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Fire Management, Managed Relocation, and Land Conservation Options for Long-Lived Obligate Seeding Plants under Global Changes in Climate, Urbanization, and Fire Regime

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Abstract: *Most species face multiple anthropogenic disruptions. Few studies have quantified the cumulative influence of multiple threats on species of conservation concern, and far fewer have quantified the potential relative value of multiple conservation interventions in light of these threats. We linked spatial distribution and population viability models to explore conservation interventions under projected climate change, urbanization, and changes in fire regime on a long-lived obligate seeding plant species sensitive to high fire frequencies, a dominant plant functional type in many fire-prone ecosystems, including the biodiversity hotspots of Mediterranean-type ecosystems. First, we investigated the relative risk of population decline for plant populations in landscapes with and without land protection under an existing habitat conservation plan. Second, we modeled the effectiveness of relocating both seedlings and seeds from a large patch with predicted declines in habitat area to 2 unoccupied recipient patches with increasing habitat area under 2 projected climate change scenarios. Finally, we modeled 8 fire return intervals (FRIs) approximating the outcomes of different management strategies that effectively control fire frequency. Invariably, long-lived obligate seeding populations remained viable only when FRIs were maintained at or above a minimum level. Land conservation and seedling relocation efforts lessened the impact of climate change and land-use change on obligate seeding populations to differing degrees depending on the climate change scenario, but neither of these efforts was as generally effective as frequent translocation of seeds. While none of the modeled strategies fully compensated for the effects of land-use and climate change, an integrative approach managing multiple threats may diminish population declines for species in complex landscapes. Conservation plans designed to mitigate the impacts of a single threat are likely to fail if additional threats are ignored.*

Keywords: climate change, fire, habitat conservation plan, managed relocation, Mediterranean climate ecosystem, obligate seeders

Manejo de Incendios, Reubicación Administrada y Opciones de Conservación de Suelo para Plantas de Vida Larga con Sembrado Obligado bajo los Cambios Globales en el Clima, la Urbanización y el Régimen de Incendios

Resumen: *La mayoría de las especies enfrentan múltiples disrupciones antropogénicas. Pocos estudios han cuantificado la influencia acumulativa de múltiples amenazas sobre las especies de interés de conservación y*

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muy pocos han cuantificado el valor relativo potencial de múltiples intervenciones de conservación a la luz de estas amenazas. Vinculamos la distribución espacial y modelos de viabilidad de población para explorar las intervenciones de conservación bajo un cambio climático proyectado, urbanización y cambios en el régimen de incendios sobre una especie de planta de vida larga con sembrado obligado sensible a las altas frecuencias de incendios; y sobre un tipo funcional de planta dominante en muchos ecosistemas propensos a incendios, incluyendo los hotspots *de biodiversidad en ecosistemas de tipo mediterráneo. Primero investigamos el riesgo relativo de la declinación poblacional para poblaciones de plantas en paisajes con y sin protección de suelo bajo un plan de conservación de hábitat existente. Después modelamos la efectividad de la reubicación de plántulas y semillas de un fragmento grande con declinaciones pronosticadas en el área de hábitat a dos fragmentos receptores desocupados con un área de hábitat incrementada en dos escenarios proyectados de cambio climático. Finalmente, modelamos ocho intervalos de retorno de incendios aproximando los resultados de diferentes estrategias de manejo que efectivamente controlen la frecuencia de incendios. Invariablemente, las poblaciones de plantas de vida larga con sembrado obligado permanecieron viables sólo cuando los intervalos de retorno de incendios se mantuvieron en o sobre un nivel mínimo. La conservación de suelo y el esfuerzo de reubicación de plántulas disminuyeron el impacto del cambio climático y el cambio de uso de suelo sobre poblaciones de plántulas de sembrado obligado en diferentes niveles dependiendo del escenario de cambio climático, pero ninguno de estos esfuerzos fue tan efectivo generalmente como la traslocación frecuente de las semillas. Mientras ninguna de las estrategias modeladas compensó completamente los efectos del uso de suelo y el cambio climático, un acercamiento integrador que maneje múltiples amenazas puede disminuir las declinaciones poblacionales para especies en paisajes complejos. Los planes de conservación diseñados para mitigar impactos de una sola amenaza tienen mayor probabilidad de fallar si se ignoran amenazas adicionales.*

Palabras Clave: Cambio climático, ecosistema climático mediterráneo, incendio, plan de conservación de hábitat, reubicación administrada, sembrado obligado

Introduction

Climate change and habitat loss currently represent the dominant concerns for the future of biodiversity globally (Periera et al. 2010; Dawson et al. 2011). Additionally, changes in disturbance regimes could rival climate and land-use change as primary biodiversity threats (Turner 2010). In particular, fire is an important disturbance for many ecosystems throughout the globe (Bowman et al. 2011), and changes to fire regimes could have significant consequences for species in high biodiversity regions such as Mediterranean-type ecosystems (MTEs) which cover 5% of Earth's surface but harbor almost 20% of all vascular plant species (Cowling et al. 1996; Syphard et al. 2009; Keeley et al. 2012). Biodiversity in MTEs is particularly vulnerable to the effects of climate change, changes in fire regime, and land-use change (Underwood et al. 2009; Keeley et al. 2012). While evidence from a variety of ecosystems highlights the independent effects of disturbance, climate change, or land-use change for populations (Brook et al. 2008), their cumulative effects are seldom studied. The full impact of multiple threats is frequently nonadditive (Didham et al. 2007), and several recent analyses have shown important cumulative effects of multiple impacts on plant species persistence in MTEs (Keith et al. 2008; Lawson et al. 2010; Conlisk et al. 2012).

Nevertheless, conservation interventions are typically targeted toward individual threats, independent of potential interactions with other stressors. The use of protected areas, for example, can effectively combat biodiversity loss via land-use changes (Bruner et al. 2001; Fuller et al. 2010). However, recent habitat protection efforts have been complicated by potential climate change impacts on the distribution of habitat (Araújo et al. 2011; Bernazzani et al. 2012). Strategies to address climate change, e.g., translocation or managed relocation, have the potential to mitigate these impacts (Richardson et al. 2009), yet they could be complicated by changing land-use patterns. Finally, managing fire regimes for the persistence of biodiversity is a critical conservation goal, but it is highly complex due to strong human influence on fire patterns, which will continue to change with altered land use (Syphard et al. 2009; Driscoll et al. 2010). Effective conservation planning must then examine multiple threats and interventions in a single framework to guide decision making. Indeed, one of the primary challenges in conservation is determining the efficacy of diverse management approaches in achieving conservation goals when facing multiple threats (Heller & Zavaleta 2009; Loss et al. 2011).

We modeled the effects of different conservation strategies, alone and in concert, on a representative of a plant functional type abundant and locally dominant in the MTE shrublands in California (U.S.A.), South Africa, Western Australia, and the Mediterranean Basin: long-lived obligate seeding shrubs and trees (Keeley 2012; Syphard et al. 2013). Soil- or canopy-stored seeds require fire to germinate, which is an evolutionary adaptation to fire regimes that are typical of MTEs (Keeley et al. 2012). We evaluated alternative conservation strategies in light of multiple threats to long-lived obligate seeding shrubs and trees through a case study within the functional type from California. Land conservation, managed relocation, and fire management were used as plausible responses to the considered threats.

Our modeled conservation strategies reflect realistic schemes being implemented or debated in southern California and other MTEs. We analyzed the potential of an existing reserve system to limit direct habitat loss through urbanization. To offset decreases in habitat under climate projections, we tested a wide range of managed relocation scenarios. We use the term *managed relocation* (following Schwartz et al. 2012) as a specific form of translocation (Seddon 2010) where the target (recipient) habitat is beyond the known historical distribution of the species. We also tested a range of fire frequencies under all threat and intervention scenarios to assess the importance of successful fire prevention relative to and in combination with the other strategies.

Methods

Study Species

Long-lived obligate seeding shrubs and trees are a dominant plant functional type in MTEs; they comprise approximately one-third of the species represented across all but one of these ecosystems (Pausas et al. 2004). We chose *Ceanothus verrucosus* as a representative for the functional type. It is a long-lived chaparral shrub narrowly distributed within coastal southern California and northern Baja California, Mexico. Like many obligate seeding species in MTEs, populations of *C. verrucosus* have been greatly reduced in California due to land-use change, in particular urban development (CNPS 2010). Increased fire frequency, continued urbanization, and climate change especially are projected to affect the species in the future (Lawson et al. 2010). We used this species as a case study to garner general insights about the effects of threats and management interventions on species belonging to the broader plant functional type.

Population Consequences of Climate Change, Urbanization, and Fire

The cumulative impacts of climate change, urbanization, and fire on *C. verrucosus* were assessed in a model developed by Syphard et al. (2013), which we used here. Modifications to the model framework and detailed methods are described in Supporting Information.

Briefly, to determine how climate change and urbanization might impact the distribution of *C. verrucosus* in the future, we used MaxEnt-based species distribution models (SDMs) (Phillips & Dudík 2008) and historic climate data. We linked SDMs with population matrix models that explicitly incorporated patch dynamics and fire-cued germination. The downscaled high-resolution (90 m) future climate data (Flint & Flint 2012) we used were based on 2 climate change scenario models, GFDL (Delworth et al. 2006) and PCM (Washington et al. 2000), under the Intergovernmental Panel on Climate Change Fourth Assessment A2 emissions scenario (Cayan et al. 2008). Urbanization scenarios were developed by simulating urban growth under alternate conservation scenarios with the SLEUTH model (Syphard et al. 2011). Using RAMAS GIS 5.0 (Akçakaya & Root 2005), we derived habitat patches and set carrying capacities for each from the SDMs applied to climate change scenarios and urbanization scenarios. This formed the basis for the stochastic projection of population dynamics. Populations in each habitat patch were simulated using a matrix model based on empirically derived *C. verrucosus* vital rates; we assumed no natural dispersal between patches. A Weibell hazard function was used to subject patches to stochastic fires with burn probabilities as a function of time since last fire (Regan et al. 2010). We examined a range of average fire return intervals (FRIs). These were a particularly important component of the fire regime in our models because fires had the dual effects of killing all plants in a burned patch while simultaneously stimulating germination.

We examined scenarios that included combinations of climate scenarios, FRIs, and management strategies. For each scenario, population dynamics were projected 100 years stochastically via Monte Carlo simulation with 1000 replications. Results are presented in the form of expected minimum abundances (EMA) (McCarthy & Thompson 2001).

Conservation Strategies

Because there is great uncertainty in how climate change will affect fire regimes (Hessl 2011) and how specific fire management actions translate to long-term FRIs, particularly in southern California (Price et al. 2012), we did not explicitly model fire management strategies. Instead, we selected a range of fire frequency scenarios, from 10- to 80-year average FRIs, that we assumed spanned both threats and potential goals for fire management strategies.

To examine the value of the San Diego County Multiple Species Conservation Plan (MSCP) lands for preserving the viability of *C. verrucosus* under the multiple threats of fire, climate change, and urbanization, we compared scenarios with and without the MSCP land protected from development. The MSCP was developed to protect biodiversity and ecosystem functioning throughout the San Diego region (Ogden Environmental and Energy Services 1998). *C. verrucosus* is covered by the MSCP because 67% of major populations are located in the planning area (Ogden Environmental and Energy Services 1998). When included as a management scenario, all MSCP protected land was restricted from development in the urban growth model, which contributed to a 51% increase in land excluded from development (Syphard et al. 2011).

Translocation (sensu Seddon 2010) is increasingly being evaluated as a potential conservation tool, particularly for the purposes of adapting to climate change (Richardson et al. 2009; Schwartz et al. 2012). Some forms of translocation, especially those involving translocations beyond a species' known historic range (e.g., managed relocation), are the subject of controversy and debate (Hunter 2007; McLachlan et al. 2007; Seddon et al. 2009). Without taking a position, we recognize its increasing visibility as a potential strategy for conservation under climate change, especially for particular plant species (Maschinski & Haskins 2012; Regan et al. 2012), and we sought to evaluate its efficacy for *C. verrucosus*.

Because we were interested in the impacts of managed relocation on population trajectories, we focused relocation effort on large patches where we would be more likely to see detectable changes in population decline. While translocations at smaller scales could be effective if one's conservation goal were restoration at a local level, we were looking for potentially intensive levels of intervention that might offset impacts from examined threats. We therefore chose the largest declining patch of habitat remaining at the end of the simulation as the source of translocated individuals (starting carrying capacity of approximately 7.30 million ≥60-year-old plants and ending carrying capacity of approximately 166,000 and 184,000 ≥60-year-old plants for GFDL and PCM, respectively) (Fig. 1). We selected 2 recipient patches based on their initial area and the magnitude of increase in habitat throughout the simulation. For the GFDL scenario, we chose 2 patches with initial carrying capacity of approximately 350,000 and 17,000, which increased to approximately 400,000 and 1.9 million ≥60-year-old plants, respectively (Fig. 1a). For the PCM scenario, we chose the same recipient patch with initial carrying capacity of approximately 350,000 and a nearby patch with initial carrying capacity of 14,000; these patches increased to approximately 1.1 and 5.3 million ≥60-year-old plants, respectively.

We tested several approaches for implementing managed relocation, including the translocation of different life stages. While seeds may be easier to transplant than seedlings and are used effectively in some plants (e.g., perennial herbs), woody plant translocations are generally more effective with older age stages, such as germinants or whole plants (Albrecht & Maschinski 2012). First, we simulated translocation of 2%, 5%, 10%, and 50% seedlings only in the year of a fire (when seedlings would be available); half were transplanted to each of the 2 recipient patches. Second, we simulated translocation of 1,000, 2,000, 10,000, and 20,000 seedlings equally across the 2 recipient patches in the year a fire occurred. Third, we simulated translocation of 2%, 10%, and 50% of seeds at regular intervals of 2, 6, or 10 years, dividing them equally across the 2 recipient patches. We assumed the same underlying vital rates for populations in the recipient patches as for the source patch.

Results

Climate Change, Urbanization, and Fire Impacts

We projected large-magnitude losses in existing habitat in the face of urbanization and climate change under both climate scenarios (PCM and GFDL; Fig. 1). Under PCM and urbanization, future *C. verrucosus* habitat was projected to decline by 41%; habitat loss declined even more at 75% decline for GFDL and urbanization. Habitat loss was concentrated in the southern portion of the distribution. Declines in this area were 80% and 92% for PCM and GFDL, respectively. Conversely, habitat extent was projected to increase in the northern part of the distribution by as much as 226% under PCM and urbanization and 45% for GFDL and urbanization.

C. verrucosus populations were projected to exhibit reduced expected minimum abundances (EMAs) as a result of all threats considered (Fig. 2). The lowest population sizes were associated with 10-year average FRIs (Fig. 2), where EMAs for the entire population were 2 to 3 orders of magnitude lower than for all other combinations of FRI, climate, and urban growth. Extinction risk was 64% and 79% with a 10-year FRI across all combinations of threat and management scenarios. For each habitat scenario, differences across EMAs were less pronounced for average FRIs greater than 20 years, with the highest predicted EMAs when average FRI was around 40–50 years under all climate and land-use scenarios (Fig. 2).

EMA was reduced by 41% by urban growth when no climate-driven habitat change was included for the optimal average FRIs of 40 and 50 years (Fig. 2). Climate-driven reductions in habitat also projected lower population sizes. Under the GFDL scenario, the EMA more than halved, resulting in 48% and 45% of the "no habitat change" EMA for the 40 and 50 year average FRIs, respectively (Fig. 2a). Population decreases under GFDL were larger than those induced by projected urbanization. The population fared slightly better under the PCM scenario with EMAs 75% and 70% of those for no habitat change for the 40 and 50 year average FRIs, respectively (Fig. 2b). In contrast to GFDL, population decreases due to PCM were less than those projected under urbanization alone (Fig. 2).

Of the landscape-level threat combinations, the cumulative impacts of climate change and urbanization were not the most dramatic across all fire scenarios, except for the 10-year average FRI, which consistently led to the worst outcomes irrespective of landscape-level threats (Fig. 2a & b). The GFDL scenario coupled with urban growth reduced EMAs for the 40 and 50 year average

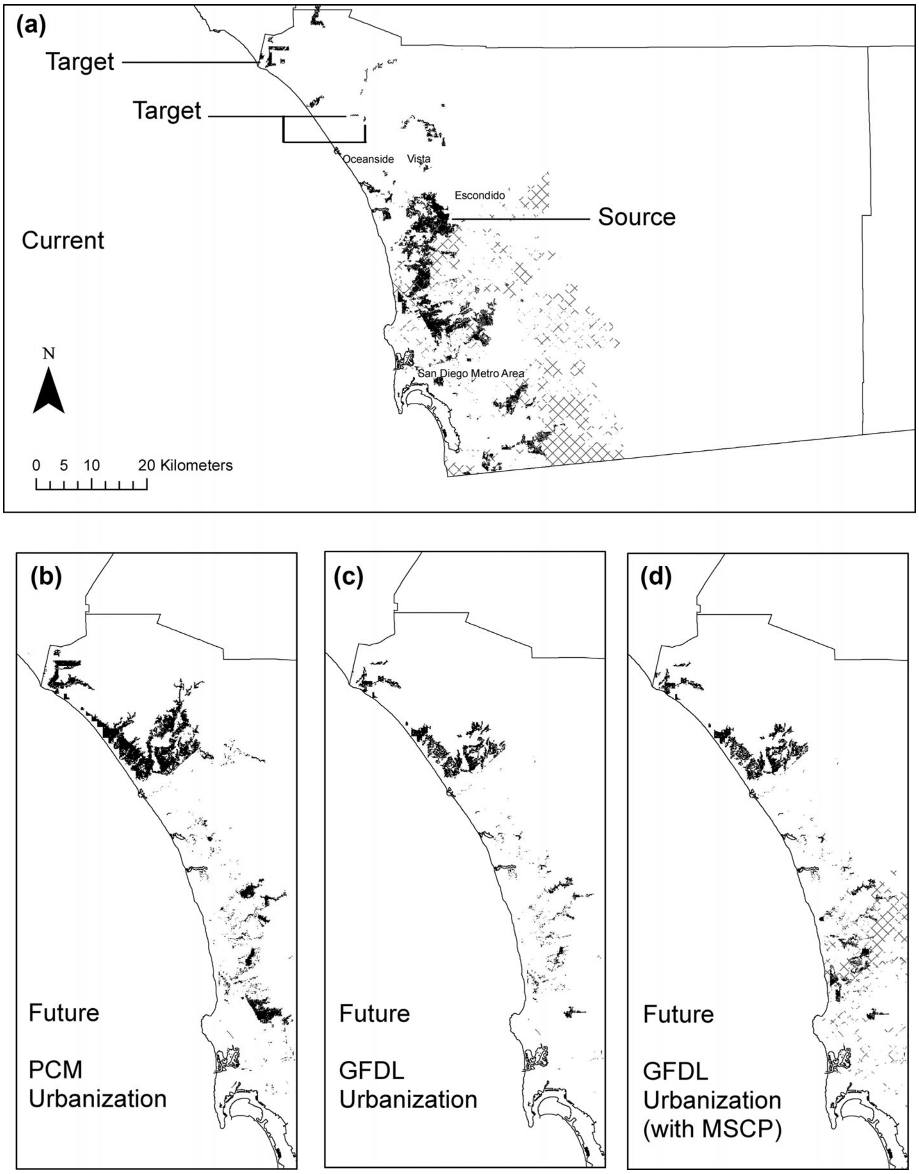

Figure 1. Modeled distribution (black) of Ceanothus verrucosus *under different climate conditions for the Intergovernmental Panel on Climate Change Fourth Assessment A2 scenario: (a) current (2000) climatic conditions (gray hatching, areas afforded land protection in the San Diego Multi-Species Conservation Plan [MSCP] reserves); source, area where individuals to be translocated occur; target, patches where individuals would be relocated; northern target, initial carrying capacity of 350,000 individuals, (b) future (2100) climatic conditions under PCM (Washington et al. 2000) and increased urbanization, (c) future (2100) climate under GFDL (Delworth et al. 2006) and increased urbanization, and (d) future (2100) climate under GFDL, urbanization, and land protection (i.e., MSCP). The northern target area is common to both PCM and GFDL scenarios. The southern target patches differed between the PCM and GFDL scenarios.*

FRIs to 17% of the EMA under no habitat change (Fig. 2a), whereas the coupled PCM and urban growth scenario reduced EMA to 36% of the no habitat change EMA (Fig. 2b).

Land Protection

The degree to which land protection mitigated population declines of *C. verrucosus* depended on climate change projections. In the absence of climate change, reserves increased EMA by 26% and 22% above the urban growth and no reserve scenario for the 40 and 50 year FRIs, respectively (Fig. 2). When climate change acted in addition to urban growth, reserves resulted in population gains of 48% and 45% for FRIs of 40 and 50 years, respectively, under the GFDL climate scenario (Fig. 2a), and of nearly 60% for the PCM scenario (Fig. 2b). There was little to no improvement to EMAs with reserves when FRIs were 10 and 20 years, irrespective of the habitat loss or land conservation scenario (Fig. 2).

Managed Relocation

Population responses under managed relocation depended upon the rate, timing, and life stage of translocated individuals. Populations under the GFDL and PCM climate change scenarios responded similarly. All rates of seedling translocation showed some benefit, albeit very small for the lower rates (Fig. 3). Surprisingly, the difference in total population EMA when 10% versus 50% of seedlings were translocated was relatively small; 10% seedling translocation increased EMA by 52%, and 50% seedling translocation increased EMA by 68% for the 40-year FRI under the GFDL climate scenario (Fig. 3a). Under the PCM climate scenario and 40-year FRI, EMA

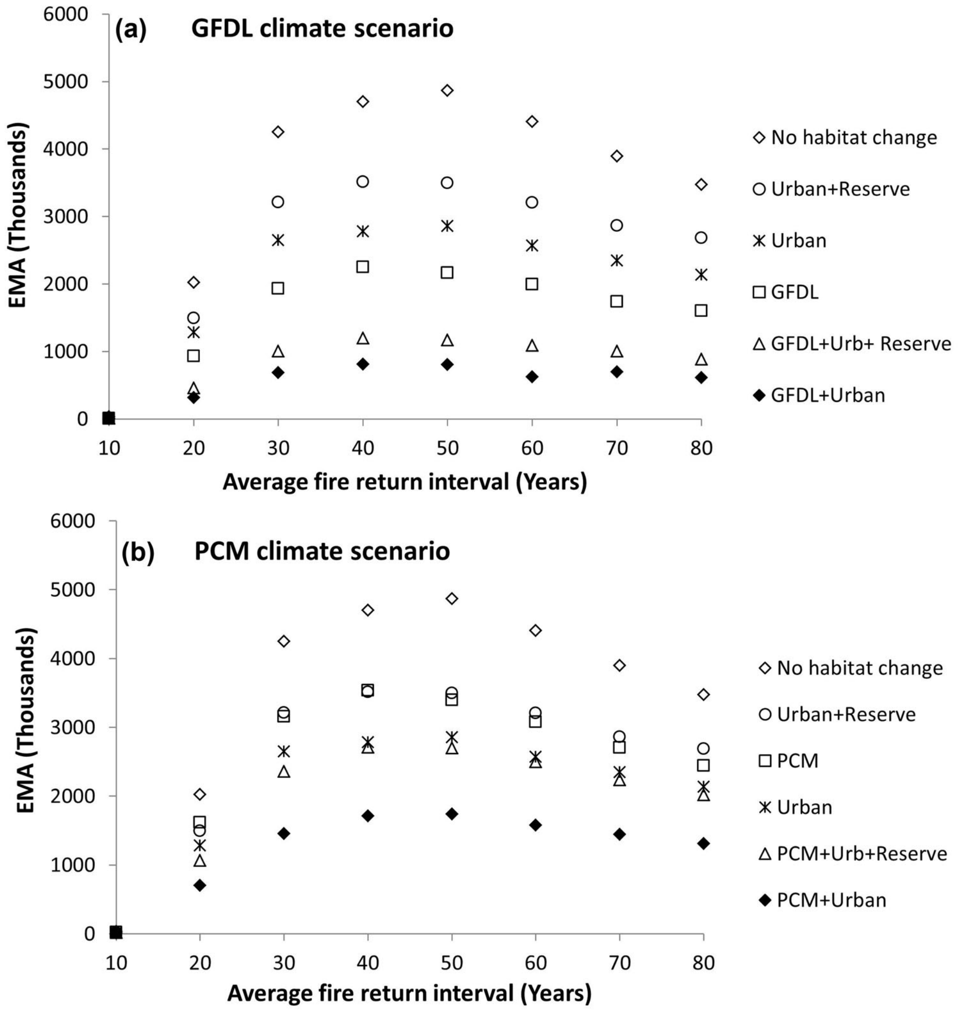

Figure 2. Extinction risk for Ceanothus verrucosus *as indexed by expected minimum abundance (EMA) as a function of fire return interval for a variety of scenarios including no habitat change (status quo), urban growth, and reserve (land protection) under the San Diego Multi-Species Conservation Plan: (a) GFDL climate model (Delworth et al. 2006) and (b) PCM climate model (Washington et al. 2000) under the Intergovernmental Panel on Climate Change Fourth Assessment A2 emission scenario.*

increased by 39% and 56% for 10% and 50% seedling translocation, respectively (Fig. 3b). No translocation option increased EMA under a 10-year average FRI. When seedling abundance (as opposed to rate) scenarios were implemented, no option increased EMA (Fig. 3c & d). This indicates that vast numbers of seedlings need to be translocated to establish viable populations given the very high background seedling mortality in our model (Supporting Information).

Managed relocation of seeds also increased population-wide EMA (Fig. 4). When 2% of seeds are translocated, more frequent translocations (every 2 years) lead to higher EMAs than less frequent translocations (every 6 or 10 years). Seed translocation of 2% every 2 years increased EMA by 75% and 47% under a 40-year FRI for GFDL (Fig. 4a) and PCM (Fig. 4b), respectively. The differences in outcomes resulting from translocations of 10% versus 50% of seeds were negligible; 10% seed translocation increased EMA up to 95%, and 50% translocation increased EMA up to 93% for the 40-year FRI under the GFDL climate scenario (Figs. 4c & e). Under PCM, EMA increased up to 74% and 73% for 10% and 50% seedling translocation, respectively (Figs. 4d & f). The effect of translocation timing on EMAs was minor for the 10% and 50% seed translocation scenarios (Fig. 4).

Discussion

Our results suggest that the relative efficacy of management strategies on mitigating extinction risk was strongly dependent upon the broader context of multiple threats. For *C. verrucosus*, the threat with by far the greatest impact was very frequent fire. This threat was so critical that management efforts to reduce habitat loss and climate change showed no benefit when the average FRIs was 10 years. The conservation importance of preventing high-recurrence fire has also been shown in models of long-lived obligate seeding trees and shrubs in other fire-prone regions (e.g., Keith et al. 2008; Wintle et al. 2011; Regan et al. 2012).

In southern California, fire frequency has increased substantially in recent decades due to anthropogenic ignitions associated with urban expansion (Syphard et al. 2007). In many areas, FRIs have been shorter than 10 years, and other obligate-seeding species have been

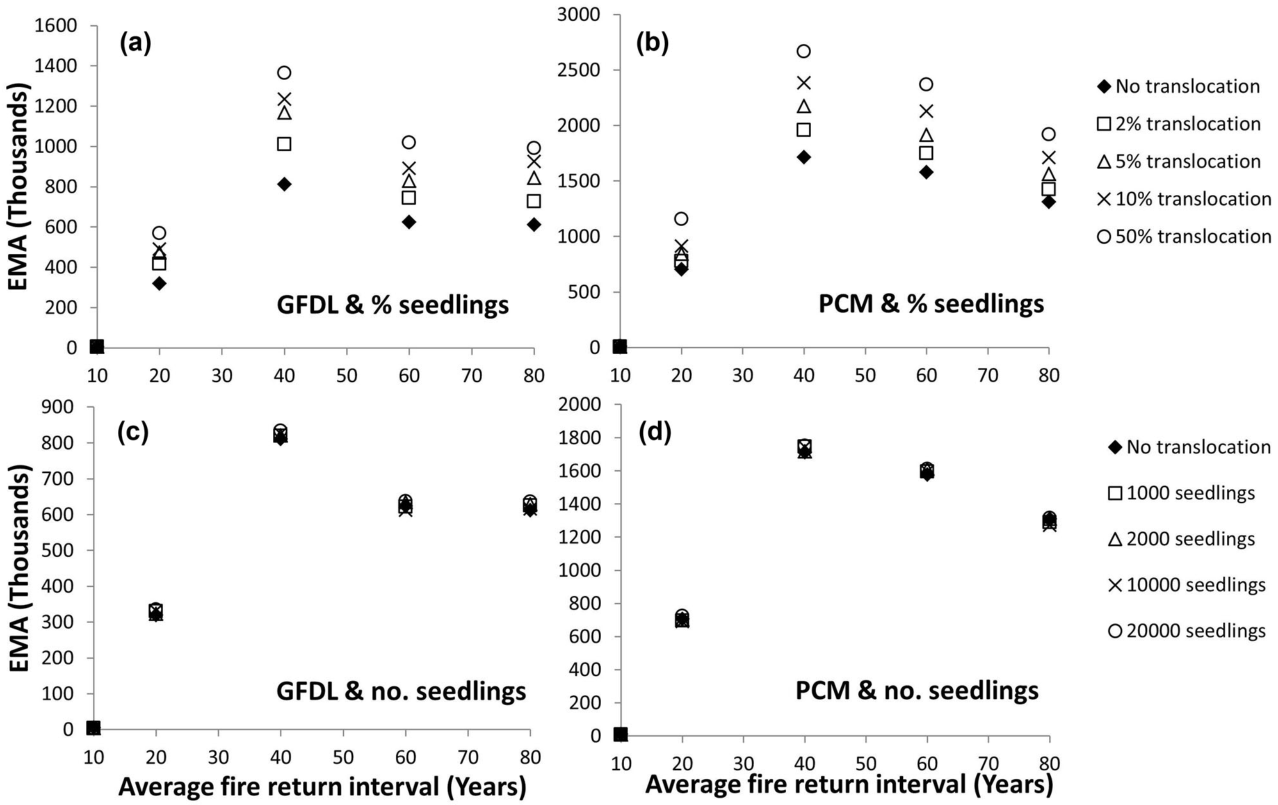

Figure 3. Expected minimum abundance (EMA) as a function of fire return interval under 2 seedling managed relocation scenarios (percentage of seedlings [a, b] and number of seedlings [c, d]) and (a, c) GFDL climate model (Delworth et al. 2006) and (b, d) PCM climate model (Washington et al. 2000) under the Intergovernmental Panel on Climate Change Fourth Assessment A2 emissions scenario.

extirpated and replaced with nonnative annuals (Zedler et al. 1983; Keeley & Brennan 2012). Although fire suppression has helped lessen fires, traditional management strategies in the form of fuel reduction have limited efficacy in southern California, particularly under the annual severe weather conditions brought by Santa Ana winds (Price et al. 2012). For meaningful improvement, alternative approaches such as land-use planning will need to be considered (Syphard et al. 2012).

With less frequent fire, the most effective management option depended on the climate scenario and, in the case of managed relocations, the life stage translocated. Under the GFDL scenario, climate change caused greater population declines than urban growth, whereas the opposite was the case under the PCM scenario. Translocation of seedlings mitigated population decline to a greater extent than land protection with GDFL, whereas under PCM the reverse occurred. This was because the net habitat area was projected to increase under the PCM scenario in the absence of urban growth; thus, existing populations declined to a lesser extent than for GFDL (Syphard et al. 2013). Translocation of 10% or 50% of seeds outranked both managed relocation of seedlings and land protection for both climate scenarios, although the land protection scenarios were only slightly inferior to seed translocation in terms of EMAs.

Our results indicate that managed relocation, especially the translocation of seeds, could be an effective management alternative to reduce population decline in the face of land-use and climate change. Seed translocations performed quantitatively better than seedling translocations because they did not have to be synchronized with uncertain fire events. Hence, they can be performed on regular intervals, accruing a seed bank until a fire event. Even decadal translocation of 10% of seeds from a patch with decreasing habitat to patches with increasing habitat increased total population size by as much as 75%, while further gains by translocating >10% of seeds in a source patch were negligible. Moreover, our results showed that even 20,000 seedling translocations made no difference to relative population size due to very high seedling mortality. When this is considered in the context of potential added translocation mortality at the recipient site (Regan et al. 2012), movement of seedlings from one patch to another may be unfeasible or unfruitful.

Regardless of how they are performed, translocations are not without complexities. Foremost they require

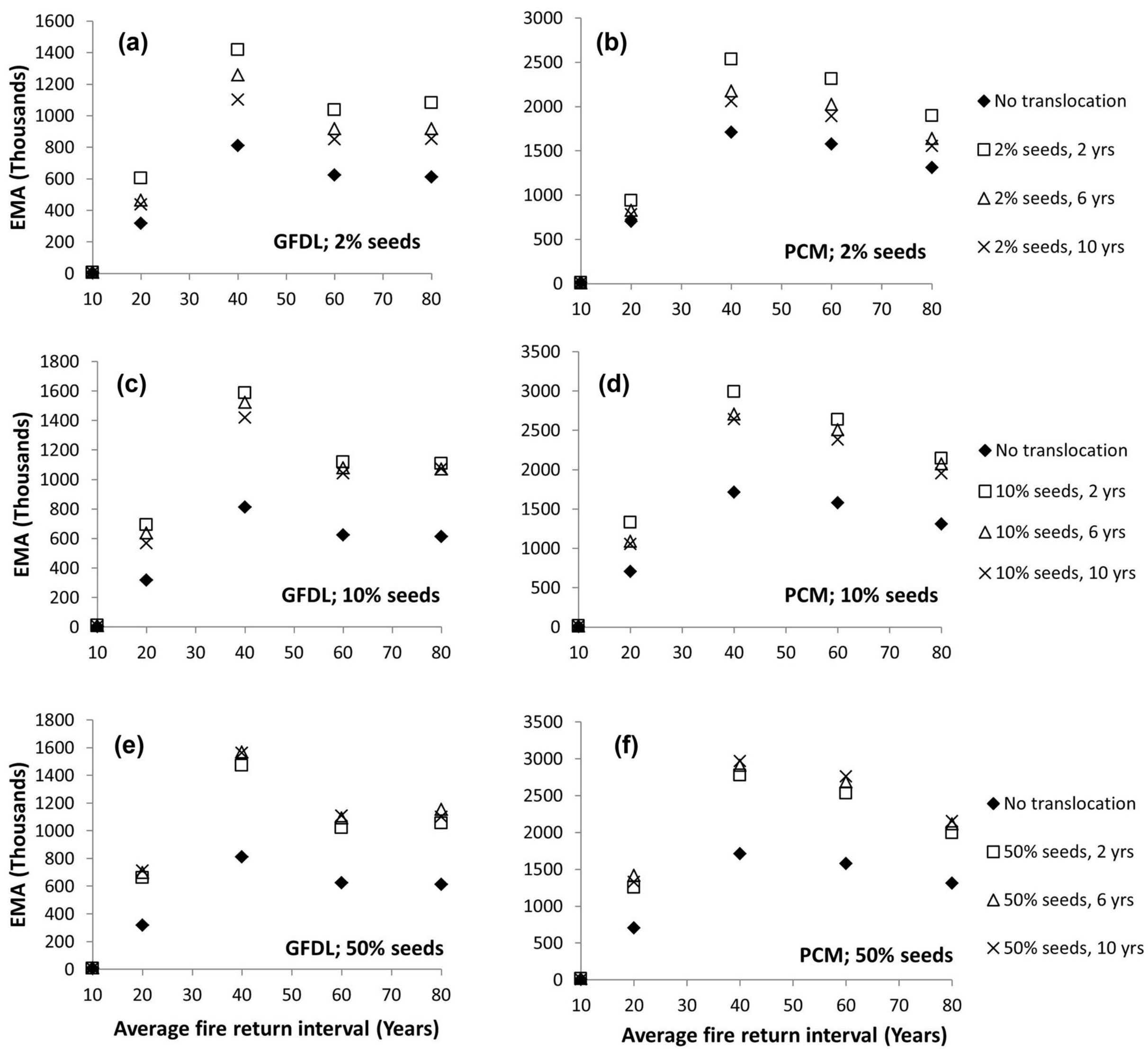

Figure 4. Expected minimum abundance (EMA) as a function of fire return interval for (a, b) 2% of source seed relocations under GFDL (Delworth et al. 2006) and PCM (Washington et al. 2000) climate models, respectively, (c, d) 10% of source seed relocations under GFDL and PCM respectively, and (e, f) 50% of source seed relocations under GFDL and PCM, respectively, under the Intergovernmental Panel on Climate Change Fourth Assessment A2 emissions scenario.

knowledge of locations of habitat. SDMs—the tools by which habitat predictions have been made—demonstrate the greatest variability in results across different model types, even more so than the choice of climate model (Conlisk et al. 2013). Added to this is the uncertainty in climate model, in this case GFDL and PCM. Uncertainties global climate models transcend regions and models. While we chose translocation recipient patches that overlapped across scenarios, uncertainty in climate models compounded the uncertainty due to SDM selection, potentially making the identification of future habitat for translocation unreliable. Of course, uncertainty lies in all components of this framework, from data collection to parameter estimation to model construction, and uncertainty is compounded across the coupled models. Rather than representing this uncertainty in full-blown uncertainty or sensitivity analyses, it may be more useful and feasible to focus on the components that impact decision making to the greatest extent. For spatial management options such as reserve design or translocation, uncertainty analysis of SDMs may be the most fruitful. For management options that focus on plant demography it may be necessary to consider greater detail on seed dormancy, the structure of temporal and spatial variation in vital rates, and changes in demographic parameters and fire frequency with climate.

In the case of *C. verrucosus*, the only sizable predicted future habitat patches were beyond the current known distribution of the species. Therefore, to reduce extinction risk, managed relocation is likely to be the only type of translocation available, presenting significant legal and administrative challenges (Schwartz et al. 2012). In particular, the target patches for the managed relocation were not on reserves and did not have management objectives pertaining to *C. verrucosus*. Additionally, the legal conservation status of *C. verrucosus* does not afford it any particular interventional protection in areas where it does not currently occur. From the perspective of land management then, the acceptability and feasibility (Richardson et al. 2009) of this managed relocation would be questionable in the absence of policy or legal intervention.

Significant ecological (Regan et al. 2012) and integrated (ethical, legal, and ecological) (Schwartz et al. 2012) questions remain for the managed relocation of *C. verrucosus* and long-lived obligate seeders in general. The target patches also happened to be located on a military base (Camp Pendleton). Although protection of endangered species is a priority at federal military installations, conservation is not their primary mission (Cohn 1996). For example, the issue of fire management could be complicated by military training priorities and the concerns of surrounding urban populations (Stein et al. 2008). Of course, fire and habitat management challenges are not unique to military bases or the species we modeled, and we anticipate that all land managers in fire-prone and developed regions will need to acknowledge the important interaction between translocation, development, and fire (Holl & Hayes 2006). Hence, irrespective of where habitat is predicted to occur and, importantly, who owns the land, early engagement and deliberation with relevant stakeholders will be necessary to craft workable conservation strategies if managed relocation is to be considered as a climate change mitigation strategy. Having reliable models in which land managers and the general public have confidence, along with establishing partnerships, is critical for relocation strategies to function.

Protection of existing habitat within the San Diego MSCP was not as effective as regular seed translocation. However, it still may be the most feasible and reliable strategy for this and other species as the MSCP planning process is already implemented. Our results demonstrate that land protection can be a viable conservation approach even in the face of decreasing or shifting habitat. Unlike managed relocation, habitat conservation benefits other species (Mawdsley et al. 2009; Shaw et al. 2012). Though climate change is rarely addressed in habitat conservation plans (Bernazzani et al. 2012), or reserve design more generally, our results show that reserves are likely important components of climate change mitigation strategies. Here too, conservation strategies will only be beneficial with an appropriate fire regime.

Climate change represents one of the biggest challenges to conservation planning because the units of conservation (populations and their habitat) are a moving target. In the United States, recent efforts to incorporate climate change mitigation into natural resource management have produced national conservation plans and strategies (USFWS 2011; CEQ, DOI 2012). Through an integrated framework that links climate data, species distributions, urban growth, fire risk, and population dynamics, we found that considering climate change alone offered an incomplete picture for a species that occurs in a region slated for future land-use change and whose life history relies on disturbance. Conservation plans could therefore be aided by integrated modeling approaches that investigate the impacts of multiple factors and evaluate the effectiveness of a variety of population-level management interventions.

Acknowledgments

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Supporting Information

A description of the modeling framework (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Akçakaya, H. R., and W. Root. 2005. RAMAS GIS 5: Linking spatial data with population viability analysis. Applied Biomathematics, Setauket, New York.

Albrecht, M. A., and J. Maschinski. 2012. Influence of founder population size, propagule stages, and life history on the survival of reintroduced plant populations. Pages 171–188 in J. Maschinski and K. E. Haskins, editors. Plant reintroduction in a changing climate: promises and perils. Island Press, Washington.

Araùjo, M. B., D. Alagador, D. M. Cabeza, D. Nogues-Bravo, and W. Thuiller. 2011. Climate change threatens European conservation areas. Ecology Letters **14:**484–492.

Bernazzani, P., B. A. Bradley, and J. J. Opperman. 2012. Integrating climate change into Habitat Conservation Plans under the U.S. Endangered Species Act. Environmental Management **49:**1103–1114.

Bowman, D. M. J. S., et al. 2011. The human dimension of fire regimes on Earth. Journal of Biogeography **38:**2223–2236.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution **23:**453–460.

Bruner, A. G., R. E. Gullison, R. Rice, and G. A. Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. Science **291:**125–128.

Cayan, D. R., E. P. Maurer, M. D. Dettinger, M. Tyree, and Hayhoe. 2008. Climate change scenarios for the California region. Climatic Change **87:**S21–S42.

CEQ (White House Council on Environmental Quality), DOI (U.S. Department of the Interior). 2012. National fish, wildlife and plants climate adaptation strategy. Public Review Draft. Available from http://www.wildlifeadaptationstrategy.gov/ (accessed July 7, 2013).

CNPS (California Native Plant Society). 2010. Inventory of rare and endangered plants (online edition, v7–09d). California Native Plant Society. Sacramento, CA.

Cohn, J. P. 1996. New defenders of wildlife. BioScience **46:**11–14.

Conlisk, E., D. Lawson, A. D. Syphard, J. Franklin, L. Flint, A. Flint, and H. M. Regan. 2012. The roles of dispersal, fecundity, and predation in the population persistence of an oak (*Quercus engelmannii*) under global change. PLoS ONE **7:**e36391. DOI:10.1371/journal.pone.0036391.

Conlisk, E., D. Lawson, A. D. Syphard, J. Franklin, L. Flint, A. Flint, and H. M. Regan. 2013. Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. Global Change Biology **19:**858–869.

Cowling, R. M., P. W. Rundel, B. B. Lamont, M. K. Arroyo and M. Arianoutsou. 1996. Plant diversity in Mediterranean-climate regions. Trends in Ecology & Evolution **11:**362–366.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science **332:**53–58.

Delworth, T. L., et al. 2006. GFDL's CM2 global coupled climate models. Part I: formulation and simulation characteristics. Journal of Climate **19:**643–674.

Didham, R., J. Tykianakis, N. Gemmell, T. Rand, and R. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology & Evolution **22:**489–496.

Driscoll, D. A., et al. 2010. Fire management for biodiversity conservation: key research questions and our capacity to answer them. Biological Conservation **143:**1928–1939.

Flint, L. E., and A. L. Flint. 2012. Downscaling future climate scenarios to fine scales for hydrologic and ecological modeling and analysis. Ecological Processes **1:**1–15.

Fuller, R. A., E. McDonald-Madden, K. A. Wilson, J. Carwardine, H. S. Grantham, J. E. M. Watson, C. J. Klein, D. C. Green, and H. P. Possingham. 2010. Replacing underperforming protected areas achieves better conservation outcomes. Nature **466:**365–367.

Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation **142:**14–32.

Hessl, A. E. 2011. Pathways for climate change effects on fire: models, data, and uncertainties. Progress in Physical Geography **35:**393–407.

Holl, K. D., and G. F. Hayes. 2006. Challenges to introducing and managing disturbance regimes for *Holocarpha macradenia*, an endangered annual grassland forb. Conservation Biology **20:**1121–1131.

Hunter, M. L. 2007. Climate change and moving species: furthering the debate on assisted colonisation. Conservation Biology **21:**1356–1358.

Keeley, J. E. 2012. Fire in Mediterranean climate ecosystems: a comparative overview. Israel Journal of Ecology & Evolution **58:**123–135.

Keeley, J. E., and T. J. Brennan. 2012. Fire-driven alien invasion in a fire-adapted ecosystem. Oecologia **169:**1043–1052.

Keeley, J. E., W. J. Bond, R. A. Bradstock, J. G. Pausas, and P. W. Rundel. 2012. Fire in Mediterranean ecosystems: ecology, evolution and management. Cambridge University Press, Cambridge, United Kingdom. 528 p.

Keith, D. A., H. R. Akçakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araùjo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters **4:**560–563.

Lawson, D. M., H. M. Regan, P. H. Zedler, and J. Franklin. 2010. Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. Global Change Biology **16:**2518–2529.

Loss, S. R., L. A. Terwilliger, and A. C. Peterson. 2011. Assisted colonization: integrating conservation strategies in the face of climate change. Biological Conservation **144:**92–100.

Maschinski, J., and K. E. Haskins. 2012. Plant reintroduction in a changing climate: promises and perils. Island Press, Washington.

Mawdsley, J. R., R. O' Malley, and D. S. Ojima. 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conservation Biology **23:**1080–1089.

McCarthy, M. A., and C. Thompson. 2001. Expected minimum population size as a measure of threat. Animal Conservation **4:**351–355.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework of debate for assisted migration in an era of climate change. Conservation Biology **21:**297–302.

Ogden Environmental and Energy Services. 1998. Final Multiple Species Conservation Program: MSCP Plan. Prepared for City of San Diego, California Department of Fish and Game, and US Fish and Wildlife Service, San Diego, CA.

Pausas, J. G., R. A. Bradstock, D. A. Keith, and J. E. Keeley. 2004. Plant functional traits in relation to fire in crown fire ecosystems. Ecology **85:**1085–1100.

Pereira, H. M., et al. 2010. Scenarios for global biodiversity in the 21st century. Science **330:**1496–1501.

Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography **31:**161–175.

Price, O. F., R. A. Bradstock, J. E. Keeley, and A. D. Syphard. 2012. The impact of antecedent fire area on burned area in southern California coastal ecosystems. Journal of Environmental Management **113:**301–307.

Regan, H. M., J. B. Crookston, R. Swab, J. Franklin, D. M. Lawson. 2010. Habitat fragmentation and altered fire regime create trade-off for an obligate seeding shrub. Ecology **91:**1114–1123.

Regan, H. M., A. D. Syphard, J. Franklin, R. M. Swab, L. Markovchick, A. L. Flint, L. E. Flint, and P. H. Zedler. 2012. Evaluation of assisted colonization strategies under global change for a rare, fire dependent plant. Global Change Biology **18:**936–947.

Richardson, D. M., et al. 2009. Multidimensional evaluation of managed relocation. Proceedings of the National Academy of Sciences, USA. **106:**9721–9724.

Schwartz, M. W., et al. 2012. Managed relocation: integrating the scientific, regulatory, and ethical challenges. BioScience **62:**732–743.

Seddon, P. J., D. P. Armstrong, P. Soorae, F. Launay, S. Walker, C. R. Ruiz-Miranda, S. Molur, H. Koldewey, and D. G. Kleiman. 2009. The risks of assisted colonization. Conservation Biology **23:**788–789.

Seddon, P. J. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology **18:**796–802.

Shaw, M. R., K. Klausmeyer, D. R. Cameron, J. MacKenzie, and P. Roehrdanz. 2012. Economic costs of achieving current conservation goals in the future as climate changes. Conservation Biology **26:**385–396.

Stein, B. A., C. Scott, and N. Benton. 2008. Federal lands and endangered species: the role of military and other federal lands in sustaining biodiversity. BioScience **58:**339–347.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, A. C. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. Ecological Applications **17:**1388–1402.

Syphard, A. D., V. C. Radeloff, T. J. Hawbaker, and S. I. Stewart. 2009. Conservation threats due to human-caused increases in fire frequency in mediterranean-climate ecosystems. Conservation Biology **23:**758–769.

Syphard, A. D., K. C. Clarke, J. Franklin, H. M. Regan, and M. McGinnis. 2011. Forecasts of habitat loss and fragmentation due to urban growth are sensitive to source of input data. Journal of Environmental Management **92:**1882–1893.

Syphard, A. D., J. E. Keeley, A. B. Massada, T. J. Brennan, and V. C. Radeloff. 2012. Housing arrangement and location determine the likelihood of housing loss due to wildfire. PLoS ONE **7:**e33954. DOI:10.1371/journal.pone.0033954.

Syphard, A. D., H. M. Regan, J. Franklin, R. M. Swab, and T. C. Bonebrake. 2013. Does functional type vulnerability to multiple threats depend on spatial context in Mediterranean climate regions? Diversity and Distributions **19:**1263–1274.

Turner, M. 2010. Disturbance and landscape dynamics in a changing world. Ecology **91:**2833–2849.

Underwood, E. C., J. H. Viers, K. R. Klausmeyer, R. L. Cox and M. R. Shaw. 2009. Threats and biodiversity in the Mediterranean biome. Diversity and Distributions **15:** 188–197.

U.S. Fish and Wildlife Service. 2011. Rising to the urgent challenge: strategic plan for responding to accelerating climate change, 1–32.

Washington, W. M., et al. 2000. Parallel climate model (PCM) control and 1% per year CO2 simulations with a 2/3 degree ocean model and a 27 km dynamical sea ice model. Climate Dynamics **16:**755–774.

Wintle, B. A., et al. 2011. Ecological-economic optimization of biodiversity conservation under climate change. Nature Climate Change **1:**355–359.

Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology **64:**809–818.