-specific data on canopy area from Zammit & Zedler (1993). The function of best fit, standardized so the largest-sized age class is weighted at 1.0 is

$$W(x) = \begin{cases} 100, & x = 1 \\ 1/(0.27 \ln(x) - 0.14), & 2 \leq x \leq 6 \\ 5.936x^{0.435}, & 7 \leq x \leq 59 \\ 1.0, & x \geq 60 \end{cases}$$

where *x* is the age of plants. When multiplied by the species-specific *K* for age 60+ years, the function above gives the carrying capacity per hectare for each age class in maximally suitable habitat. Patch-specific carrying capacities in each time step were then calculated as the sum of habitat suitability indices across all cells in the patch for the relevant time step multiplied by the appropriate age-specific carrying capacity for the area of a cell (1 ha), which is how the effects

of climate change on habitat suitability were incorporated into the population model (Keith *et al.*, 2008). Density dependence was implemented by reducing rates of survival and growth (due to intra-specific competition) such that abundance declined faster than the self-thinning function, $W(x)$, as plant age increased whenever a population exceeded the carrying capacity of its habitat patch. Initial abundances in occupied patches were set at 80% of K for age 16 plants to correspond with average observed densities: 207 individuals/ha for *C. greggii* and 1623 individuals/ha for *C. verrucosus*. The initial seed bank was calculated to be commensurate with the initial number of age 16 plants to give 2811 seeds per ha for *C. greggii* and 7511 seeds per ha for *C. verrucosus*.

Stochasticity was incorporated through Monte Carlo simulations for 1000 replications over a 100-year time period to account for natural variation in the fire events and the population demographic rates. Expected minimum abundances (EMA) across the 1000 replications were used to compare all treatments (McCarthy & Thompson, 2001).

RESULTS

Habitat change

The SDM of current habitat for *C. verrucosus* had a training accuracy of 0.99, as measured by the area under the curve (AUC) of the receiver operating characteristic. The AUC for

C. greggii was 0.93. Both species showed ‘ecologically sensible’ unimodal responses to climate variables (Austin, 2002), and *C. verrucosus* exhibited a narrower range of tolerance to mean annual precipitation and was limited to substantially drier conditions (optimum 300 mm) than *C. greggii* (optimum 800 mm; see Appendix S1). *Ceanothus verrucosus* also showed a warmer optimum winter temperature and cooler optimum summer temperature than *C. greggii*, consistent with its coastal distribution. Both species had upper limits of summer maximum temperature tolerance of 32–34°C.

For both *C. verrucosus* and *C. greggii*, the largest area of projected habitat loss occurred under the GFDL future climate change scenario that predicts substantially hotter and drier climate conditions (Figs 1& 2). Only a small proportion of *C. greggii* habitat was projected to remain by 2100. Under the PCM climate change scenario that predicts hotter and wetter climate conditions, *C. greggii* habitat was also projected to decline, but there was a slight gain in habitat projected for *C. verrucosus*. In addition to net changes in habitat extent, habitat distribution was also projected to shift under projected future climate conditions, reflecting both gains and losses for both species (Fig. 2).

Because most urban development in the next 50 years was projected to occur in the western portion of the study area, only the habitat of *C. verrucosus* was substantially affected by urban development in the simulations (Figs 1& 3). *Ceanothus verrucosus* was predicted to lose 4163 ha, or 27% of its

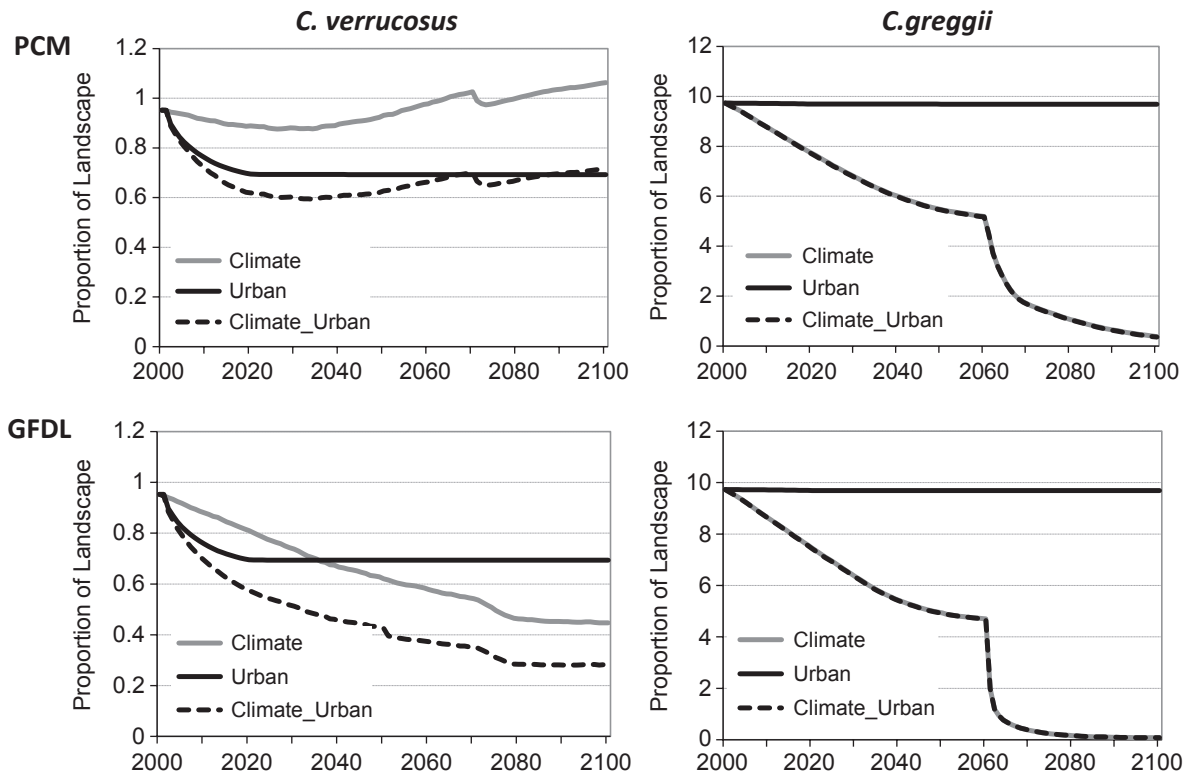


Figure 1 Proportion of landscape occupied by suitable habitat for *Ceanothus verrucosus* and *C. greggii* under scenarios of climate change only, urban growth only and urban growth combined with climate change for the Parallel Climate Model and Geophysical Fluid Dynamics Laboratory models. Note difference in y-axes.

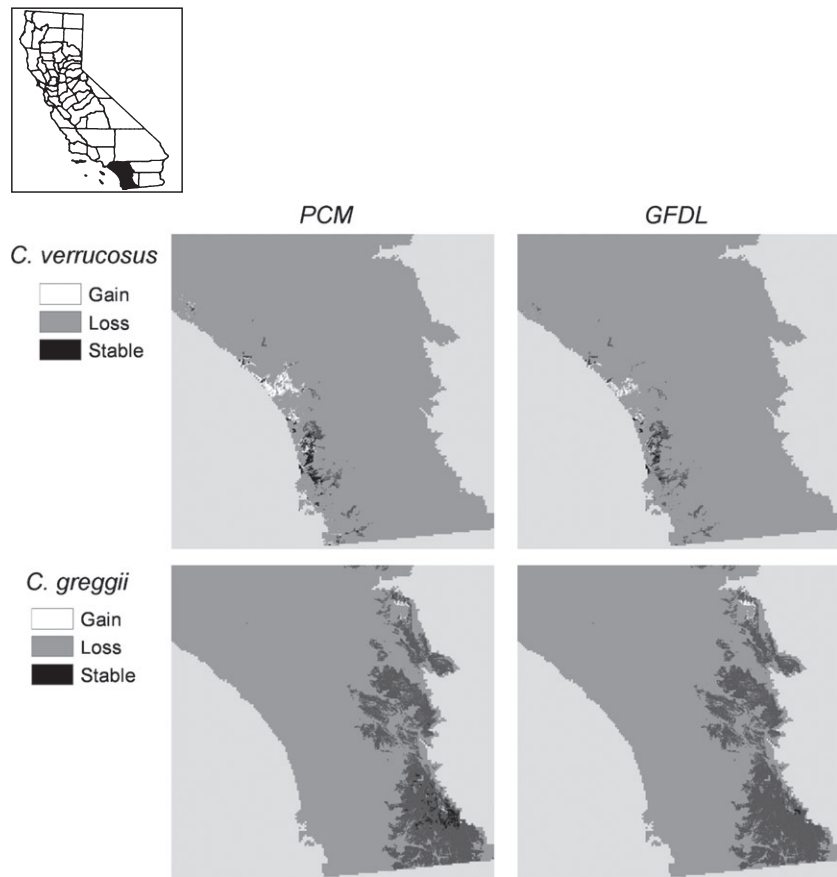


Figure 2 Maps of *Ceanothus verrucosus* and *C. greggii* habitat projected as gained, lost or stable after 100 years of climate change for the Parallel Climate Model and Geophysical Fluid Dynamics Laboratory general circulation models. Study area contains most of San Diego and Orange Counties, as well as portions of Riverside, Los Angeles and San Bernardino Counties, CA, USA (see inset).

current extent, to urban growth by approximately 2020, after which the rate of habitat loss subsided. Less than 1% (650 ha) of *C. greggii* habitat was projected to be converted into urban development.

Although urban development contributed to the largest initial habitat loss for *C. verrucosus* under both climate scenarios, the rate of habitat loss due to a combination of climate change and urban development in the GFDL scenario rapidly exceeded that due to urban growth alone, while habitat loss under climate change without urban growth occurred more slowly (Fig. 1). In the PCM scenario, urban growth offsets the net gain in *C. verrucosus* habitat that otherwise occurred with climate change alone.

Population projections under altered fire regimes

When population dynamics under a range of average fire return intervals were simulated in addition to habitat changes, both species were most sensitive to high fire frequency (Fig. 4). However, if average fire return intervals were longer than 10–20 years for *C. greggii*, the EMA was most strongly affected by the projected habitat decline under climate change, particularly under the GFDL scenario. The sensitivity to short fire return intervals was more pronounced under the PCM scenario and scenarios with no climate change (urban growth and status quo with static maps). *Ceanothus greggii* population abundance closely mirrored the

decline in habitat under climate change when the average fire return interval was ≥ 30 years.

For *C. verrucosus*, the projected difference in EMA was substantially less pronounced among the climate change and urban growth scenarios than for *C. greggii*, and fire was clearly the most substantial threat when average fire return intervals were shorter than approximately 30 years (Fig. 4). When the climate change scenarios were modelled without urban growth and the average fire return interval was ≥ 30 years, the EMA mirrored the habitat decline predicted through the SDMs, as it did for *C. greggii*. The projected EMA was similar under the PCM-only and urban growth-only scenarios across most fire return intervals. However, when PCM and urban growth were modelled together, the projected EMA was substantially lower.

DISCUSSION

Our comparison of how two species of the same functional type responded to a range of stressors revealed that the disturbance that defines their classification, fire, is likely to have the most significant negative impact on population persistence at short fire return intervals. Under all climate change and urban growth scenarios, average fire return intervals shorter than 10–20 years resulted in similarly low-estimated minimum abundances. At longer fire return intervals, however, the

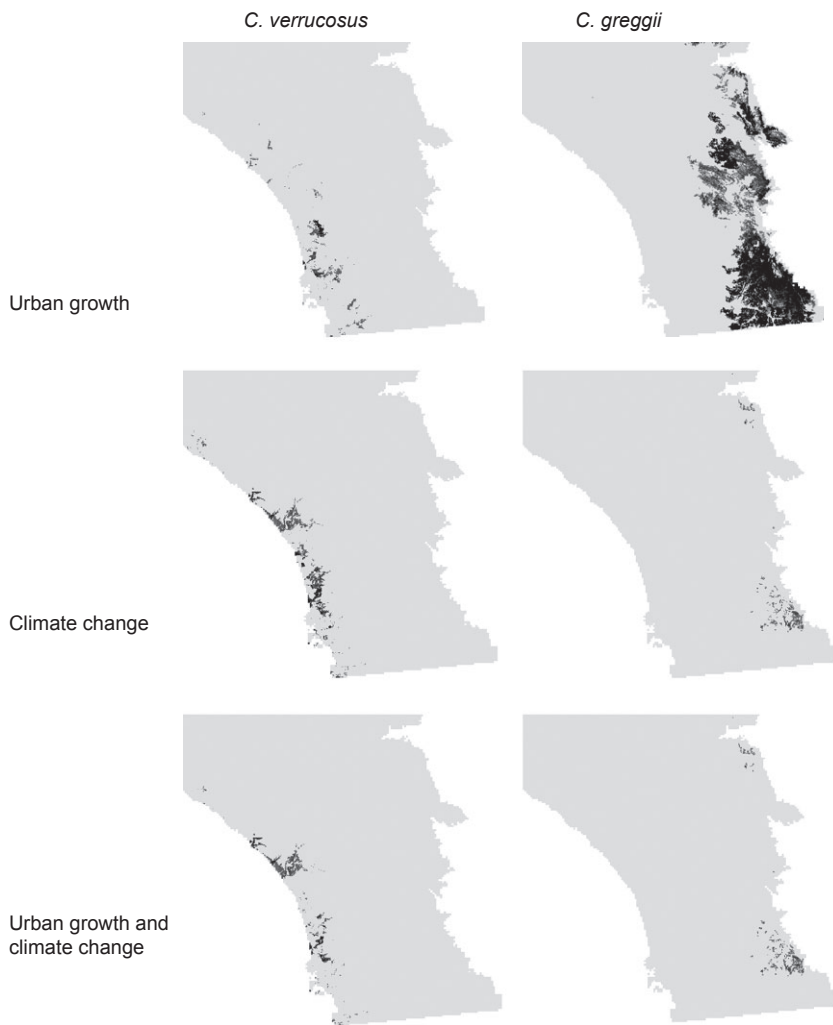


Figure 3 Maps of suitable habitat probability (low-to-high probability as a gradient from white to black) for *Ceanothus verrucosus* and *C. greggii* under scenarios of urban growth only, climate change only and urban growth combined with climate change for the Parallel Climate Model.

dominant threats to the species differed in rank and magnitude. Therefore, if fire becomes increasingly frequent in the future, it will likely override the influence of other threats for this functional type, regardless of where the species is located on the landscape. Otherwise, the spatial context of the threat and species distribution could make substantial difference in these obligate seeders' vulnerability to multiple stressors.

The sensitivity of obligate seeder shrub species to high fire recurrence has been widely documented (Zedler *et al.*, 1983; Haidinger & Keeley, 1993; Regan *et al.*, 2010; Swab *et al.*, 2012). This vulnerability ironically results from the fire-dependent reproductive trait of these species. Obligate seeders rarely germinate between fires and thus require fire for recruitment. Yet, they require sufficient time between fires to reach reproductive maturity and to replenish their seed bank, without which they will be locally extirpated and potentially replaced with exotic annual grasslands. In all Mediterranean regions, and particularly in southern California, average fire return intervals have been decreasing largely due to population growth and increased human-caused ignitions (Keeley *et al.*, 1999; Syphard *et al.*, 2009); and climate change could

exacerbate this situation (Mouillot *et al.*, 2002; Moriondo *et al.*, 2006). Altered fire regimes are thus a serious current and ongoing threat for obligate seeders.

Despite the similar response to short fire return intervals, the species differed in their relative vulnerabilities to projected climate change and land-use change. Although *C. greggii* currently has a much broader distribution than *C. verrucosus*, climate change projections suggest that its habitat proportion and area could contract to a greater extent than that of *C. verrucosus*. This discrepancy is particularly the case in the PCM scenario, in which precipitation is not predicted to decline as much and in which *C. verrucosus* was projected to have a net increase in available habitat.

The species' modelled responses exhibited different estimated tolerances to the climate variables in the model. The reason for the extreme contraction of *C. greggii* but not *C. verrucosus* is that the combination of temperature and precipitation conditions in the current realized niche of *C. greggii* is projected to be less extensive under climate change than the combination of climate conditions for the realized niche of *C. verrucosus*. This underscores the complexity in forecasting the effects of future threats and the importance of considering

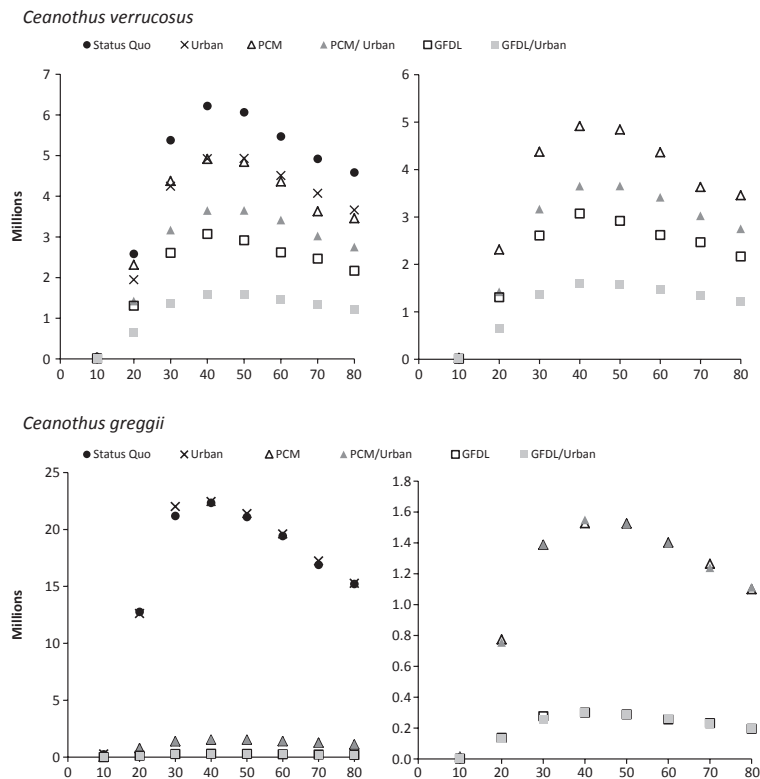


Figure 4 Estimated minimum abundance for *Ceanothus verrucosus* and *C. greggii* under status quo (no urban growth or climate change); climate change with Parallel Climate Model and Geophysical Fluid Dynamics Laboratory models only and combined with urban growth; and urban growth only and climate change.

spatial context in future conditions, as *C. greggii* is currently considered common and widespread, while *C. verrucosus*, a species of conservation concern, has a limited distribution already fragmented and reduced by historical land-use change. Future habitat suitability maps are based on the assumption that species are limited to those conditions under which they are currently distributed; however, it is unknown the extent to which they could tolerate a broader range of climate conditions. Although we presented only the results of one SDM in this study, a comparison with projections from other commonly used SDMs showed similar projections. Also, although there were differences in habitat projections between the two GCMs that we used, particularly for *C. verrucosus*, these differences did not change the overall conclusions of the study regarding the relative rankings of multiple stressors on the two species.

The other clear difference in impacts was that *C. greggii* was not expected to experience substantial habitat decline from urban development, while urban development may be more of a threat to *C. verrucosus* than climate change. This is because most urban development was predicted to occur closer to the coast near the current urban footprint, where current and projected future *C. verrucosus* habitat is located. Much of the *C. greggii* habitat also overlaps national forest land, which was assumed to be protected from development. Although the fire-response functional type classification indeed captures the similarity in these species' vulnerability to very high fire frequencies, even in the presence of other stressors, the spatial context becomes much more important when fire is projected to be less frequent. At longer fire

return intervals, the ranking of threats differs between the species such that the most serious projected threat for *C. verrucosus* is still fire, followed by urban growth, then climate change; whereas climate change is the most serious projected threat for *C. greggii*, followed by fire, then urban growth.

It is therefore important in the context of conservation management in Mediterranean-climate regions to understand where and how fire regimes are likely to change in the future. Documented increases in fire frequency, particularly in southern California, are spatially distributed such that fire is most frequent where there are intermediate levels of population and urban development, likely due to a juxtaposition of high human ignitions with continuous vegetation and poorer fire-fighter access (Syphard *et al.*, 2007, 2009; Lampin-Maillet *et al.*, 2010). If population increases in the less-developed areas around *C. greggii* habitat, future urban growth could have larger impacts on *C. greggii* than on *C. verrucosus* due to this indirect effect on fire regimes rather than direct habitat loss. On the other hand, although fire was consistently the biggest threat to *C. verrucosus*, fire frequency will likely be lower in the isolated urban habitat remnants where it occurs (Gill & Williams, 1996). In addition to interactions between urban growth and fire, there is potential for strong, yet uncertain, interactions between climate change and fire. If climate change contributes to the recurrence of prolonged drought conditions in the region, the potential for increased fire hazard could increase, as most megafires in southern CA (individual fires larger than 50,000 ha) have been associated with anomalously long antecedent droughts (Keeley & Zedler, 2009).

In Mediterranean-climate regions, functional types centred on fire response substantially improve capacity to predict vegetation change under altered fire regimes. However, elsewhere and for other global change drivers, other combinations of traits may better define functional response (Lavorel *et al.* 2007). Despite ongoing efforts to identify which suite of species' characteristics best captures overall variation in vegetation response to global change, the results of this study call into question the efficacy of doing so when species face multiple, simultaneous threats. This is because the ranking of the threat, and consequently the best conservation actions, may depend on spatial context. More work is therefore needed, using a broader range of species and regions, to illuminate the robustness of different functional classifications under a range of simultaneous drivers of change and to better understand the role of spatial context. For example, for different groups of *Banksia* species, spatial context influenced relative vulnerability to projected climate change, particularly in relation to land transformation (Yates *et al.* 2010). Further demographic data collection is also needed for both *Ceanothus* species studied here, particularly responses of early plant stages to changes in temperature and precipitation (while species-specific data were used to estimate survival rates for *C. greggii*, composite data from other obligate seeding *Ceanothus* species were used for early *C. verrucosus* survival.)

Regarding conservation in Mediterranean regions, it may be useful to consider the distribution of vulnerable species in relation to land-use change, areas of 'high-velocity' climate shifts (Loarie *et al.*, 2009) and places where altered fire regimes are likely to interact with other threats. There is potential to incorporate these considerations into emerging frameworks for biodiversity conservation in Mediterranean regions based on attributes of resilience and resistance (Prober *et al.* 2012). In conclusion, our results show that threats in combination may exacerbate any one threat in isolation, and it is important to consider them simultaneously.

ACKNOWLEDGEMENTS

This work was supported by National Science Foundation (NSF-DEB-0824708), Department of Energy (DE-FC02-06ER64159) and California Landscape Conservation Cooperative (5288768). The work represents the findings of the authors and does not reflect the opinion of the sponsors. We are grateful to A. and L. Flint for providing access to downscaled climate data and to S. Ferrier and an anonymous reviewer for providing helpful suggestions on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details of species distribution modelling and population modelling methods.

BIOSKETCH

Alexandra D. Syphard's research focuses on interactions among human and natural disturbances and their effects on landscape change and the persistence of native biodiversity. She is especially interested in vegetation dynamics and wild-fire in Mediterranean ecosystems; the influence of humans on fire regimes; and the distributional dynamics of native plants.

Author contributions: A.D.S., H.M.R. and J.F. conceived the ideas; A.D.S., H.M.R., J.F., R.M.S. and T.C.B. constructed the models, generated results and analysed the data; A.D.S., H.M.R. and J.F. led the writing.

Editor: Simon Ferrier