

# Linking spatially explicit species distribution and population models to plan for the persistence of plant species under global change

**THEMATIC SECTION**  
Spatial Simulation Models  
in Planning for Resilience

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## SUMMARY

Conservation managers and policy makers require models that can rank the impacts of multiple, interacting threats on biodiversity so that actions can be prioritized. An integrated modelling framework was used to predict the viability of plant populations for five species in southern California's Mediterranean-type ecosystem. The framework integrates forecasts of land-use change from an urban growth model with projections of future climatically-suitable habitat from climate and species distribution models, which are linked to a stochastic population model. The population model incorporates the effects of disturbance regimes and management actions on population viability. This framework: (1) ranks threats by their relative and cumulative impacts on population viability, such as land-use change, climate change, altered disturbance regimes or invasive species, and (2) ranks management responses in terms of their effectiveness for land protection, assisted dispersal, fire management and invasive species control. Too-frequent fire was often the top threat for the species studied, thus fire reduction was ranked the most important management option. Projected changes in suitable habitat as a result of climate change were generally large, but varied across species and climate scenarios; urban development could exacerbate loss of suitable habitat.

*Keywords:* biodiversity, California, climate change, fire, land-use change, population model, population viability, rare plant species, species distribution model, urban growth model

## INTRODUCTION

Habitat loss and fragmentation resulting from human land use has historically been the primary cause of species extinctions (Foley *et al.* 2005). In the coming century, land-use change and climate change are expected to be the two main drivers of

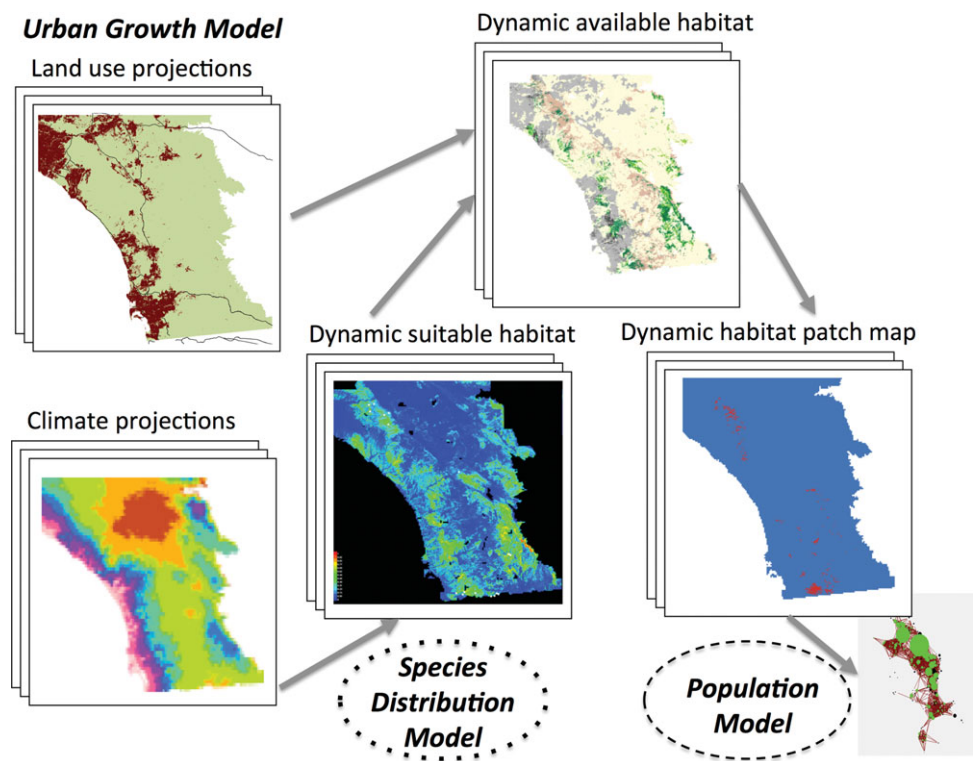
global biodiversity loss (Alcamo 2006), with climate change predicted to result in species' habitat shifts or loss (see for example Iverson & Prasad 1998). Although extinction typically results when habitat across a species' entire range is lost, substantial range reduction due to habitat degradation and fragmentation can also lead to extinction if populations become small or isolated enough for demographic stochasticity, inbreeding depression or Allee effects to be significant. Extinction may also be facilitated by species traits (such as specific requirements for survival or recruitment) or from synergistic effects of multiple interconnected threats (Hobbs 2001; Davies *et al.* 2004). For instance, altered fire regime (Syphard *et al.* 2009) and invasive species (D'Antonio & Vitousek 1992) can interact with habitat loss (Syphard *et al.* 2005), and may ultimately drive fragmented populations to extirpation.

For conservation managers and policy makers to anticipate and respond to the effects of projected patterns of global change on biodiversity, models are required that can simulate and project the impacts of multiple interacting threats on population viability and rank those threats so that management responses can be identified and prioritized. We thus used an integrated modelling framework that linked (1) species distribution models that track the effects of climate changes on habitat suitability, (2) an urban growth model that projects plausible future urban development patterns, and (3) spatially explicit population models that incorporate demographic data and responses to global change scenarios. We have extended this framework, pioneered to examine climate change impacts on plant population persistence (Keith *et al.* 2008; Brook *et al.* 2009), to explicitly address multiple factors important in a highly urbanized Mediterranean-type ecosystem (MTE) and planning context.

MTEs are found in five regions globally, and are characterized by high plant species diversity and endemism (Cowling *et al.* 1996), and by plants with functional adaptations to regionally-specific fire regimes (Keeley 1986). Habitat loss, altered fire regime and invasive species are among the top threats affecting plants in MTEs (Regan *et al.* 2008; Underwood *et al.* 2009). Although plants in MTEs are resilient to natural fire regimes (Bond & Keeley 2005), land-use change and increased human ignitions have altered the

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**Figure 1** Components and products of the modelling framework depicting the study region in south-western California. The urban growth model yielded spatially and temporally explicit land-use change projections. Climate change projections are linked to a species distribution model (dotted ellipse, details in Fig. 2) to make spatially and temporally dynamic projections of climatically suitable habitat. Combining these with urban growth projections yields dynamic maps of habitat that are both climatically suitable and available (not lost to urban growth). These projections are further constrained to delineate patches of potentially occupied habitat based on species minimum patch area requirements, such that the resulting dynamic habitat patch maps, input to the population model (dashed ellipse), reflect the impacts of habitat shifts, loss and fragmentation on population (Fig. 3).



distribution of fire frequency, size and location in all MTEs (Syphard *et al.* 2009). The trend of increased fire frequency particularly threatens those organisms that require substantial time between fires to mature and reproduce (Syphard *et al.* 2009), but can also threaten species that have adapted in different ways to a different fire regime. Human-altered fire regimes may interact with climate change, but the nature of the effect remains highly uncertain (McKenzie *et al.* 2004).

We adopted a distinctly geographical perspective to evaluate synergies among multiple interacting threats that affect biodiversity at landscape and regional scales and in examining the effectiveness of alternative management responses. We focused on plant species in the highly urbanized, topographically diverse, species-rich and wildfire-prone MTE of southern California (USA), which supports a mosaic of evergreen shrubland (chaparral and sage scrub), grassland and oak woodland; the dominant shrublands experience periodic stand-replacing crown fires. The management responses considered included managing the fire regime, establishing corridors or landscape linkages through land-use planning (and relying on natural dispersal and *in situ* conservation), removing invasive species and assisting dispersal through assisted colonization. Assisted colonization (also called managed relocation, assisted migration and translocation) is the transport of individuals by human agency from where they are currently found to other presently unoccupied habitats predicted to provide better prospects for future survival (Regan *et al.* 2012). It has been both promoted

and strongly criticized as an aggressive adaptation strategy for biodiversity management under global change.

We describe the components of the framework and their linkages (Fig. 1), and provide examples of its application in several case studies in southern California, namely plant species with traits that make them vulnerable to altered fire regimes, which have been reduced by historic land-use change and are threatened by future habitat loss. We emphasize the generality of the approach for examining species, threats and management actions beyond those presented as case studies here. We discuss the strengths, data requirements and challenges of this framework, and conclude with future directions for improving and applying this framework to support timely management decisions and actions.

## METHODS

Our approach linked the following steps (Table 1):

- (1) Urban growth scenarios: We developed spatially and temporally explicit urban growth projections for decades into the future using a cellular automaton model. Lands were considered unsuitable habitat for focal species if development was projected within species' habitats within the time horizon considered.
- (2) Species distribution models: Species distribution models (SDMs) were used to create maps of suitable habitat for our focal species (Franklin 2010). SDMs extrapolate

**Table 1** Steps for analysing multiple threats to species persistence under global change, including: modelling components, data requirements, links between models, and selected references providing more details and examples of applications.

<i>Objective</i>	<i>Modelling approach</i>	<i>Data requirements</i>	<i>Links</i>	<i>References</i>
1. To project patterns of future land use where urban land use constitutes habitat loss	Urban growth model	All required model-specific input to run a spatially explicit, cellular automaton urban growth model; OR, existing spatial data representing temporally explicit projection of future land use.	Dynamic urban growth projections are overlaid with climatically suitable habitat projections to incorporate direct habitat loss.	Syphard <i>et al.</i> (2005); Syphard <i>et al.</i> (2011a)
2. To model current species distribution based on habitat factors, including current climate	Species distribution models	Representative sample of species localities; digital maps of environmental variables, including climate (Fig. 2)	Models of distributions under current climate conditions are applied to future climate projections	Franklin (1998); Franklin (2010)
3. To project distribution of suitable habitat under future climate scenarios	Apply species distribution model to climate change scenarios	Future climate projections, downscaled to appropriate scale for species distribution modelling	Dynamic projections of climatically suitable habitat serve as input to population model	Flint & Flint (2012); Franklin <i>et al.</i> (2013); . . . and many others
4. To simulate species persistence, based on demographic factors, under scenarios of habitat change, disturbance (fire) frequency and management response	Spatially explicit population viability analysis using stochastic population models	Species' age/stage-specific vital rates; frequency distribution for stochastic vital rates or threats; estimated initial distribution and size of populations, carrying capacity and appropriate density dependence function	Time series of maps of suitable habitat (one per time step), that dynamically track changes in habitat due to urban growth and climate change	Akçakaya <i>et al.</i> (2005); Regan <i>et al.</i> (2003); Regan <i>et al.</i> (2010)

species location data in space based on correlations of species localities with environmental variables thought to influence habitat suitability. Potential habitat maps for focal species were modelled from species location records and environmental predictor maps (including climate variables) using statistical and machine learning methods.

- (3) Climate change scenarios: SDMs are widely used to delineate climatically suitable future habitat that matches climatic conditions where the species is currently found (Pearson & Dawson 2003) (Fig. 1). Climate change projections from global circulation models (GCMs) were used with the SDMs to predict the distribution of climatically-suitable habitat in the future.
- (4) Population viability models: Stochastic population models employ Monte Carlo simulations to incorporate variation in demographic parameters in order to provide a set of population trajectories, from which the chance of extinction or decline can be calculated (Regan *et al.* 2003). They provide quantitative measures for the likely fate of populations contingent on underlying assumptions. They have proved to be invaluable tools to test hypotheses relating to the consequences of habitat loss and other threats (Henle *et al.* 2004; Akçakaya *et al.* 2005). Spatially explicit stochastic simulation models of

species' population viability incorporated the effects of disturbance, threats and management actions.

### Urban growth scenarios

Because we were concerned with the impact of future land use on habitat extent and pattern, and because virtually all land-use change in our study region was due to urban growth, we used a cellular automaton model known as SLEUTH (Clarke 2008) that predicts the spatial extent of future urban expansion at an annual time step. These temporally explicit predictions were needed to delineate habitat that was both suitable and available (Fig. 1) at the time step of the population model (Table 1). The predictive strength of SLEUTH results from rigorous calibration that associates future development with historic growth patterns, and it has accurately hindcast urban growth for several cities in the USA.

The spatial context of a threat and a species distribution can make a substantial difference in species' vulnerability to multiple threats and the success of spatial conservation measures. Land-use planning is a well-established conservation strategy, and includes land acquisition (protecting land in existing or new habitat preserves), conservation easements (restricting private lands

to uses that are compatible with conservation) and establishing corridors or landscape linkages (preserving lands specifically configured to link core habitat preserves). Land-use planning may not only prevent direct habitat loss from urban development, but it also shows promise for reducing fire hazard in southern California (Syphard *et al.* 2011b). We simulated urban growth under three land conservation scenarios to compare the relative effects of location and extent of protected areas. In Scenario A, development was not allowed on public lands, but allowed in areas currently designated as reserves; in scenario B, development was not allowed on public lands or reserves; and in scenario C, development was not allowed in areas protected in scenarios A and B, with additional habitat protected in small strategically-located reserves closer to the city (Syphard *et al.* 2011a).

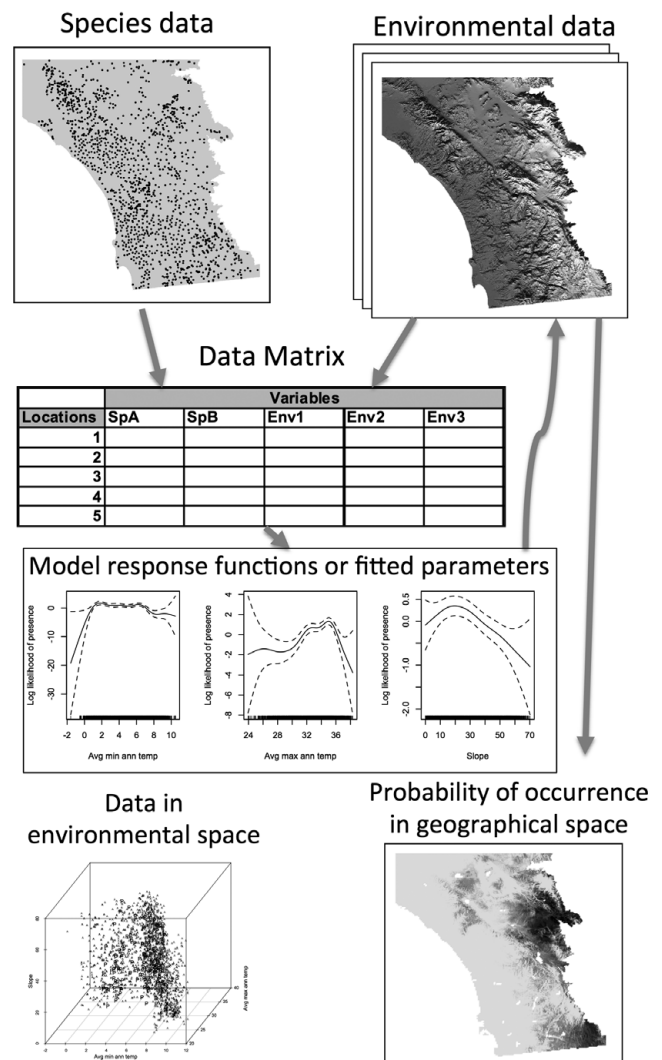
### Species distribution models

We selected species with a range of traits (for example, varying life forms and reproductive responses to fire) to build a suite of models for representative species ('exemplar taxa' *sensu* Fordham *et al.* 2012) of broader functional types (Gillison & Carpenter 1997) that may be applicable to other species with similar traits, but for which fewer demographic data are available (Table 2).

We used species occurrence records and maps of environmental predictors to develop statistical learning models (Franklin 1995) of species distributions (Fig. 2), relying on various sources of species occurrence data such as plant community surveys (recording species presence and absence), natural history collections and conservation databases (with 'presence-only' records). Modelling approaches included generalized additive models (GAMs), decision trees (random forests [RFs]) and maximum entropy (using the MaxEnt modelling platform) models because they spanned statistical, machine learning and presence-only methods, respectively (Franklin 2010), and because they are among the best performing methods (Elith *et al.* 2006). We relied on MaxEnt (Phillips *et al.* 2006) for several species because their occurrence data only included presences and comprised small samples, conditions for which MaxEnt is particularly useful (Phillips & Dudík 2008).

Based on previous research (Franklin 1998, 2002), we selected candidate predictors related to the primary environmental regimes (light, water, nutrients, temperature) determining plant distributions (Mackey 1993). These environmental data (Fig. 2) included digital maps of climate variables, terrain-derived variables (solar insolation, topographic moisture), and variables related to substrate (soils, geology). Because independent evaluation data do not exist for many species, we used bootstrapping to evaluate model predictive performance based on a range of metrics (Fielding & Bell 1997).

Applying SDMs to future climate projections (Table 1) should be done cautiously because SDMs are correlative models that, when used for projection, extrapolate an



**Figure 2** Steps in species distribution modelling. Species occurrence data (such as presence-only, presence-absence or abundance) are the response variable and environmental variables are the predictors used in a multiple-regression like modelling framework. Model can be fit in data space using a wide variety of statistical learning methods. Estimated parameters are then applied back to environmental data layers (mapped grids) to predict probability of species occurrence in geographical space.

empirical relationship between species and environment into novel (non-analogue) environments (Wiens *et al.* 2009). Because choice of SDM method is an important source of uncertainty (Thuiller 2004), ensemble forecasting (averaging of several SDMs; Araújo & New 2007), or carefully controlling model fit and integrating information from models of physiological tolerances (Elith *et al.* 2010), have been recommended. SDMs are most useful for estimating exposure to climate change rather than consequences to population fitness as determined by species' demographic and physiological sensitivity to climate (Dawson *et al.* 2011).

**Table 2** Modelled plant species of southern California Mediterranean-type ecosystem, their functional classification, status, management actions or responses considered in modelling, main findings regarding the ranking of multiple threats, and references where details are published. The sequence of threats is ordered from the most to the least serious threat with respect to population size decline. IUCN = International Union for the Conservation of Nature; CNPS = California Native Plant Society, Inventory of Rare and Endangered Plants of California (<http://www.rareplants.cnps.org/>); US ESA = United States Endangered Species Act, United States Fish and Wildlife Service. \*Urban growth did not affect this species as it occurred on protected lands. \*\*Of the threats listed, number indicates variability in population projections due to models from highest (1) to lowest (3) uncertainty. The ranking of urban growth and climate change depends on the climate model considered: for the US Department of Energy’s parallel climate model (PCM), urban growth is a greater threat than climate change; for the National Oceanic and Atmospheric Administration’s Geophysical Fluid Dynamic Laboratory’s CM.2 model (GFDL), climate change is a greater threat than urban growth.

<i>Common name</i>	<i>Scientific name</i>	<i>Functional type</i>	<i>Status</i>	<i>Management actions</i>	<i>Threats</i>	<i>References</i>
Wart-stemmed lilac	<i>Ceanothus verrucosus</i>	Obligate-seeding long-lived perennial	Rare, globally vulnerable (G3; CNPS), C2 candidate species under US ESA	Reduce fire; habitat protection	Very frequent fire > (climate change + urban growth) > climate change > urban growth	Lawson <i>et al.</i> (2010); Conlisk <i>et al.</i> (2013); Syphard <i>et al.</i> (2013)
Cup-leaf lilac	<i>C. greggii</i> var. <i>perplexans</i>	Obligate-seeding long-lived perennial	Range largely restricted to the ecoregion, common and widespread there	Reduce fire; habitat protection	Very frequent fire > climate change > urban growth	Regan <i>et al.</i> (2010); Syphard <i>et al.</i> (2013)
Tecate cypress	<i>Hesperocyparis (Callitropsis) forbesii</i>	Obligate-seeding long-lived perennial	Rare, threatened in California (1B.1; CNPS) and globally imperilled (NatureServe)	Reduce fire; assisted colonization	Frequent fire > climate change > urban growth*	Regan <i>et al.</i> (2012)
Engelmann oak	<i>Quercus engelmannii</i>	Obligate resprouting long-lived perennial	Endemic to the ecoregion, moderately common; vulnerable (IUCN Red List)	Reduce fire; landscape linkages to promote dispersal	Climate change > frequent fire > urban growth	Conlisk <i>et al.</i> (2012)
San Diego thornmint	<i>Acanthomintha ilicifolia</i>	Annual herb	Rare and endangered species under US ESA	Remove invasive species; reduce fire; habitat protection	** Frequent fire (3) > urban growth (2) > climate change (1)	Conlisk <i>et al.</i> (2013)

### Climate change scenarios and the shifting distribution of suitable habitat patches

We used two general circulation models (GCMs) and two emissions scenarios that have been widely used to project climate change impacts on water supply, energy, fire risk and ecosystems in California (Franco & Sanstad 2008; Westerling & Bryant 2008; Flint & Flint 2012). The GCMs we used were the US Department of Energy's Parallel Climate Model (PCM) and the GFDL climate model (from the National Oceanic and Atmospheric Administration's Geophysical Fluid Dynamic Laboratory's CM.2 model), and the emissions scenarios were A2 (medium high) and B1 (low). These four scenarios have been used in impact analysis in southern California because (1) they successfully simulate the region's recent historical climate, including the distribution of temperatures and strongly seasonal precipitation (Cayan *et al.* 2008), and (2) the two GCMs differ in their sensitivity to greenhouse gas (GHG) forcing, therefore they encompass the range of conditions that would be projected by a larger ensemble of climate models (see Lenihan *et al.* 2008). Further, statistically and spatially downscaled current and future climate maps based on these four scenarios were available for our region at very fine scales, namely to 100-m resolution (Flint & Flint 2012; Franklin *et al.* 2013). Combining SDMs and climate change scenarios with spatially explicit land-use change due to urban growth (Fig. 1) allowed us to predict the separate and combined effects of these factors on the extent of suitable habitat and to evaluate the magnitude of uncertainty in projections resulting from different sources (Table 1). To create a time series of dynamic suitable and available habitat, the maps of climatically suitable habitat in year 0 (present) and year 100 (future) were linearly interpolated to produce a time series that we subsequently overlaid with the annual urban growth maps (Fig. 1). We delineate patches of potentially occupied habitat based on the most appropriate probability threshold criterion (Freeman & Moisen 2008) used to distinguish suitable from unsuitable habitat (for details see references in Table 2).

### Population viability analysis: the impact of threats and effectiveness of management scenarios

The projected landscape dynamics of climatically suitable habitat from the previous steps captures the dynamics of the spatial structure of the metapopulation (for example changing size, number and location of habitat patches) for population models (Fig. 1). We used stochastic, spatially explicit, age/stage-based metapopulation models to simulate fragmented populations under different threats and management scenarios. We used the RAMAS<sup>®</sup> geographic information system (GIS) (Akçakaya & Root 2005) modelling software to link the population model to the time series of habitat suitability maps to produce spatially structured, age/stage-based models of metapopulations. RAMAS<sup>®</sup> GIS also allows a variety of realistic density dependence

mechanisms (Akçakaya *et al.* 2004), and episodic threats such as fire, flood and drought.

Models were constructed for species covering a range of regionally significant plant functional types, threats and corresponding management responses (Table 2). Obligate seeders are plants with long-lived seeds that only reproduce from seed, through fire-stimulated germination. They require sufficient time between fires to develop an adequate seed bank and are therefore sensitive to too-frequent fire (Keeley 1986). For obligate-seeding, long-lived trees and shrubs (Table 2), we constructed a spatially explicit stochastic age-based matrix model, with age classes ranging from seedlings to plants > 99 years old (Lawson *et al.* 2010; Regan *et al.* 2010, 2012). Survivorship was estimated by fitting functions to published data for the focal species or closely related species. Recruitment for these species only occurs following fire and was estimated from the average number of seeds or post-fire seedlings per adult plant in available data sets. Average dispersal distance was set to 0 for the obligate seeders we studied, as dispersal occurs on the order of tens of metres, much shorter than the average distance between habitat patches. Carrying capacity was calculated as a function of age (and therefore size) of the plants; as plants grow older and larger, carrying capacity (the maximum abundance a patch could support) is reduced. Density dependence was incorporated in a variety of ways; for some species it was a strict ceiling carrying capacity, for others a time lag was introduced where population abundance gradually reduced to carrying capacity when it exceeded carrying capacity.

Another plant fire-response strategy in MTEs is obligate resprouting; plants survive fire by vigorous vegetative reproduction, but only sexually reproduce in the absence of fire. Seeds are not long-lived and tend to be killed by fire. A stage-based model was developed for a long-lived obligate resprouter (Table 2) with five stages (seed, small seedling, large seedling, sapling and adult tree), chosen to match available demographic data (Conlisk *et al.* 2012). Vital rates depended on time since last fire and masting (episodic high seed production). Seed predation was assumed to occur prior to dispersal, and post-dispersal predation was accounted for in germination rates. Seeds for the focal obligate resprouter are dispersed metres to kilometres by small mammals and birds attempting to eat or cache them, and dispersal distances were taken from the literature (for example see Scofield *et al.* 2010). Because dispersal distance is highly uncertain, a range of values was tested.

An important component of plant diversity in MTEs is a rich annual flora (Cowling *et al.* 1996). Demographic data are often lacking for many of these herbs despite their endangered and protected status. Our demographic model for an annual herb (Table 2) was constructed specifically to assess threats and rank management strategies in light of this uncertainty. A two-stage matrix model was developed for seeds and plants in which fire affects the mean vital rates. The additional threats of invasive (non-native) plant species via competition and the facilitation of invasives by fire were incorporated into the

demographic model for this species using several scenarios (because the effect of invasives is highly uncertain) by lowering vital rates according to different trajectories following fire.

Threats can be included by invoking changes in demographic rates, carrying capacity or population abundance; for threats that occur well outside the typical range of variability in demographic rates, a probabilistic function can be linked that acts on vital rates. Scenarios of different fire frequencies were incorporated into our models as stochastic events governed by a Weibull hazard function (Moritz 2003). We constructed different hazard functions (Regan *et al.* 2010) to simulate a range of average fire return intervals from very short (10 years) to longer ‘natural’ intervals (80 years) in our study region.

The population models were linked to the dynamic habitat (Fig. 1). Carrying capacity for each patch in the metapopulation model was determined by patch size and habitat suitability predicted by the SDM: the unit of carrying capacity should match the cell size in the input maps, in this case number of individuals per hectare. As habitat suitability and patch size change through time (due to climate change and urban growth), so does carrying capacity. If the population abundance exceeds carrying capacity then density dependence is invoked, lowering survival rates of the population; the mechanism for this is species-dependent.

We analysed the effects of compounding parameter uncertainty on broad conclusions through sensitivity analysis, perturbing key parameters in all modelling components to determine how uncertainty affected the ranking of species vulnerability to the threats being considered. We also examined the effect of model choice (be it GCM, emissions scenario, SDM or population) on the integrated model output, and, in particular, which model type contributed the greatest to variability in output.

## RESULTS

### Fire management

Increased fire frequency was consistently highly ranked as a threat to the plant types we considered (Table 2), especially long-lived obligate seeders (Fig. 3). In some cases, even if predicted habitat losses or shifts due to climate change were dramatically large, too-frequent fire was still the largest threat to persistence.

### Land-use planning

Urban growth simulated using the three land conservation scenarios (A: development not allowed on public land, but allowed on large private reserves, B: development not allowed on public lands or large private reserves, C: development not allowed on A and B and also not allowed on small, strategically placed reserves) suggested that, although large, existing reserves are extensive, and excluding them from development (Scenario A versus B) did not have the proportional effect

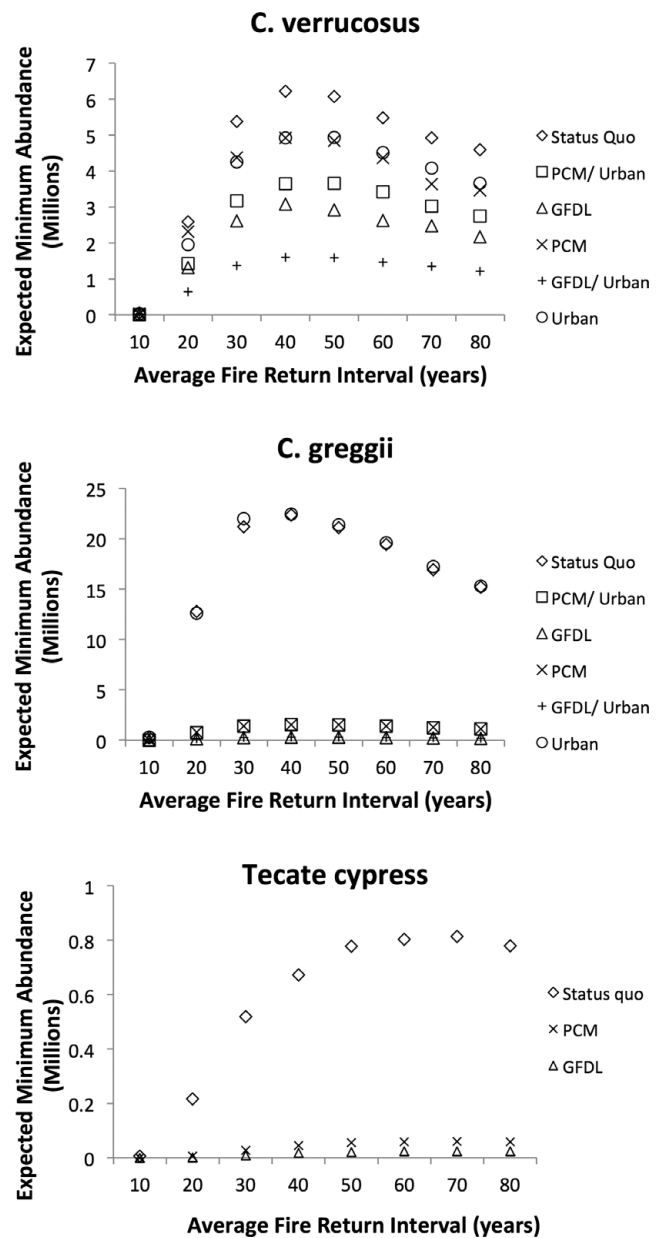
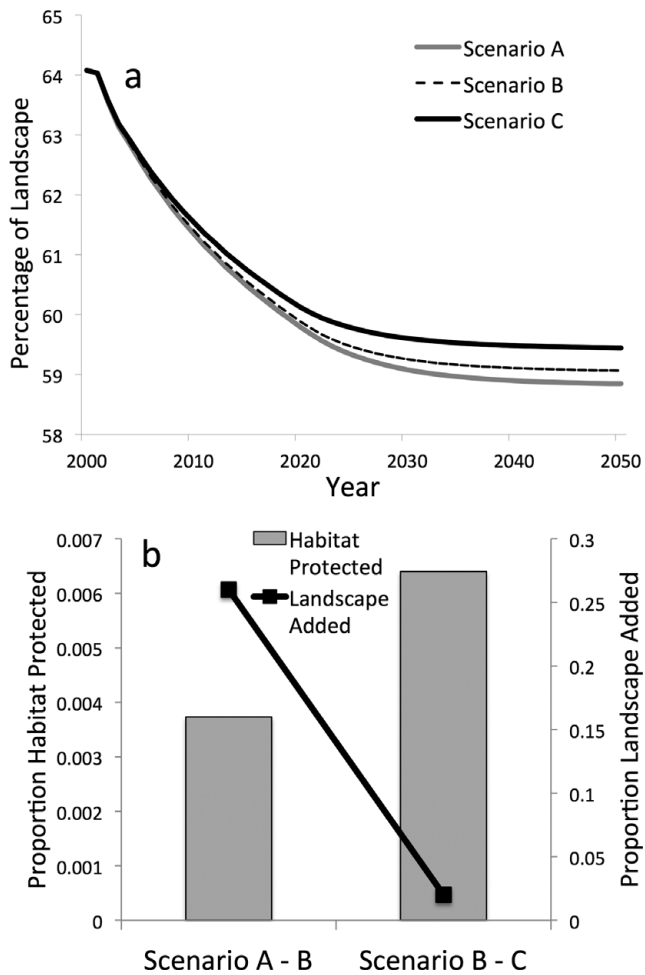


Figure 3 Expected minimum abundance at different average fire return intervals for three long-lived obligate seeder plant species (Table 2), *Ceanothus verrucosus*, *C. greggii* and Tecate cypress (*Hesperocyparis (Callitropsis) forbesii*) under status quo conditions (no urban growth or climate change), under climate change scenarios for the US Department of Energy’s parallel climate model (PCM) and the GFDL climate model (from the National Oceanic and Atmospheric Administration’s Geophysical Fluid Dynamic Laboratory’s CM.2 model) only, for the models combined with urban growth, and for urban growth only. (Tecate cypress habitat was unaffected by urban growth alone, so these scenarios are not shown.)

that smaller reserves in strategic locations did on habitat conservation (Scenario B versus C; proportion of landscape added to protected areas) because of the high likelihood



**Figure 4** (a) Percentage of vegetated habitat (natural plant communities) on the landscape for three development scenarios: Scenario A = public lands restricted from development; Scenario B = public lands and large conservation reserves restricted from development; Scenario C = public lands, large conservation areas and small strategically-placed reserves restricted from development. (b) Proportion of the landscape added to protected areas among different development scenarios versus the proportion of additional habitat that was actually protected in the simulations.

of those locations becoming urbanized otherwise (Fig. 4) (Syphard *et al.* 2011a).

When comparing effects of multiple threats on two obligate-seeding shrubs in the genus *Ceanothus* (Table 2), we found that, although too-frequent fire posed a large threat to both species (Fig. 3), the ranking of other threats differed between them, especially under scenarios of longer fire intervals (Syphard *et al.* 2013). Despite the broader current distribution of *C. greggii* than *C. verrucosus*, climate change projections suggested that its habitat could contract to a greater extent than that of *C. verrucosus* because climate conditions typical of the coastal areas were not projected to shift as greatly as those inland. Conversely, urban growth was projected to be more of a threat to *C. verrucosus* than *C. greggii* (Fig. 3), especially under scenarios of climate change, because future

urban development is expected to overlap future suitable habitat (Fig. 5).

We predicted dramatic reduction in abundance of a long-lived obligate resprouting oak under increased fire frequency and climate change (Table 2). Habitat suitability predictions alone underestimated the impact of these global change scenarios on the population by roughly five-fold. Dispersal allowed Engelmann oak to establish in habitat predicted to become more suitable over time, mitigating to a limited extent predicted global change effects. When we assumed that masting lowered seed predation rates, increased masting frequency led to higher expected minimum abundances (for details see Conlisk *et al.* 2012). It is not known how climate change may affect masting frequency.

### Assisted colonization

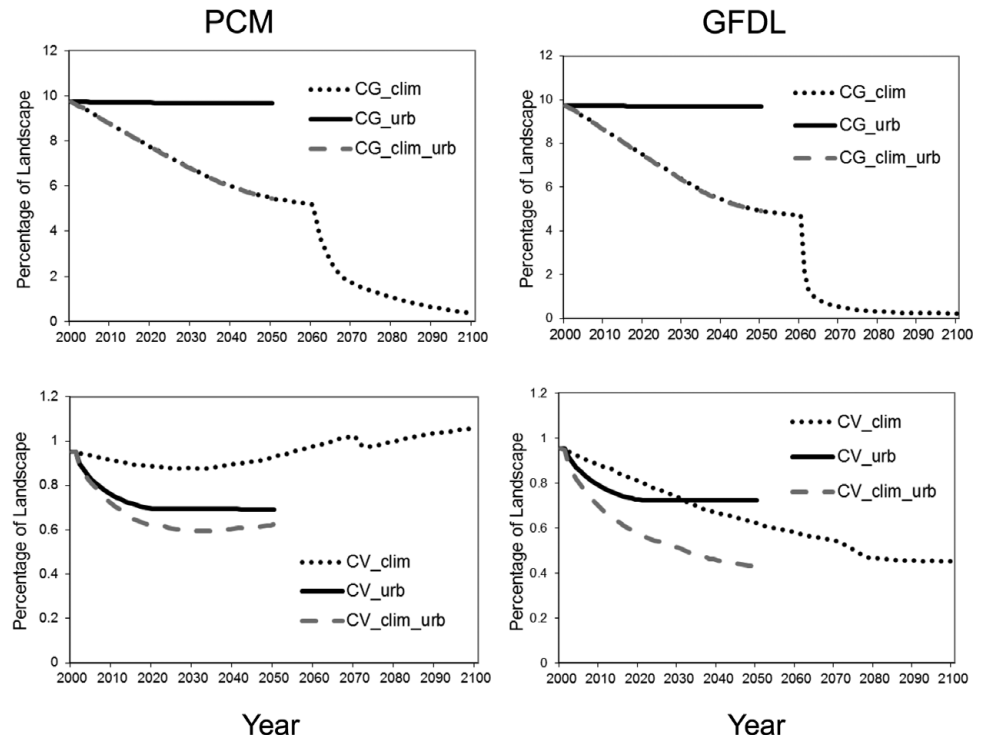
We asked how much assisted colonization would be necessary to minimize risk of population decline of a rare obligate seeding tree, Tecate cypress (Table 2), in the face of potential climate change impacts and other existing threats (Fig. 3), and under what conditions could it be an effective climate change adaptation response. We found that assisted colonization could minimize risk of decline or extinction for Tecate cypress when: (1) large source populations are projected to decline dramatically due to habitat contractions, (2) multiple nearby sites are predicted to contain suitable habitat, (3) the species has minimal natural dispersal, (4) rates of successful establishment of translocated individuals are high, and (5) non-climatic threats such as altered fire regimes are absent (Table 2). However, when serious ongoing threats exist, such as too-frequent fire, assisted colonization is ineffective at boosting population numbers (for details see Regan *et al.* 2012).

### Uncertainty

We examined compounding uncertainty across model types and parameters for the rare annual plant species San Diego thornmint (Table 2), and found that the type of SDM contributed most to overall uncertainty in model output. Climate change models and scenarios, and population model parameters were the next most important source of uncertainty (roughly equal to each other), followed by urban growth scenarios, type of population model used and fire regime scenarios (Conlisk *et al.* 2013). Although different combinations of SDM, climate and population model assumptions led to different rankings of management actions, invasive species control and fire suppression consistently ranked highly among the most beneficial options across scenarios (Table 2). This information is useful to regulatory agencies that suspect fire promotes invasive species that compete with San Diego thornmint (Anon. 2009), and managers who are already removing non-native plants on their preserves (J. Vinje, personal communication 2012).



**Figure 5** Time trajectory for percentage of landscape occupied by two shrub species that are obligate seeders (*Ceanothus greggii* [CG, upper panels] and *C. verrucosus* [CV, lower panels]), with dynamic habitat loss due to urban growth (\_urb, solid line) modelled for the period 2000–2050, climate change modelling 2000–2100 (\_clim, dotted), and combined losses (\_clim\_urb, dashed), based on the US Department of Energy’s parallel climate model (PCM) and the National Oceanic and Atmospheric Administration’s Geophysical Fluid Dynamic Laboratory’s CM.2 model (GFDL).



**DISCUSSION**

**Management actions: fire management, land use planning and assisted colonization**

Too-frequent fire and climate change were almost always the greatest threats to the plant functional types we examined (Table 2). Because of the time needed for plants to mature and to establish a sufficient seed bank following fire, it is not surprising that too-frequent fire was a highly-ranked threat to long-lived obligate seeding species (Lawson *et al.* 2010; Regan *et al.* 2010, 2012; Syphard *et al.* 2013). However, even obligate resprouter abundances were predicted to decline by 50–60% with high fire frequency (Conlisk *et al.* 2012). For an annual herb without any particular fire adaptations, fire suppression also ranked highly as a management response aimed towards increasing population persistence (Conlisk *et al.* 2013).

Although fire management through prevention or suppression would be an effective conservation strategy in these cases, its feasibility may be challenging due to continued increases in human-caused ignitions at the developing wildland–urban interface (WUI) (Syphard *et al.* 2007). The largest wildfires occur every year under extreme fire weather conditions, which is also when fuel manipulation projects have limited effectiveness and suppression efforts are overwhelmed (Syphard *et al.* 2011b). These challenges in reducing regional fire frequency were acknowledged in a 2010 workshop aimed at developing conservation strategies for Tecate cypress. Land managers and agency personnel focused primarily on the potential of assisted colonization for this species. Nevertheless, evaluation of traditional and alternative management approaches for reducing fire hazard

and impacts to biodiversity is an area of active research (see for example [www.werc.usgs.gov/socalfirerisk](http://www.werc.usgs.gov/socalfirerisk)).

The counterintuitive result that the widespread *Ceanothus* species is more vulnerable to habitat loss due to climate change than the rare *Ceanothus* species resulted from the juxtaposition of their current spatial distributions with the distribution of the threats and the ramifications of climate change on distribution projections. *C. greggii* is widespread in rural foothills, is mainly found on public lands, and therefore is not considered vulnerable to habitat loss due to urban growth. Model projections suggested that its foothills distribution makes it vulnerable to climate warming. In contrast, *C. verrucosus* is considered rare and managed for conservation, and has a restricted fragmented distribution in the urbanized coastal area (Regan *et al.* 2008; Franklin *et al.* 2011). Our projections suggest that future urban growth is a greater threat than climate change because climates are not projected to shift dramatically in coastal areas. We found that adding small areas of conservation lands in strategic (coastal) locations was disproportionately beneficial compared to the addition of larger *ad hoc* conservation areas in (inland) locations less likely to develop in the future. For a resprouting oak species, dispersal has the potential to offset the negative effects of climate change if average dispersal distances are large enough; therefore land use planning that promotes landscape linkages is likely to be a useful adaptation strategy. The importance of land-use planning as a conservation tool for preservation of future critical habitat varied among species as a function of the location and extent of their spatial distribution. In addition to direct habitat protection, however, land use planning has also shown substantial promise for reducing fire

impacts and minimizing future fire frequency (Syphard *et al.* 2012).

The efficacy of assisted colonization as a climate adaptation strategy depended not only on species demographic characteristics but also on mitigation of other threats. If individuals are translocated to areas with frequent fire, then assisted colonization is a waste of effort, irrespective of the future habitat suitability of the recipient sites or how many individuals are translocated.

### Uncertainty

All landscape and population models, indeed models of all kinds, incorporate trade-offs between the detail required to achieve a desired level of realism and the uncertainty that compounds through multiple parameters and model components (Regan *et al.* 2002, 2003). A number of studies have found, as we did, that projections of species range change under climate change scenarios, based on SDMs alone or SDMs linked to demographic models, vary most with the type of SDM used (Thuiller 2004; Fordham *et al.* 2012). However, while we found large differences in results across model and scenario choices for a rare annual plant species, the ranking of management actions was fairly robust to these uncertainties.

Spatial resolution of climate data is an additional source of uncertainty. We were able to generate predictions of climatically suitable habitat at fine scales because of the fortuitous availability of fine-scaled climate maps (Flint & Flint 2012). Because the modelling framework was used to address spatially explicit threats and management scenarios for individual species, fine-scale climate data were necessary to capture population dynamics of the species in question as well as management actions and responses at a scale relevant to conservation managers. Recently it was shown that as climate data resolution (ranging from 90 m to 4 km) became coarser, SDMs based on those data predicted larger habitat areas with diminishing spatial overlap between fine- and coarse-scale predictions (Franklin *et al.* 2013). Habitat captured using finer scales, but missed using coarser-scale data, could have serious implications when predictive maps are used for regional conservation decision-making. However, the management question may drive the resolution requirements; for example, fine spatial scale may be necessary for considering assisted colonization but is perhaps less essential for fire management.

### Strengths of the framework

The framework presented uses an integrated landscape approach that links population models to projections of the shifting distribution of suitable habitat under climate and land-use change scenarios, derived from species distribution and urban growth models (Anderson *et al.* 2009; Fordham *et al.* 2012). In fire-prone ecosystems, models of fire events and the demographic effects of fires on populations are also an essential part of this framework (Keith *et al.* 2008).

Nevertheless, the framework can be generally applied to any region provided sufficient data exist to construct each composite model. We have presented an overview and results of this framework applied to plants in a fire-prone MTE, but threats could include extreme weather events, altered hydrological regimes, agricultural expansion, poaching and harvesting, while species may include both animals and plants. By linking models that address each of these important drivers, realistic future projections can be made that would not be possible if each driver were considered in isolation. For example, for the species we studied (Table 2), projected population declines that accounted for population dynamics were greater than if population loss were simply proportional to habitat losses predicted from species distribution models under global change scenarios. Using this framework, threats can be ranked individually and in combination, as can the effectiveness of integrated management responses in promoting population persistence.

This is a flexible framework for species-specific questions and therefore especially useful for species with protected status that are monitored and managed under legal mandate, and all of the models can be updated as new information becomes available. We have also demonstrated that population models may be developed for groups of species that share demographic traits, for example functional types based on disturbance response, and used to characterize risk for a broader group of species with similar traits (see also Keith *et al.* 2008). With the right skill set, dedicated time and data availability, the development, linkage and execution of these models could be expected to span six analyst-months per species, assuming (say) the urban growth modelling results were available.

### CONCLUSIONS AND FUTURE DIRECTIONS

SDMs may overestimate species decline through range contraction by underestimating species' likelihood of persisting *in situ*, and may thus be used for identifying areas of increasing habitat suitability under future climate scenarios (Schwartz 2012). Scenarios incorporating current plus future gains in habitat could be evaluated alongside 'no climate change' and climate change net effects (gains and losses) on habitat distribution within the modelling framework presented in this paper. Further, SDM projections could be modified using information about ecophysiological tolerances to better characterize the species' fundamental niche and potential distribution on environmental gradients (Kearney & Porter 2009; Dormann *et al.* 2012); this approach was pioneered decades ago in our study region (Malanson & Westman 1991).

Within the framework described here, climate change effects on population dynamics were included via the SDM-based predictions of the location and quality of habitat patches, determining carrying capacity. Alternatively, population models might be constructed that use local within-patch data to define how growth and survival rates vary across

the landscape as climate changes (also discussed by Fordham *et al.* 2012). If such data on the relationship between climate and vital rates were available, the impact of climate change could be estimated using richer, more detailed local ecological mechanisms (Conlisk *et al.* 2013). Types of threats other than those discussed here may be incorporated, such as the effects of floods, disease, predation and harvest.

An area of future development would be to address interactions and feedbacks among threats and responses. For example, climate change might affect fire frequency or land use. Fire regimes might also be affected by other types of disturbance, such as insect outbreaks or wind blowdown of forests, as well as land-use changes associated with population growth or urban expansion (Syphard *et al.* 2007).

As the number, magnitude and spatial extent of threats to biodiversity increase, integrated modelling frameworks are needed to link information from a variety of sources and across a range of scales of ecological organization. We have described one such framework that has been rising in prominence in the literature over the past five years, a framework that couples climate models, species distribution models, urban growth models, fire models and population models to provide a mechanism for exploring species responses and potential management strategies in the context of multiple threats. Ongoing studies within this framework, coupled with meaningful collaboration with conservation managers and practitioners, can guide future research to reduce uncertainties, close data gaps and align scenarios closely with on-the-ground conservation management goals. The creation of frameworks that integrate the vast body of data and models currently available to examine threats and explore the effectiveness of intervention strategies, goes a long way towards providing robust management actions to mitigate the myriad threats experienced by biodiversity.

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