# Evaluation of assisted colonization strategies under global change for a rare, fire-dependent plant

HELEN M. REGAN*, ALEXANDRA D. SYPHARD†, JANET FRANKLIN‡, REBECCA M. SWAB*, LISA MARKOVCHICK§, ALAN L. FLINT¶, LORRAINE E. FLINT¶ and PAUL H. ZEDLER**

*Biology Department, University of California Riverside, 900 University Avenue, Riverside, CA 92521, USA, †Conservation Biology Institute, 10423 Sierra Vista Avenue, La Mesa, CA 91941, USA, ‡School of Geographical Sciences and Urban Planning, Arizona State University, 975 S. Myrtle Avenue, Tempe, AZ 85287, USA, §Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182, USA, ¶U.S. Geological Survey, 6000 J St., Sacramento, CA 95819, USA, **U.W. Arboretum and Nelson Institute for Environmental Studies, The University of Wisconsin-Madison, 550 N. Park St., Madison, WI 53706, USA

## Abstract

As a clear consensus is emerging that habitat for many species will dramatically reduce or shift with climate change, attention is turning to adaptation strategies to address these impacts. Assisted colonization is one such strategy that has been predominantly discussed in terms of the costs of introducing potential competitors into new communities and the benefits of reducing extinction risk. However, the success or failure of assisted colonization will depend on a range of population-level factors that have not yet been quantitatively evaluated – the quality of the recipient habitat, the number and life stages of translocated individuals, the establishment of translocated individuals in their new habitat and whether the recipient habitat is subject to ongoing threats all will play an important role in population persistence. In this article, we do not take one side or the other in the debate over whether assisted colonization is worthwhile. Rather, we focus on the likelihood that assisted colonization will promote population persistence in the face of climate-induced distribution changes and altered fire regimes for a rare endemic species. We link a population model with species distribution models to investigate expected changes in populations with climate change, the impact of altered fire regimes on population persistence and how much assisted colonization is necessary to minimize risk of decline in populations of Tecate cypress, a rare endemic tree in the California Floristic Province, a biodiversity hotspot. We show that assisted colonization may be a risk-minimizing adaptation strategy when there are large source populations that are declining dramatically due to habitat contractions, multiple nearby sites predicted to contain suitable habitat, minimal natural dispersal, high rates of establishment of translocated populations and the absence of nonclimatic threats such as altered disturbance regimes. However, when serious ongoing threats exist, assisted colonization is ineffective.

*Keywords:* assisted colonization, bioclimate envelope, climate change, fire, population model

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## Introduction

In light of the results of global climate models and species distribution models (SDMs), or bioclimatic envelopes (Keith *et al.*, 2008), a clear consensus has emerged on the effects of climate change on species distributions – climatically suitable habitat for many species is forecast to dramatically reduce, increase or shift (Iverson *et al.*, 1999; Beaumont & Hughes, 2002; Midgley *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Sekercioglu *et al.*, 2008; Lawler *et al.*, 2009). Therefore, attention has recently focused on managing species that seem unlikely to persist in their present habitats (Heller &

Zavaleta, 2009; Lawler *et al.*, 2010). The most aggressive of these strategies, widely discussed in the literature and public media, is assisted colonization (also referred to in the literature as managed relocation and assisted migration). It is simply the transport of individuals by human agency from existing natural habitats to other presently unoccupied habitats predicted on some basis to provide better prospects for future survival.

There has been much debate in the scientific literature about the ethics, feasibility and potential pitfalls and benefits of assisted colonization (Schwartz *et al.*, 2009; Minteer & Collins, 2010). Most opposition centers on the potential for invasive spread and competition with native biota in recipient habitat, the level of uncertainty associated with introducing organisms to new environments and the redirection of valuable

Correspondence: Helen Regan, tel. + 1 951 827 3961,
fax + 1 951 827 4286, e-mail: helen.regan@ucr.edu

conservation resources away from potentially more serious threats and more promising conservation actions (Fazey & Fischer, 2009; Ricciardi & Simberloff, 2009). Proponents of assisted colonization counter that the risk of invasive escape and excessive dominance is low for short-distance intracontinental dispersal (Schlaepfer *et al.*, 2009), that the worst case costs of altering the composition and function of ecosystems are tolerable when weighed against the benefits of forestalling extinction (Sax *et al.*, 2009), and that assisted colonization can fill the role natural dispersal would normally play in a landscape less fragmented by human land use (Vitt *et al.*, 2009).

Although decision frameworks have been developed to address many of these complexities (McLachlan *et al.*, 2007; Hoegh-Guldberg *et al.*, 2008; Richardson *et al.*, 2009), a complicating issue that has received less attention in the literature is that climate change impacts will not occur in isolation. Depending on the region and species, a suite of other threats has the potential to seriously impact species survival and patterns of biodiversity. These existing threats are no less potent because climate change has come to the fore; in fact, many threats are predicted to be exacerbated under climate change, and hence, adaptation strategies need to be devised in the context of multiple threats. In this article we couple dynamic SDMs, which track the impact of projected climate change on species habitat suitability through time, with stochastic population models and fire hazard functions to evaluate the ability of a range of assisted colonization strategies to mitigate the effects of climate change on the availability of climatically suitable habitat for a rare fire-dependent plant.

Interactions among multiple threats may be particularly devastating in Mediterranean ecosystems (Midgley *et al.*, 2003; Underwood *et al.*, 2009). Mediterranean ecosystems are biodiversity hotspots and, while they only occupy <5% of the earth's surface, they make up 20% of the world's flora (Cowling *et al.*, 1996). They are among the most threatened ecosystems in the world because they are particularly sensitive to the most prevalent and dominant threats: habitat loss, altered natural disturbance regimes (particularly fire), invasive species and anthropogenic climate change (Cincotta *et al.*, 2000; Sala *et al.*, 2000; Underwood *et al.*, 2009). It is not clear which threat will have the most serious consequences for species in Mediterranean ecosystems or what the cumulative impact of multiple threats will be. The many rare and endemic plant species of these regions are likely to be disproportionately affected by climate change (Midgley *et al.*, 2002; Loarie *et al.*, 2008). Impacts to Mediterranean systems could therefore seriously deplete global biodiversity. Evaluation of

adaptation strategies therefore should account for the cumulative impact of multiple threats.

Fire has played some role in all Mediterranean ecosystems and is of central importance in Australia, the Pacific Coast of North America, South Africa and portions of the Mediterranean basin (Bond & Keeley, 2005). However, anthropogenic land-use change has altered fire regimes in all five Mediterranean ecosystems (Cincotta *et al.*, 2000; Syphard *et al.*, 2009). Most significantly, fire frequency has increased in many regions because there are more ignition sources. These altered regimes may interact synergistically with climate change, likely through changes to fuel properties, although the nature of the effect remains uncertain (McKenzie *et al.*, 2004). Nevertheless, if fires become more frequent, as expected, in Mediterranean shrublands (Lavorel *et al.*, 1998; Westerling *et al.*, 2003), the effect may be devastating for rare and endemic obligate seeding plants, that is, plants with large seed banks that require fire for germination, already threatened by anthropogenically increased fire frequency.

Assisted colonization is akin to translocation in traditional single-species conservation management (i.e., the movement of individuals from one location to another, including introduction and reintroduction), the success of which depends on a number of practical, demographic and habitat-related factors such as the quality of the recipient habitat, the number and life stages of translocated individuals, the rate at which translocated individuals establish and reproduce in their new habitat and whether or not the recipient habitat is subject to threats that could impinge on the translocated population. Hence, examination of the expected suitable habitat under climate change is insufficient to gauge the likelihood of success of assisted colonization programs; the demography of the species and the dynamics of populations in new patches should also be considered. Any assessment of the likely success of assisted colonization must necessarily rely on population projections and must be considered in the context of likely habitat loss due to climate change and ongoing threats to populations.

In this article we focus on a long-lived rare endemic obligate seeding tree, Tecate cypress [formerly *Cupressus forbesii* Jeps., currently *Hesperocyparis forbesii* (Jeps.) Bartel or *Callitropsis forbesii* (Jeps.) D.P. Little; the common name is used in this article for simplicity given the recent taxonomic changes]. Tecate cypress is representative of a common functional group of plants found in most Mediterranean ecosystems: long-lived obligate seeders. It is an ideal case study because it is rare and highly threatened, it occurs in a landscape fragmented by urban growth and other land-use changes, its life history cycle is dependent on fire regime which is also

expected to change with climate change, it is a poor disperser and large reductions in its populations are likely, deeming global extinction in the next century possible in the absence of intervention.

We do not take one side or the other in the debate over whether assisted colonization is worthwhile. Rather, we focus on the likelihood that assisted colonization will promote population persistence in the face of climate-induced distribution changes for a rare endemic species. Our purpose is twofold. First, we aim to apply foundations in population viability analysis and biogeography to provide a framework to quantitatively analyze the potential population-level effects of climate change on a species and evaluate assisted colonization strategies under variability and uncertainty. Second, we wish to highlight the importance of considering the effects of climate change in the context of existing threats to the persistence of species. Although we assess, separately and in combination, the effects of climate change on habitat availability and altered fire regime, we do not explicitly predict complex interactions between climate and fire. We address the following questions: How is the distribution of Tecate cypress expected to change with climate change? How sensitive are Tecate cypress populations to fire regimes, and especially how vulnerable are they to more frequent fire? What effect would assisted colonization have on the risk of population decline under climate change and altered fire regime?

## Materials and methods

### Species background

Tecate cypress is a long-lived (>100 years) rare fire obligate species located in the highly urbanized region of southern California, USA and Baja California, Mexico, usually above 400 m in elevation associated with chaparral plant communities (Armstrong, 1966; Zedler, 1977; Dunn, 1985, 1987; Esser, 1994). There are only four major populations in the United States: Otay Mountain, Guatay Mountain, Sierra Peak and Tecate Peak (Fig. 1), most on Federal land or other land reserves (Dunn, 1986). Reproduction occurs almost entirely through the seed released from canopy-stored cones during fires that simultaneously kill all adult trees. Although Tecate cypress accrues a canopy-stored seed bank, it shares fire response and other life history traits typical of other long-lived obligate seeding shrub species with fire-cued germination from a persistent underground seed bank (Zedler *et al.*, 1983; Syphard & Franklin, 2010). Seed dispersal is limited, and occurs minimally via erosion or water flow across denuded slopes.

Tecate cypress is ranked as rare, threatened or endangered and seriously threatened in California and elsewhere (1B.1) by the California Native Plant Society and globally imperiled by NatureServe. Past and present threats include habitat
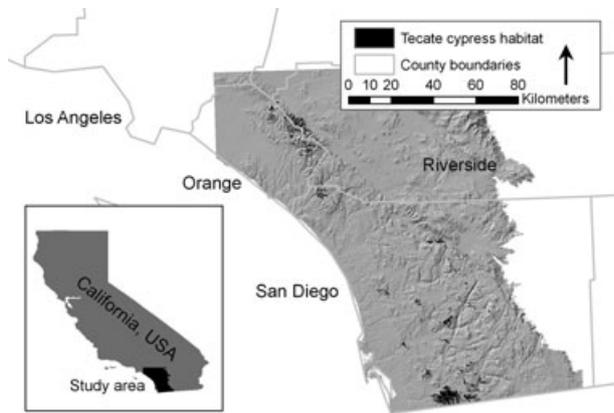


**Fig. 1** Map of study area within region (inset). Gray shading in main map shows the study area, black shading shows the currently occupied Tecate cypress populations; gray shading in inset shows the state of California, black shading orients the study area.

fragmentation, degradation and destruction and increased exposure to anthropogenic fire ignition sources.

### Coupled modeling approach

We developed SDMs (Franklin, 2009) for Tecate cypress under current and future climate scenarios using geographically referenced herbarium records of species occurrence and maps of occupied habitat, digital maps of climate, terrain and soils and the MaxEnt modeling method (Phillips *et al.*, 2006). To project future climate we applied results from two General Circulation Models (GCMs) used for forecasting the impacts of climate change in California (Cayan *et al.*, 2008), the Parallel Climate Model from the National Center for Atmospheric Research and the National Oceanic and Atmospheric Administration's Geophysical Fluid Dynamics Laboratory CM2.1 model (GFDL), for the A2 scenario that is based on medium high greenhouse gas emissions. Predictive maps of current and future suitable habitats were temporally interpolated and used to provide the patch structure for each time step of a spatially explicit stochastic age-based matrix population model for Tecate cypress in the platform RAMAS GIS® (Akçakaya & Root, 2005). This model was used to simulate the effects of fire regime and assisted colonization scenarios on the expected minimum abundance of Tecate cypress both with and without the effects of climate change on the distribution, extent and quality of suitable habitat. Descriptions of each component of this modeling framework are provided next.

### Species distribution models

An SDM was developed for Tecate cypress to describe the statistical association of its contemporary distribution with mapped climate, terrain and soil factors. Strictly speaking, this model predicts the geographical distribution of suitable habitat (Franklin, 2009) defined only by abiotic environmental factors (ignoring biotic factors), but for brevity we will use the

term 'suitable habitat' in this article. We used species occurrence data from 37 geolocated herbarium collections (Consortium of California Herbaria; http://ucjeps.berkeley.edu/consortium/) provided to us by SDNHM, and from the California Natural Diversity Database (http://www.dfg.ca.gov/biogeodata/cnddb/). As these observations represented presence-only records and not a probability-based sample, we used MaxEnt (Phillips et al., 2006; Elith et al., 2011a) which has been shown to be particularly effective for this type of data (Elith et al., 2006; Phillips & Dudik, 2008).

Abiotic environmental predictors included three climate, three soil and four topographically derived variables (Table 1). These were selected because they represent the primary environmental regimes affecting plant distributions (Franklin, 1995; Guisan & Zimmermann, 2000) and have shown to correlate strongly with the distributions of chaparral-associated woody plants in the study region (Franklin, 1998; Syphard & Franklin, 2010). SDMs assessing the impact of climate change are improved when they include landscape (terrain, soil) variables in addition to climate predictors (Austin & van Niel, 2011). Climate grids were derived from 1971 to 2000 parameter-elevation regressions on independent slopes (PRISM) data (Daly et al., 2002; Daly, 2006), spatially downscaled using a 90 m Digital Elevation Model (DEM), using a validated, modified gradient-inverse-distance square interpolation method (Flint & Flint, 2007), and resampled to 100 m resolution and averaged over the 30-year time series.

**Table 1** Environmental predictors and the sources of gridded digital maps

| Environmental predictor (units) | Source |
| --- | --- |
| Average annual precipitation (1971–2000) | PRISM |
| Average minimum January temperature (1971–2000) | " |
| Average maximum July temperature (1971–2000) | " |
| Soil order | 13 categories |
| Soil depth (m) | STATSGO[*] |
| Soil available water capacity (cm cm$^{-1}$) | STATSGO[*] |
| Soil pH | STATSGO[*] |
| Slope angle (°) | USGS 30 m DEM |
| Potential winter solstice solar insolation (Watt hr m$^{-2}$) | From DEM using Solar Analyst |
| Potential summer solstice solar insolation (Watt hr m$^{-2}$) | From DEM using Solar Analyst |
| Topographic moisture index (unitless) | From DEM |

DEM, Digital Elevation Model; USGS, U.S. Geological Survey; Solar Analyst, an ArcView extension for modeling solar radiation at landscape scales.
[*]State Soil Geographic (STATSGO) database for California, U.S. Department of Agriculture Natural Resources Conservation Service (http://gis.ca.gov/catalog/BrowseRecord.epl?id=21237).

Although the Tecate cypress range extends south of the US–Mexico border into Baja California, Mexico (Minnich & Franco Vizcaino, 1998), management based on translocation within the United States would be implemented based on the status of the US populations. Therefore, we have only considered these populations in our study (see Fig. 1). There are 24 mapped populations in Baja California between elevations of 300 m and 900 m, and from 30 15′ 25″N to the border (~31 33′ 56″N) (Minnich & Franco Vizcaino, 1998). The error that could be introduced by not using all the current distribution data from the full range to model the future suitable habitat under climate change is that, by omitting locations from the southern portion of their range, if it were warmer there, we could potentially underestimate the high temperatures that the species can tolerate. Therefore, we could overestimate the loss of habitat in the trailing edge of the range under the increased temperatures predicted through climate change. However, we compared current maximum temperature of the warmest period (from WORLDCLIM data; http://www.worldclim.org/) for 16 collections record locations (obtained from San Diego Natural History Museum; SDNHM) from Baja California, with those within the US border (31 locations), and the maximum temperatures were within the same range, and actually slightly lower, for Baja (mean: 29.7 °C, range: 27.6–32.0 °C) than for the United States (mean: 31.0 °C, range: 29.9–32.8 °C). As maximum temperature was the only climate variable important in the SDM, including modeling locations from Baja California would not have changed the projected future distribution. Furthermore, the soil and terrain variables that we found to be very important for modeling Tecate cypress distribution in California were not available (at the same resolution) for Mexico.

The SDM was evaluated using the commonly applied area under the curve (AUC) of the receiver operating characteristic plot (Fielding & Bell, 1997; Barry & Elith, 2006) based on training data (there were not enough observations to split into train and test). The AUC was 0.88, indicating that the model had a very good ability to discriminate occupied locations from background locations, and the most important environmental predictors were the terrain and soil variables. The only important climate predictor was average maximum July temperature (Table 2). The model was then applied to digital maps of these predictors to predict the distribution of suitable habitat, and then applied to the same variables but substituting maps of future climate simulated by two GCMs to predict the effect of climate change on the distribution of suitable habitat. The two GCMs, Parallel Climate Model (PCM) and the GFDL model, were selected by the State of California for assessing climate change impact because they produced realistic simulations of California's recent climate but show different levels of sensitivity to greenhouse gas forcing (Cayan et al., 2008). GFDL and PCM predict warmer conditions for southern California by the end of the 21st century, but PCM predicts a more modest annual temperature increase (2.5 °C for PCM vs. 4.4 °C for GFDL) and winter precipitation change (+8% for PCM vs. −26% for GFDL) based on the A2 emissions scenario. We used the moderately high A2 emissions scenario as this has been used by California and other studies similar to ours to assess the impacts of climate change (Sork et al., 2010). Grids

**Table 2** Percent contribution of predictors to MaxEnt Species Distribution Model for Tecate cypress. Shape of marginal response curve is described for variables with contribution >0

| Variable | Percent contribution | Response curve type |
|---|---|---|
| Slope angle | 41.4 | Monotonic increasing suitability up to 60° |
| Soil order | 21.3 | Highest suitability on entisols, aridisols and terraces |
| Winter solar insolation | 15.2 | Monotonic decreasing; suitability highest at very low values |
| Soil pH | 8 | Unimodal with peak at pH = 5.3 |
| Soil available water capacity | 6.9 | Monotonic increasing |
| Average maximum July temperature | 6.7 | Unimodal with peak suitability at 34 °C, declining to 0 above 36 °C |
| Average annual precipitation | 0.2 | Monotonic increasing |
| Soil depth | 0.2 | Unimodal with peak at 0.4 |
| Average minimum January temperature | 0 | – |
| Topographic moisture index | 0 | – |
| Potential summer solstice solar insolation | 0 | – |

Percent contribution: relative contribution to MaxEnt model gain (average log probability of the presence samples minus a constant).

of climate variables for 2071–2100 were downscaled using a Digital Elevation Model (DEM) and the same methods described before, after first downscaling from very coarse GCM resolution using the constructed analog method (Hidalgo *et al.*, 2008), as described by Sork *et al.* (2010). They were then averaged for the time period.

MaxEnt predicts a continuous probability value that approximates the likelihood of species presence (Elith *et al.*, 2011b) or the relative habitat suitability. In the population model this probability value is used to characterize the carrying capacity of the habitat patch. Generating a time series of habitat suitability maps for the population simulations required three maps: one depicting habitat patches that are currently occupied, one depicting currently suitable habitat patches and one depicting future suitable habitat patches for each time step interpolated from current and future habitats projected from the GCMs based on 2071–2100 climate. Therefore, a minimum probability threshold (Liu *et al.*, 2005) was first applied to the continuous predictions from MaxEnt to distinguish suitable (values above the threshold) from unsuitable habitat to derive discrete habitat patches required for population modeling.

Currently and historically occupied habitat of Tecate cypress has been well documented (Armstrong, 1966; Zedler *et al.*, 1984; Stephenson & Calcarone, 1999a; SWCA Environmental Consultants, 2008). Although we used both current and historic data to model suitable habitat, we only wanted to delineate current habitat for the initial conditions of our simulations. One possible threshold criterion is to select the probability that results in a predicted extent of suitable habitat equal to the observed extent (Cramer, 2003; Freeman & Moisen, 2008), if this has been independently derived. Currently occupied patches of Tecate Cypress derived from two datasets (San Diego County 1995 vegetation map, www.sandag.org; State of California 1997–2002 vegetation data, frap.cdf.ca.gov/data) cover approximately 5,700 ha. As this species has declined in recent decades (Zedler, 1981; SWCA Environmental Consultants, 2008), we assumed that there is suitable but unoccupied habitat in the region, and we adjusted the threshold criterion by selecting

the probability, 0.75, which predicted a current extent of suitable habitat about twice the area currently occupied. Setting the threshold any lower resulted in predictions of suitable habitat in locations well outside the known current or historic distribution. In our study, probability values below the threshold were set to 0.

This threshold (0.75) was then applied to the future habitat suitability maps derived from each GCM. Unoccupied suitable habitat patches <25 ha were deleted from these current and future suitable habitat maps because they were considered to be of insufficient size to support viable populations and hence would not be selected as recipient patches for translocation. The current and future suitable habitat maps were then linearly interpolated, resulting in a habitat suitability map for each time step of the population simulation. The same 0.75 threshold was applied to each map. Habitat suitability is invoked in the population model (see next) by setting a carry capacity for patches proportional to the number of grid cells in a patch and the habitat suitability of those cells. As the relationship between population size, habitat suitability and carrying capacity for Tecate cypress is uncertain, and because the threshold applied in the map development was relatively high, a habitat suitability of 1.0 was then applied to all cells of suitable habitat (i.e., to cells with habitat suitability ≥ 0.75) in each map. Hence, all suitable habitat was treated as maximally suitable for Tecate cypress populations so as not to be overly conservative.

*Population model structure and parameterization*

We constructed a spatially explicit stochastic age-based matrix model using field data and supplemented with available data on Tecate cypress from the literature (Zedler, 1977; Dunn, 1986). Age classes ranged from seedlings to plants >99 years old. To estimate survival rates, a Wiebull function was fit to data from (Dunn, 1986),

$$S = \exp\left(-\left(\frac{x}{17}\right)^{0.675}\right), \tag{1}$$

where $x$ is the age of plants in years and $S$ denotes survivorship. Bounding Weibull functions, $S_{lower} = \exp(-(x/6)^{0.52})$ and $S_{upper} = \exp(-(x/30)^{0.9})$, which enveloped all data from Dunn (1986) were used to approximate an upper bound and a lower bound, respectively, on survivorship. For each age class, the difference between the upper bound, and the difference between the lower bound, and the mean survival was calculated; the greatest of these was assumed to be 1 SD for that age-specific survival rate. Survival rates for each age class were then represented as lognormal distributions with average rates and standard deviations as described.

Recruitment was represented as average replacement in a fire (measured as number of seedlings per prefire tree) and was estimated using data from Dunn (1986) and from the field as

$$F = \begin{cases} 0, & \text{for } x \leq 6 \\ \frac{15.7 \times \exp(-12.3 + 0.287x)}{1 + \exp(-12.3 + 0.287x)} & \text{for } x > 6 \end{cases}, \quad (2)$$

where $F$ is fecundity (or replacement) and $x$ is the age of the prefire tree in years. As replacement in the absence of fire is rare for this species (Zedler, 1977; Dunn, 1986; Esser, 1994) we set it to $10^{-7}$. The coefficient of variation in recruitment was set to 10%. Environmental stochasticity was represented through a lognormal distribution with average rates and standard deviations as described above. Dispersal capacity for this species is minimal, and average dispersal distances are much shorter than the resolution of the data we used for the SDMs, that is, several meters vs. 100 m. Given these short distances relative to the grain of our data, it is reasonable to assume dispersal to be 0 in the population model. Demographic stochasticity was applied to survival rates and fecundities.

Density dependence in populations was modeled as a ceiling carrying capacity; as trees grew older and larger, carrying capacity (i.e., the maximum abundance a patch could support) was reduced. We used data on maximum densities from field estimates (1480.7 adult trees per hectare) to calculate age-based carrying capacity per hectare of maximally suitable habitat as

$$K = \begin{cases} 1480.700 \times 10.035 \times \left(1 - \frac{\exp(-4.663 + 0.149x)}{1 + \exp(-4.663 + 0.149x)}\right) & \text{for } 1 \leq x \leq 44 \\ 1480.700 & \text{for } x > 44 \end{cases}, \quad (3)$$

where $x$ is plant age. While this may underestimate carrying capacity it provides a consistent upper bound for the purposes of comparing the relative effects of treatments. When the populations exceeded carrying capacity survival rates were reduced by the following amounts: 60% (1–2 years), 50% (3–4 years), 40% (5–6 years), 30% (7–8 years), 20% (9–18 years) and 10% (>19 years). This has the effect of a gradual decline over time toward carrying capacity which is expected in the field. Further details of the field data and other data sources used for model parameterization, as well as sensitivity analyses, appear in Markovchick-Nicholls (2007).

## Fire probabilities

Stochastic fire events were incorporated via a hazard function based on the Weibull function (Polakow et al., 1999; Moritz, 2003)

$$\lambda(t) = \frac{ct^{c-1}}{b^c}, \quad (4)$$

where $\lambda(t)$ is the probability of fire in a given time step, $t$ is the time since last fire, $b$ is a scale parameter related to the average fire return interval and $c$ is the shape parameter which reflects the degree to which fire hazard changes with time since the last fire. To represent the fire regime in southern California we used a shape parameter developed by Polakow et al. (1999) for mixed chaparral ($c = 1.42$). We constructed different hazard functions for a range of average fire return intervals (10, 20, …, 80 years) by changing the value of the scale parameter, $b$ (see Regan et al., 2010). Fires events occurred independently across patches. When a fire occurred, all plants in the patch were killed, recruitment was triggered and the time since last fire was reset to 0 in the fire hazard function for that patch. As the patch representing Otay Mountain was so large (5168 ha) we simulated fires to burn half the patch, that is, half of the standing plants were killed, recruitment was halved and fires occurred within the patch twice as often as in smaller patches to maintain an average fire return interval across the entire patch to be consistent with the average fire return interval in smaller patches. It is worth mentioning that, aside from the largest patch, our simulated fires burned across entire patches at a time, varying by different intervals between fires. In reality, fires are likely to have heterogeneous patterns, will range in size and may potentially leave behind remnants of unburned trees within a fire perimeter. Nevertheless, chaparral-dominated areas like those where Tecate cypress is distributed tend to exhibit low spatial complexity in burn patterns, with few unburned islands and uniform fire severity across a fire perimeter (Sugihara et al., 2006).

## Assisted colonization scenarios

The Otay Mountain population was chosen as the source from which individuals were translocated as it was by far the largest population at the beginning of the simulation. We simulated translocation of seedlings after a fire event in the source patch. Translocation events (i.e., seedlings removed from the source patch and donated to the recipient patch) were limited to the first 60 years of the simulation, after which time habitat suitability in the Otay Mountain population declined substantially. To limit the number of seedlings translocated from the source population, and evaluate if populations in the recipient patches were self-sustaining, seedlings were only translocated when more than 100 Tecate cypress seedlings existed in the source patch, and fewer than 500 Tecate cypress individuals of any age occupied the recipient patch. Recipient patches were chosen based on the following criteria: (1) the patch had suitable habitat which remained suitable throughout the entire simulation (100 years); (2) the patches of suitable habitat were common to both climate scenarios; and (3) the patch was as close as possible geographically to the original patch, to

mimic, as much as possible, natural dispersal (albeit over many generations for this dispersal-limited species). In different simulations, we translocated 10%, 20% and 30% of seedlings across 1, 2 and 3 different patches, respectively, that is, each recipient patch received 10% of seedlings from the source patch. For each translocation scenario we applied a range of average fire return intervals (20, 40, 60 and 80 years) and survival rates of translocated seedlings in the recipient patch for the first two years (100%, 80%, 60%, 40%, 20% and 0% of the seedling survival rate in the source patch). It was assumed that if seedlings survived the first two years in the recipient patch and plants became established then the population would adopt the survival rates of the source patch. The coefficient of variation of seedling survival rate in the source patch was applied to the modified survival rates in the recipient patches to incorporate environmental stochasticity.

### Simulations

We used RAMAS GIS® (Akçakaya & Root, 2005) to link the spatial arrangement of patches in each time step, the population model and the fire functions. Initial time since last fire was set to reflect the actual time since last fire in each occupied patch. For stands 35 years or older the initial population sizes of patches were calculated as 1000 individuals per hectare based on average observed densities of 35-year-old Tecate cypress stands. For younger stands, this value was modified (i.e., increased) for each age class using the ratio of carrying capacity for 35-year-old stands to the younger stands, according to Eqn (3).

In each time step of the population model, the spatial configuration of populations was updated based on the map for that time step. The effects of this on population dynamics was invoked via changes in the amount of suitable habitat available which in turn invoked changes in carrying capacity. Density dependence was implemented by reducing rates of survival and growth (due to intraspecific competition) independently for particular life stages whenever a population exceeded the carrying capacity of its habitat patch. Stochasticity was incorporated through Monte Carlo simulations for 1500 replications over a 100-year time period to account for natural variation in the fire events and the population demographic rates. Expected minimum abundances (EMAs) across the 1500 replications were used to compare treatments (McCarthy & Thompson, 2001).

## Results

### Habitat suitability under current and future climate conditions

The current distribution of Tecate cypress is most highly correlated with soil properties and topographic variables, and only weakly with climate, but it does correspond to where mapped July maximum temperature averages about 34 °C, and is less than 35 °C. The predicted extent of suitable habitat (above the 0.75 proba-

bility threshold) is 25 833 ha, while imposing the 25 ha minimum patch size eliminated 8114 ha, resulting in 17 719 ha of suitable habitat in patches large enough to support viable subpopulations.

The predicted extent of suitable habitat in 2100 based on the A2 emissions scenario and the two GCMs, is greatly reduced in both scenarios. This is rather remarkable because the temperature variable (average maximum July temperature; $T_{max}$) only contributes 6.7% to the MaxEnt model (Table 2). However, the estimated response function to temperature was unimodal, and while the estimated optimum July $T_{max}$ was 34 °C, probability of species occurrence reduces to 0 above 36 °C and the proportion of the study area with July $T_{max} > 36$ °C increases dramatically in the GCM simulations. The predicted distribution of suitable habitat in 2100 is restricted to areas with predicted July $T_{max}$ less than 36 °C, which excludes the central, foothills portion of the study area (Fig. 2a). When a threshold was applied to the continuous probabilities estimated by the SDM [to eliminate habitat of low suitability], and small patches that could not support viable populations were also eliminated, the currently occupied patches (four patches, 6398 ha) were predicted to shrink to one patch, 57 ha or 138 ha, respectively, under the GFDL and PCM scenarios, by 2100 (Fig. 2b). We set the habitat suitability threshold very high (0.75); this is the value below which the habitat was deemed to be unable to support new postfire populations. In reality Tecate cypress populations may still be supported in patches with low habitat suitability, hence our results are precautionary and most likely overestimate the effects of climate change on populations.

### Effect of fire frequency on population persistence

Frequent fire had similar impacts on Tecate cypress abundance whether or not climate change was included in the predictions of suitable habitat. The highest fire frequencies, 10-year average fire return intervals, resulted in dramatically reduced EMAs across our modeled populations (reduced to approximately 6000 individuals for no climate change and 15 individuals under both climate models), whereas average fire return intervals of 60–80 years maximized EMAs (Fig. 3).

The GFDL climate model consistently resulted in the lowest EMAs for all average fire return intervals considered, followed by the PCM climate model and the no climate change scenario. Climate change, whether projected under the GFDL or PCM climate models, is shown to have dramatic effects on EMA (Fig. 3) because it substantially reduces habitat suitability (Fig. 2).
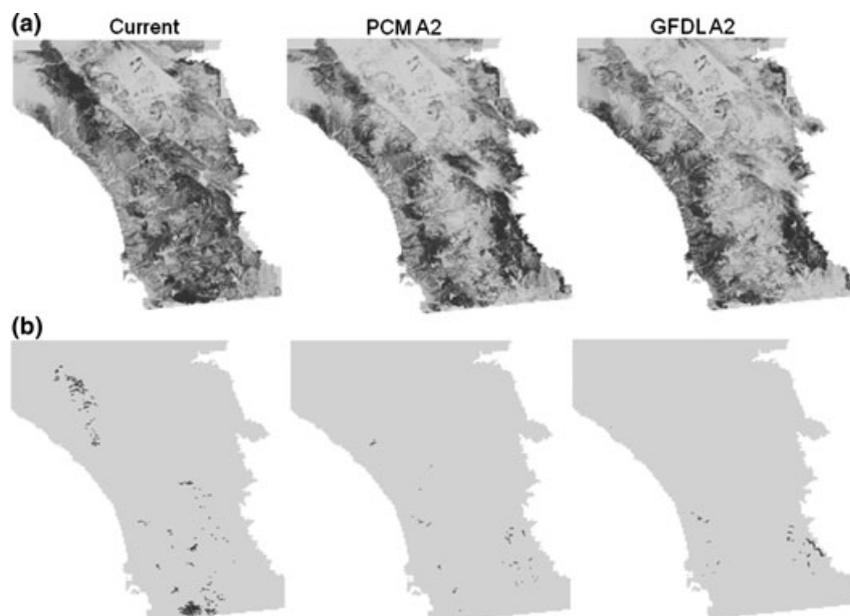
**Fig. 2** Maps showing (a) continuous distribution of predicted suitable habitat of Tecate cypress for current climate conditions (1970–2000) and projected climate conditions (2070–2099) for the Geophysical Fluid Dynamics Laboratory CM2.1 model and Parallel Climate Model, the two General Circulation Models under the A2 emissions scenario. These are scaled evenly from low values of 0 (white) to high values of 1 (black), but because absence data were not available for modeling, these values cannot be interpreted directly as probability of occurrence. As described in the text, the threshold value of 0.75 corresponded to the minimum probability value corresponding to a suitable habitat, based on independent information about species extent. Corresponding thresholded patch maps (b) are shown directly underneath the continuous maps.
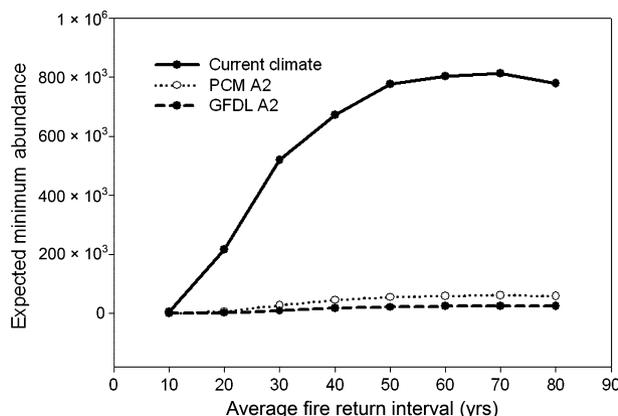


**Fig. 3** Expected minimum abundances for a range of average fire frequencies for habitat suitable under current climate conditions and habitat under Parallel Climate Model A2 and Geophysical Fluid Dynamics Laboratory A2 climate scenarios projected for 100 years.

*Effect of assisted colonization*

The relative effects of average fire return interval on EMA are maintained under all assisted colonization strategies for both climate change models (Fig. 4 for the PCM climate model; Fig. 5 for the GFDL climate model). Failed translocation attempts (i.e., 0% translocation success) have no impact on EMA, irrespective of the percentage of seedlings translocated (Figs 4a and 5a). As the translocation success and the percentage of seedlings translocated increases, the EMA increases; 30% translocation and 100% translocation success increases EMAs by approximately 50% for 60-year average fire return intervals (Figs 4d and 5d). In summary, removing up to 30% of the seedlings from the source patches does not reduce EMA even if those seedlings do not establish in the recipient patch and it offers a good chance of increasing EMA if they do establish.

The effects of very frequent fires outweigh the potential increase in abundance afforded by translocation; translocation has no noticeable impact on EMAs under 20-year average fire return intervals (Figs 4 and 5). Unless translocation and success rates are both high the effects of frequent fires outweigh the increase in EMA due to translocation; for example, a 10% translocation rate with 100% translocation success under a 40-year average fire return interval results in EMAs lower than those for no translocation under a 60-year average fire return interval for both climate models (Figs 4d and 5d).

In summary, these results show that as habitat suitability declines, thereby reducing the carrying capacity
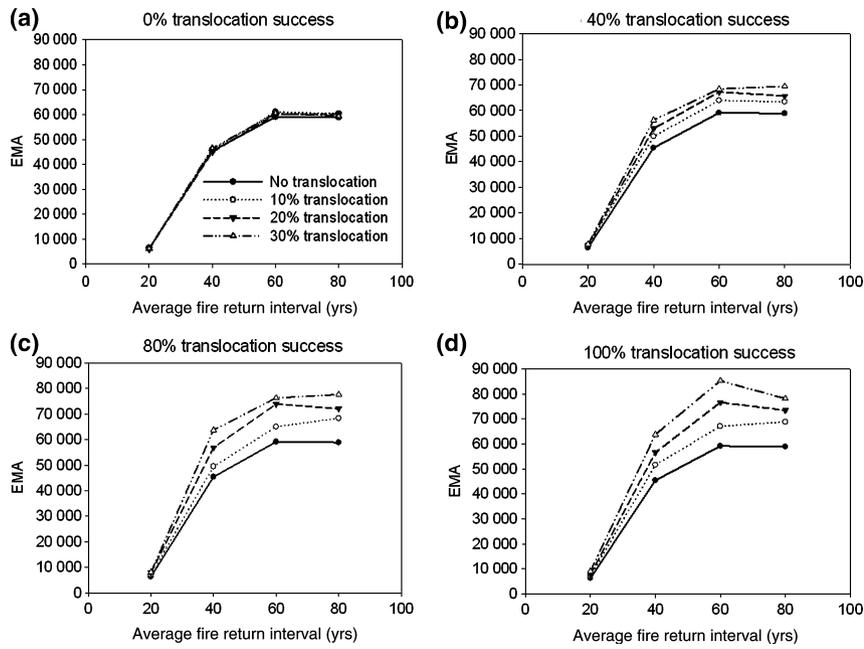
**Fig. 4** Expected minimum abundances for a range of translocation treatments and average fire frequencies for suitable habitat under Parallel Climate Model A2 projected for 100 years.
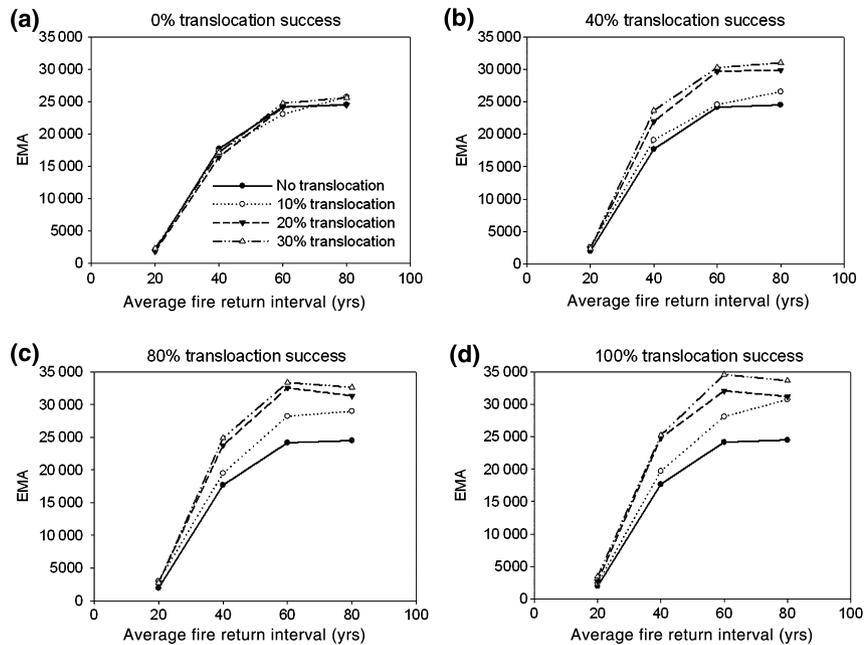


**Fig. 5** Expected minimum abundances for a range of translocation treatments and average fire frequencies for suitable habitat under Geophysical Fluid Dynamics Laboratory A2 climate model projected for 100 years.

of the patch, removing and translocating some postfire seedlings can have population-level benefits. Self-thinning as stand age increases kills some individuals due to intraspecific competition which is exacerbated by habitat (and hence carrying capacity) reductions due to climate change; it is essentially these individuals that would have died due to intraspecific competition that are translocated. It is clear from these results that loss of suitable habitat is by far the more serious impact to the source patches than loss of individuals due to translocation.

## Discussion

In view of the fact that many managers are already considering implementation of assisted colonization programs, there is a clear need for research that evaluates the potential success and the uncertainties of these strategies (McLachlan *et al.*, 2007; Ricciardi & Simberloff, 2009). An important result of our study, therefore, is that any evaluation of assisted colonization needs to account for the fact that impacts of climate change are unlikely to occur in isolation; and thus a research framework is needed that considers assisted colonization in light of the impacts of interacting threats. In particular, our results show that for a long-lived Mediterranean obligate seeder, implementing assisted colonization to mitigate the effects of distribution shifts or contractions due to climate change will be useless if the prevailing threat of frequent fire is not moderated. This conclusion is robust to climate change scenario, the amount and success rate of translocation strategies and uncertainty in future suitable habitat. Therefore, integrated management will be necessary to address the cumulative effects of multiple threats in the context of climate change.

Our results showed that if nothing is done and fires are frequent existing populations will nonetheless shrink drastically. Regional fire frequency has increased substantially due to increased ignitions associated with human population growth and urban expansion (Keeley *et al.*, 1999). This trend could be exacerbated by climate change and by the increase in abundance of fire-promoting exotic grasses (Keeley, 2006). Hence, future management must consider what can be done to protect Tecate cypress stands, whether translocated or natural, from experiencing damaging fires at short intervals.

Although our results show a dramatic effect of fire frequency on Tecate cypress persistence, it is possible that small subpopulations may continue to persist in isolated areas, or 'fire refugia', which remain unburned even though surrounding areas burn with high frequency (Zedler, 1981; Schwilk & Keeley, 2006). In our simulations, fires burned across entire patches at a time (except for the largest patch), varying by different intervals between fires, and we did not simulate the potential influence of fire refugia on population persistence. Burn patterns in chaparral-dominated areas generally exhibit low spatial complexity with few unburned islands (Sugihara *et al.*, 2006), although spatial heterogeneity and unburned patches may increase with more frequent fire. Nevertheless, we believe that the influence of fire refugia would not substantially affect the conclusions of the study.

Regardless of the postfire response, climate change is likely to interact with a suite of other threats. Therefore, considering all the many uncertainties at this stage of understanding, assisted colonization must be evaluated on a case-by-case basis depending on risks particular to the species and the primary threats occurring in the region. For example, assisted colonization may have very different implications depending on the degree of urbanization in a region. In areas highly fragmented by human land uses, assisted colonization may involve short distance movements across dispersal barriers and this may be less likely to result in some of the negative potential impacts of assisted colonization on the recipient ecological community (Vitt *et al.*, 2010). On the other hand, accidental fire may be more probable in a fragmented suburbanized landscape.

Despite the insights this study provides on assisted colonization in the context of climate change, it does not shed light on the effect that populations of translocated individuals may have on native biota in the recipient habitat. Recipient areas may need to be burned prior to translocation to provide a suitable environment for translocated seedlings, and this may have negative long-term consequences for the native biota present in the patch. As many other regional native species are also sensitive to repeated fire (Zedler *et al.*, 1983; Syphard *et al.*, 2006), it would be important to first consider the species composition and fire history of the recipient areas. We echo the caution expounded in McLachlan *et al.* (2007) that common garden experiments should be considered to garner insights about potential competition in recipient and donor patches.

Whether to implement assisted colonization or not, and how aggressively, is essentially an exercise in decision making under risk and uncertainty (Ricciardi & Simberloff, 2009; Richardson *et al.*, 2009). While there will be a fact of the matter about what the optimal strategy should be, the uncertainties inherent in GCMs, SDMs, population models and the field data they rely on preclude unambiguously identifying a clear and certain course of action. Under a risk-averse approach, we should assess the risks and uncertainties as best we can and choose a strategy that minimizes the risk of failure (what constitutes 'failure' should be carefully and explicitly defined and should weight extant populations highly). In doing so, we accept acts that are less likely to achieve the best outcomes if our pessimism is unjustified. This might not increase the population in the future, but it should minimize the probability of extinction. This is the price we pay for risk aversion but under uncertainty it is more likely to minimize failure, and probable extinction, than higher risk tolerance (Regan *et al.*, 2005). Linking single-species SDMs with population dynamics allows us to quantitatively examine the risk tradeoffs involved in active adaptation to climate change. Given the levels of uncertainty

associated with spatially explicit climate change impacts and adaptation strategies, coupled with a paucity of regulation that makes it relatively easy to move species around legally (McLachlan *et al.*, 2007), a risk-averse attitude toward assisted colonization policy is prudent; risk-averse decision making is not a new concept to conservation biologists.

While there is no 'one size fits all' strategy for assisted colonization (Vitt *et al.*, 2009), our study shows that under certain conditions, assisted colonization could be an appropriate adaptation response for increasing population abundance of species whose distributions contract or shift due to climate change. When there are large source populations that are expected to decline dramatically due to suitable habitat contractions, multiple nearby sites that are predicted to contain stable suitable habitat in the future, high expected rates of establishment of translocated populations, minimal dispersal due to natural or anthropogenically created barriers and the absence of more serious ongoing threats, assisted colonization may increase population abundances and persistence, provided translocated individuals actually establish in the recipient habitat. But, as with the uncertainties with climate predictions, we stress that our results cannot by themselves be taken as justifying more than modest experiments in translocation. A theoretical model cannot anticipate all the risks and practicalities of implementation inherent in assisted colonization; speculation about an ideal program is one thing, it is another matter to actually implement it.

The results of this study also do not address the ethics, social values, socio-economics and practicalities of wholesale assisted colonization policies that would arise if more than just a handful of the multitudes of species affected by climate change are considered for translocation. Scientists alone cannot resolve the issue of whether assisted colonization is a desirable adaptation response to climate change – it will require interdisciplinary and multiagency consideration of the full costs and benefits of this strategy (Richardson *et al.*, 2009). We have merely provided one important piece of scientific information that can shed some light on the risks and benefits of adaptation under climate change in the face of ongoing threats.

## Acknowledgements

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