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Increasing Understanding of Species Responses to Global Changes Through Modeling Plant Metapopulation Dynamics

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Increasing Understanding of Species Responses to Global Changes Through Modeling Plant Metapopulation Dynamics

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by

Rebecca Marie Swab

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ABSTRACT OF THE DISSERTATION

Increasing Understanding of Species Responses to Global Changes Through Modeling Plant Metapopulation Dynamics

by

Rebecca Marie Swab

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, March 2014
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Understanding species responses to climate change is a topic of increasing concern given climate change projections. Niche models evaluate species vulnerabilities to climate change using current locations to project future habitat suitability under climate scenarios. However, these models are simplified and ignore other factors such as life history traits, catastrophes, or variability of vital rates. Therefore, in these three studies, I have used spatially explicit metapopulation models to evaluate species responses to global changes and variability in vital rates. The first study linked metapopulation models including stochastic fire events with niche models to evaluate the response of an obligate fire seeding shrub to simultaneous altered fire frequencies and shifting habitat due to climate change. For this species, altered fire regimes greatly reduced expected minimum abundances (EMAs). Climate change, on the other hand, only negatively affected the species under extreme scenarios. Therefore, altered fire regimes were the bigger threat to the species. The second study integrated fecundity and survival information from a translocation experiment into metapopulation models incorporating habitat suitability changes from a niche model. While the niche model projected overall increases in habitat for the species, the metapopulation model projected declining abundances within currently occupied patches due to declines in habitat suitability. Increased fecundity and survival rates sometimes mitigated the impact of these declines. The third study was an extensive sensitivity analyses of metapopulation models for two species, one obligate fire seeding shrub and one resprouter. Changes in the variability and means of vital rates, as well as changes in fire regime, dispersal, and variability of carrying capacity were integrated in separate scenarios. The obligate seeder was more vulnerable to altered fire regimes while the resprouter was more vulnerable to changes in vital rates. Both species were sensitive to increased variation of carrying capacity. Overall, all of the three studies indicate increasing the complexity of models can change the direction of results, and that different factors are influential for different species. Species were vulnerable to altered fire regimes and vital rates in particular, while habitat suitability changes caused by climate change sometimes affected minimum abundances.

Table of Contents

Supplemental Material from Chapter 1

Supplemental Material from Chapter 2

List of Figures

List of Tables

Introduction:

Global climate change is predicted to alter soil moisture, soil temperature, litter quality (Ayres 1993), fire regimes (Flannigan et al 2000), modify hydrology (Peterson et al 1997), temperature, and precipitation, (IPCC 2007), affecting plant growth and reproduction (Ayres 1993), permeability and infiltration rates of soil (Lavee et al 1998) and ecosystem biodiversity, function and resilience (Peterson et al 1997, Williams et al 2008). Organisms may be affected by and respond to climate change in a number of ways (Hughes 2000), including persistence, migration, and extinction (Davis et al 2005). Climatic variability is also predicted to increase, with more extremes of temperature in particular (Easterling *et al.* 2000, Schär *et al.* 2004, IPCC 2007, Wigley 2009). These extremes could affect species at local levels, affecting fecundity (Davison *et al.* 2010, Evans *et al.* 2010), plant population dynamics (Marrero-Gomez *et al.* 2007), and population growth rates (Buckley *et al.* 2010, Torang *et al.* 2010, Evju *et al.* 2011). Thus even within areas projected to remain suitable habitat for a species under climate change, abundances could decline if climatic fluctuations affect vital rates.

Ecologists have long sought to understand how vegetation relates to climate (Merriam 1898, McIntosh 1985, in Breshears 2008). Explanations range from the physiological to the community level (Andrewartha & Birch 1954, MacArthur 1972, Griffith & Watson 2006). At regional and global scales, climate defines the broad limits to the distribution of plant taxa and the dominance of plant life forms (Peters 1990, Vetaas 2002, Walther 2003, Witkowski & Lamont 2006, Williams et al 2007). Climate change is not a new occurrence, modern plant taxa have persisted through periods of variable climate for at least the past 2.5 million years (Davis & Shaw 2001). Historic responses of plant species to climate change include migration, adaptation, and extinction (Davis et al 2005). Given current climate change, all three responses are expected, though extinction is of the highest concern.

Under increasing temperature scenarios, species are predicted to generally shift their distributions poleward or upslope (Peters 1990, Breshears et al 2008, Loarie et al 2008). Over the past century, range margins of many species have already responded to warming in such a fashion (Hughes 2000, Parmesan 2006, Root et al 2003). Empirical examples of historic changes in geographic distribution resulting from climate change have been recorded for numerous taxa (Peters 1990, Loarie et al 2008), as evidenced by fossils, pollen, and pack rat middens (Davis & Shaw 2001). Most data indicate that species respond individually to climate change, as has been theorized for some time (Gleason 1926, Graham & Grimm 1990). Historically, the most exceptional examples of ranges shifts were 100 to 150 km per century; however, current climate projections may necessitate shifts of 300 to 500 km per century (Davis & Shaw 2001). Therefore, projecting future changes is crucial to planning for and mitigating the impacts of climate change on biodiversity (Loarie et al 2008).

Species are not expected to respond to climate change as a whole; species experience environmental variation across broad spatial gradients and thus have evolved ecotypes in response to these differences (Clausen *et al.* 1948, Jain & Bradshaw 1966, Waser & Price 1985, Schmitt & Gamble 1990, Galen *et al.* 1991, Kindell *et al.* 1996; Nagy & Rice 1997). Additionally, climatic extremes are predicted to increase, and may impact species viabilities. For example, temperature and precipitation extremes can decrease survival rates (Saccone *et al.* 2009, Torang *et al.* 2010, Andrello *et al.* 2012) and fecundity (Herrera 1991, Andrello *et al.* 2012). Thus it is difficult to capture a species response to climate change by simply mapping changes in habitat suitability.

Climate change does not operate in isolation from other factors. For example, interactions of climate change with extinction drivers, disturbance regimes, species dispersal, diseases or pests, and nutrient and water availability jointly influence species (Peters 1990). The most severe impacts of climate change are likely to stem from associations with other stressors rather than climate acting in isolation (Peters 1990, Thomas et al 2004, Parmesan 2006, Williams et al 2007, Preston et al 2008). Whereas the primary risk to species under climate change is typically considered to be shifting ranges (Peters 1990, Pearson & Dawson 2003), climate is also predicted to affect natural processes such as fire regimes (Whelan 1995). Additionally, anthropogenic processes such as urbanization affect fire regimes (Keeley 2004) and increase the difficulty of species migrations (Brook et al 2008). Interactions between threats are expected to increase given anthropogenic disturbance and climate change (Brook et al 2008), and are predicted to have critical impacts on biodiversity (Pimm 1996).

Most projections of species response to climate change ignore other global changes, varied responses of species across different parts of their range, and life history factors. The most common method of predicting species responses to climate change, bioclimatic modelling, uses knowledge of individual species responses to present climate conditions to predict future habitat (Vetaas 2002). Projections derived from bioclimate models have shown that species distributions may be altered dramatically under future climate regimes through range expansion, contraction, fragmentation, or shifts (Peterson et al 1997, McLaughlin et al 2002, Williams et al 2001, Beaumont et al 2007). These models have a number of limitations- they typically assume a linear relationship between abundance and range area (Ayres 1993); fail to account for other processes that influence extinction risk (Keith et al 2008); discount biological interactions; underestimate the importance of species dispersal (Pearson & Dawson 2003); and assume static tolerance ranges of species (Davis & Shaw 2001, Thuiller et al 2005). These criticisms have been addressed in several ways, including using multiple models within an ensemble forecasting framework (Araujo & New 2007), and incorporating ecological theory along with statistical models (Austin 2002). Increasingly, models include previously ignored factors such as invasive species spread, biotic interactions, local adaptation, fragmentation, changing land use patterns (Loarie et al 2008), and changing fire regimes (Keith *et al.* 2008). In order to increase the realism of predictions, it is necessary to continue to incorporate important factors such as life history characteristics, variability in vital rates, and responses to other stressors or catastrophes in predictions of species responses to climate change. This dissertation attempts to address these issues through three different studies, which address the following questions.

Chapter 1: Which is a greater threat to an obligate fire seeding shrub- range shifts due to climate change or altered fire frequency, and how do they interact?

Chapter 2: How do differences in vital rates across subpopulations interact with climate change to affect population viability?

Chapter 3: How does variability in life history traits and processes such as fire affect the viability of obligate fire seeders and resprouters?

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Chapter 1- Niche models tell half the story: spatial context and life history traits influence species responses to global change

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Abstract:

Aim: While niche models are typically used to assess species vulnerability to climate change, they have been criticized for their limited assessment of threats other than climate change. We attempt to evaluate this limitation by combining niche models with life history models to investigate the relative influence of climate change and a range of fire regimes on the viability of a long-lived plant population. Specifically, we investigate whether range shift due to climate change is a greater threat to an obligate seeding fire-prone shrub than altered fire frequency and how these two threatening processes might interact.

Methods: The study species is *Leucopogon setiger,* an obligate seeding fire-prone shrub. A spatially explicit stochastic matrix model was constructed for this species and linked with a dynamic niche model and fire risk functions representing a suite of average fire return intervals. We compared scenarios with a variety of hypothetical patches, a patch framework based upon current habitat suitability, and one with dynamic habitat suitability based on climate change scenarios A1fi and A2.

Results: *L. setiger* was found to be sensitive to fire frequency, with shorter intervals reducing expected minimum abundances (EMAs). Spatial decoupling of fires across the landscape reduced the vulnerability of the species to shortened fire frequencies. Shifting habitat, while reducing EMAs, was less of a threat to the species than frequent fire.

Main conclusions: Altered fire regime, in particular more frequent fires relative to the historic regime, was predicted to be the main threat to this species, which may reflect a vulnerability of obligate seeders in general. Range shifts induced by climate change were a secondary threat when habitat reductions were predicted. Incorporating life history traits into habitat suitability models by linking species distribution models with population models allowed for the population-level evaluation of multiple stressors that affect population dynamics and habitat, ultimately providing a greater understanding of global change impacts than would be gained by niche models alone. Further investigations of this type could elucidate how particular bioecological factors can affect certain types of species under global change.

Introduction:

Anthropogenic climate change is projected to shift, fragment, contract or increase the distributions of many of species, likely leading to redistributions (Peterson *et al.,* 1997; Pearson & Dawson, 2003) and extinction for some species (Thomas *et al.,* 2004). At the same time, fire frequency, size, and intensity are expected to interact with climate change, which in turn is expected to have serious consequences for species that have adapted to particular fire regimes (Keeley, 1995, Montenegro *et al.,* 2004). This leads to important management questions: will preparing for range shifts driven by climate change outweigh fire management as a key mediator of species persistence of fire adapted species?

The main method of investigating species vulnerability to range shifts due to climate change thus far has been niche modelling, also called habitat suitability or bioclimate envelope modelling (Pearson & Dawson, 2003). Niche models use present-day species-climate relationships to project potential suitable habitat, which may be altered by changing climate (Williams *et al.,* 2001; McLaughlin *et al.,* 2002; Thomas *et al.,* 2004; Beaumont *et al.,* 2007). However, a species' ability to track shifting habitat is potentially limited by natural and anthropogenic factors such as species dispersal capabilities, habitat fragmentation, and species interactions (Peters, 1990; Walther, 2003), all of which are typically not included in niche models. Additionally, niche models often ignore factors such as disturbances and life history characteristics (Pearson & Dawson, 2003; Keith *et al.,* 2008; Thuiller *et al.,* 2008), and do not account for synergisms with other threats, which may drive extinction dynamics (Brook *et al.,* 2008). In order to develop effective climate change adaptation strategies, it is necessary to assess species vulnerabilities to climate change and explore the implications of alternative management responses for population persistence. Given that climate change is expected to act in concert with other threats, which may interact synergistically to hasten extinction dynamics (Brook *et al.,* 2008), considering the impact of climate alone will not adequately address conservation issues.

Altered disturbance regimes (Salafsky *et al.,* 2002; Regan *et al.,* 2010) and climate change have been identified as important threats to biodiversity (Thomas *et al.,* 2004; Auld & Keith, 2009). Fire prone ecosystems in particular are expected to be highly sensitive to both global climate change and altered disturbance (fire) regimes (Moreno & Oechel, 1995, Tague *et al.,* 2009). In these ecosystems, altered fire regimes have the potential to overshadow the importance of other more direct effects of global warming on species that are sensitive to the timing and intensity of fires (Pausas, 1999; Flannigan *et al.,* 2000). In Australia in particular, the frequency of extreme fire weather is projected to increase as the climate warms (Lucas *et al.,* 2006). In addition, many fire prone ecosystems have experienced high levels of habitat loss and fragmentation, pollution, and exotic species introductions, all of which may weaken the resilience of the species that are most sensitive to climate change and/or adverse fire regimes (Field *et al.,* 1999). In this paper we focus on a species within a plant functional type that is dominant in many fire-prone ecosystems and is sensitive to changes in fire regime—long-lived obligate seeding shrubs.

Obligate seeders, plant species that are killed by fire and rely only on seed for regeneration, have been shown to be particularly sensitive to shortened fire intervals (Bradstock *et al.,* 1998; Pausas *et al.,* 2004; Regan *et al.,* 2010). However, it is unclear whether generalizations about fire regime in conjunction with climate change can be made for this plant functional type. While one study concludes that fire return interval is the main factor influencing viability of obligate seeders (Keith *et al.,* 2008), another concludes that climate plays a larger role (Lawson *et al.,* 2010), though each study shows that both fire and climate are likely to be important. There is also evidence that spatial structure of populations plays a large part in determining vulnerability of obligate seeders to changing fire return intervals (Regan *et al.,* 2010). Furthermore, dispersal defines a species ability to reach suitable habitat, and thus can mitigate a species response to shifting habitat (Engler *et al.,* 2009, Regan *et al.,* 2011). Overall, it is uncertain how fire regime changes or range shifts will interact, and whether one will have greater influence than the other on species persistence. More case studies of obligate seeders under different spatial contexts are needed to further explore these questions.

The existing studies on obligate seeders outlined above have built a foundation for explaining in greater detail the responses of functional types to climate change. However, there is much left that is unexplored. Therefore, we use the same methodologies in Keith *et al.* (2008) and Anderson *et al.* (2009) to delve further into explaining species responses to global change. Specifically, we incorporate life history traits into investigations of different climate, dispersal, and spatial structure scenarios.

We determine how these factors interact to impact species viability when faced with altered fire regimes and climate induced range shifts. We combine dynamic habitat suitability models with a spatially explicit age/stage-based model (hereafter referred to as spatially dynamic life history models) for an Australian obligate seeder, *Leucopogon setiger.* This species has been the subject of a number of field studies devoted to understanding and quantifying demography and responses to fire (Ooi, 2007, 2010; Ooi *et al.,* 2004, 2006, 2007). Therefore it is an ideal species for this type of modelling approach.

While niche models have been used to infer extinction rates by tallying species whose niches are projected to disappear (Thomas *et al.,* 2004; Williams *et al.,* 2007), spatially dynamic life history models can quantitatively compare the viability of populations in scenarios even where extinction risk is zero. These models can also be used to investigate the influence of habitat suitability thresholds, dispersal, and age specific survival rates and fecundities on species vulnerabilities, providing greater scope to address questions about global change and potential management responses. Other climate related feedbacks, in particular rising CO_2 levels, may affect plant allocation and thus feedback into demographic function by impacting fecundity or maturation. Such feedbacks can only be addressed in this type of modelling through sensitivity analyses incorporating changes in demographic parameters.

The response of species to threats in general (Pimm *et al.,* 1988; Isaac & Cowlishaw, 2004; Henle *et al.,* 2004), and fire in particular, has been shown to depend upon life history traits and species distributions (Keith *et al.,* 2008; Lawson *et al.,* 2010;

Regan *et al.,* 2010). However, insights into how the response of species to climate change depends on demographics are still limited by the number and diversity of case studies. Currently, many recommendations for adaptation to climate change in conservation plans, such as increasing habitat connectivity and establishing reserves, are based primarily on projected species distributions (Beale *et al.,* 2008, Heller & Zaveleta, 2009). However, the cumulative and synergistic nature of multiple threats necessitates adaptation strategies based on life history characteristics in addition to species distributions.

In this context, we set out to answer the following questions for *Leucopogon setiger*: 1) How do altered fire regimes impact this species and what role does spatial structure play in species vulnerability to fire? 2) What is the cumulative impact of species distribution shifts, contractions and fragmentation due to climate change and altered fire regimes? 3) How robust is the response of the species to changes in climate, dispersal, and spatial structure?

Methods

Study Species

Leucopogon setiger R. Br. is a fleshy fruited endemic of New South Wales, in southeastern Australia. Its core habitat is in fire-prone dry sclerophyll forests (Harden, 1992). *Leucopogon setiger* is an obligate seeding woody shrub with a soil stored seed bank. Therefore, populations tend to grow as even-aged cohorts with germination and seedling establishment rarely occurring in the absence of fire. The maximum life span is uncertain but is thought to range from 40 to 60 years. *Leucopogon setiger* has been the focus of a demographic study (Ooi, 2007). The model was parameterized using published demographic data and from additional field data describing post fire response, collected for the purpose of this current study.

Current and Future Spatial Distribution

Projected future climate maps were obtained from the Australian National University. These were generated based on an ensemble of 23 global climate models that were used by the IPCC (2007), and derived for years 1990, 2030, 2050, and 2070 using projected climate scenarios interpolated using ANUCLIM 5.1 (Houlder *et al.,* 2003) for two emissions scenarios, A1FI and A2. For each scenario, climate predictions were generated for 10th percentile, median, and 90th percentile climate values (hereafter referred to as pc10, pc50, and pc90, respectively). The advantage of composite climate models is that variations and uncertainties of individual models are reduced. For this composite, twenty-seven climatic variables were generated including a range of annual and quarterly statistics for temperature, precipitation, and solar radiation (variables 1-27 in http://fennerschool.anu.edu.au/publications/software/anuclim/doc/params.html). The environmental data was rescaled to 30 second (app. 1 km) cells by interpolation. We also used a geology layer to model edaphic relationships.

To evaluate the effects of projected climate change, habitat suitability for the current time was modeled using Maxent Version 3.3.3e (Phillips *et al.,* 2006; Phillips & Dudik, 2008). Maxent has proven very effective for habitat suitability modelling and performs better with presence only data than most other available methods (Elith *et al.,* 2006). Using the above climatic projections, 278 presence locations from vegetation survey data and herbarium records (NSW Office of Environment & Heritage), current suitable habitat was predicted using Maxent and then projected for future conditions in years 2030, 2050, and 2070. Maxent was used to determine which climatic, topographic, and substrate variables were the best predictors of species presence. Non-influential factors (those below two percent contribution to modeled predictions), including multiple climate factors, were removed. The remaining variables were evaluated by species experts for their suitability in regards to *L. setiger*, and then used to predict current suitable habitat. A road layer was used as unsuitable habitat to separate the suitable habitat into multiple patches since average patch size was far larger than average fire size across the landscape.

A minimum threshold of habitat suitability for occupancy of 0.249 was established using the equal training sensitivity and specificity parameter for *L. setiger* (Liu *et al.,* 2005). For comparison, the minimum training presence value, 0.007, was used as an alternative threshold for occupancy. Future habitat suitability was determined using the same climatic factors and future climate projections, assuming the same relationship between species and climate. Model goodness of fit was evaluated using the area under the receiver operator characteristics curve (AUC). Linear interpolation between the four time slices created species distribution maps for annual time steps with changing habitat suitability.

Metapopulation model

A stochastic matrix metapopulation model with four age classes and five stages was created in RAMAS GIS (Akcakaya, 2005). Seedlings were divided into four age classes, with survival rates available from previous field studies (Ooi, 2010). Field measurements assigned older plants to one of five stages, based on vertically projected canopy area assuming elliptical shape such that mean bud production varied by approximately an order of magnitude between stages (Figure 1). While populations are primarily age structured, given that fire induces germination, seed production varies depending upon the size of the individual, and thus a stage-structured population is more appropriate for mature plants. Both environmental and demographic stochasticity were incorporated into vital rates; the former via a lognormal distribution for each mean vital rate in the stage matrix and specified standard deviation, the latter via a Poisson distribution.

Survival rates

Background survival rates (in the absence of fire) for seedlings up to four years old were parameterized with data from a post-fire study (Ooi, 2010). The majority of *L. setiger* mortality (65%) occurs in the first year, leveling off to around 95% annual survival thereafter (Ooi, 2010). Thus our survival rate was set at 35% for the first year and 95% thereafter (Table 1.1). The 95% survival rate beyond age 4 was verified by estimating frequencies of recent deaths in field populations of ages 7-15 years. The coefficient of variation for survival rates was set at 15%, based on variability recorded by Ooi (2007).

Table 1.1 Age- and stage-based population matrix including fecundity and transition rates used in the metapopulation model of the Australian woody shrub *Leucopogon setiger.*

	Seeds	Year 1	Year 2	Year 3	Year 4	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Seeds	0.793	0	0	0	0	0.2	1.58	12.26	81.41	536.36
Year 1	0.000001	0	0	0	0	0	0	0	0	0
Year 2	0	0.35	0	0	0	0	0	0	0	0
Year 3	0	0	0.94	0	0	0	0	0	0	0
Year 4	0	0	0	0.94	0	0	0	0	0	0
Stage 1	0	0	0	0	0.457	0.857	0	0	0	0
Stage 2	0	0	0	0	0.334	0.08	0.8475	0	0	0
Stage 3	0	0	0	0	0.158	0.01	0.0855	0.886	0	0
Stage 4	0	0	0	0	0	0	0.0095	0.057	0.943	0
Stage 5	0	0	0	0	0	0	0	0.005	0.0095	0.94

Fecundity and seed survival

The number of seeds produced per plant is a function of canopy area, which is an indirect function of plant age. To determine the fecundity for each stage, four stands aged seven and 15 years were sampled. Bud counts were recorded for 20-25 shrubs per stand, and used to determine seed production by stage (Figure 1.1). Previous work found approximately 11% of flowers developed into mature fruits (Ooi, unpubl. data) and that 83.88 % of seeds (one per fruit) produced by *L. setiger* shrubs in each year were viable (Ooi *et al.,* 2007). Removal rates of seeds were up to 98% (Ooi, 2007), however not all of the seeds taken were lost to predation, as predators consume the fleshy fruit, while the seed itself tended to be dispersed by endozoochory. To estimate each individual's contribution to the seed bank annually, the bud numbers determined through field work were reduced by the proportion of buds that become seeds, and further reduced by predation. The number of seeds entering the seed bank per year was drawn from a

Poisson distribution with these calculated means and standard deviations. The seed bank was estimated to decay exponentially at a rate of 0.156 (±0.070) annually (Ooi *et al.,* 2007), and an additional 6% of those remaining fail to germinate. Thus, annual seed survival was set at 79.3% with an estimated half life of 2.99 years.

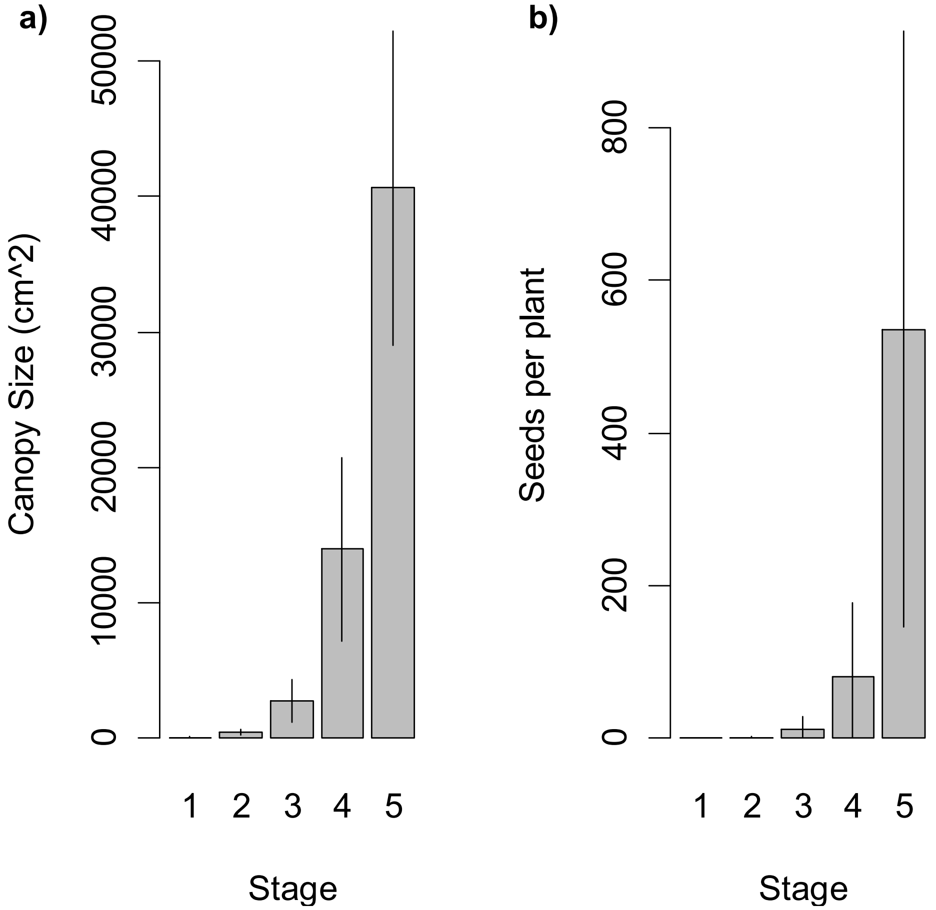

Figure 1.1. A) Canopy size and B) Seed production by stage for *Leucopogon setiger*.

Post-fire recruitment

During a fire event 76.8% of seeds in the seed bank are killed by indirect heat or burning (Ooi, unpubl. data). When fire mortality and predation are accounted for, germination of the stored pre-fire seed bank occurs at a rate of 0.068. Seedlings emergence is delayed until autumn irrespective of the season in which the fire event occurred (Ooi *et al.,* 2004). Therefore, the model is structured around a post-emergence census, with first year seedling death incorporated into the first year transition rate.

Carrying capacity and self-thinning

Density dependent effects on survival, growth and fecundity were implemented in the model to ensure that simulated population densities remained within biologically realistic bounds. Carrying capacity (*K*) was determined by calculating the maximum number of *L. setiger* individuals in a monospecific stand (size of one 30 second cell) based on the average canopy size of the largest size class. Field sampling of wild populations showed competitor species to occupy on average 9.5 times more space than conspecifics. Therefore, the threshold density was divided by 9.5 to account for unavailable space occupied by neighbours. Each stage was weighted by size (i.e. canopy area), so individuals of smaller stages occupied less space than those of larger stages. Weights were as follows: 0.043, 0.043, 0.053, 0.053, 0.063, 0.107, 0.18, 0.64, 1 for ages 1 to 4 and stages 1 to 5, respectively. Seeds were not subject to carrying capacity. The carrying capacity (*K*) per cell (1200 individuals) was multiplied by the summed habitat suitability across each cell within a patch, which changed through time with climate. In each time step, if population size exceeded carrying capacity, due to natural fluctuations or reduced suitable habitat caused by climate change, a density dependence function (adapted from Keith *et al.,* 2008) reduced survival, growth and fecundity of particular life stages by a proportion varying from 0.9 (for seedlings) to 0.1 (for full sized plants), until population size was at or below *K*.

Fire events

To investigate the effects of changing fire regimes, we compared the impacts of seven different average fire return intervals (5, 10, 15, 20, 25, 30, 35 years) on abundances of *L. setiger*. Average fire return interval was implemented in the population model through a hazard function—an annual probability of fire as a function of time since last fire. The fire, in turn, resulted in mortality of all (in most simulations) or most (90, 95, and 99%, in sensitivity analyses) standing individuals, and triggered germination from the seed bank. To determine the annual fire probability, we used hazard functions based on McCarthy *et al.* (2001),

$$h(t) = \frac{h}{1 + c \times \exp(t)}$$

where h =1/mean fire interval, c is 'skewness' or a shape parameter affecting the slope of the curve (set to 1000), and t is time since last fire. Each time a fire occurred, the fire function was reset to $h(0)$. Fixed fire intervals (i.e. fires occurring exactly every n years with no wildfires) were also implemented for some simulations (see below).

Dispersal

L. setiger is dispersed by ants and birds (Keighery, 1996, Stansbury, 2001; Ooi, 2007). Potential dispersal rates of seeds from *L. setiger* calculated based upon the average daily distance travelled by dispersers of the seeds predict that only 0.6% of seeds were estimated to reach distance of over 300 metres, 7% over 50 metres, 17% over 15 metres, and 95% less than 15 metres. This means that no seeds would disperse between patches. However, given that dispersal is highly uncertain, and rare long distance events are thought to play a key role in species movement to new habitats (Higgins *et. al.* 2003, Engler *et. al.* 2009), we modeled extreme dispersal at ten times the amount predicted above to determine whether long distance dispersal would increase the species viability. The probability of a seed dispersing from one patch, *i*, to another patch, *j*, is given by the equation:

$$M_{ij} = \begin{cases} a \times \exp\left(-D_{ij}^{\frac{c}{b}} \right) & \text{if } D_{ij} \leq D_{\max} \\ 0 & \text{if } D_{ij} > D_{\max} \end{cases}$$

where *a*, *b*, *c*, are function parameters, D_{ij} is the distance between the two populations, and $D_{\max}$ is the maximum distance any individual can disperse in one time step (Akçakaya, 2005). For the simulations including dispersal, *b* was set to 0.88, *c* to 0.34 and $D_{\max}$ to 600. These values best simulate the ten times extended dispersal kernel expected for this species. Since dispersal estimates are uncertain, we varied the parameter *a* (which represents the maximum amount of dispersal between two patches) to take values between 1 and 0.1 to compare the effect of different rates of dispersal on minimum abundance. For a stable patch structure, the total amount of seeds dispersing from each population averaged 43%, 21.9%, 6.1%, and 4.4% for a=1, 0.5, 0.25, and 0.1, respectively.

Simulations

Each simulation was run for 1500 replications with a 100 year time interval (i.e. 2000-2099). Population viability was assessed using expected minimum abundance (EMA), or the smallest population size averaged across all 1500 population trajectories of 100 years (excluding population size at $t = 0$). EMA is useful for identifying threats to species which face population decline over time scales too short to observe extinction (McCarthy & Thompson, 2001). Multiple sensitivity analyses were carried out by individually perturbing germination, fecundity, transition, and survival rates (with and without fire) for each stage or age step. These identified the life history characteristics most influential on species viability under the effects of climate change and highlighted where uncertainties might affect model results (Regan *et al.,* 2003).

Experiment 1

Two experiments were conducted. First, a hypothetical landscape was developed under a stable climate. This allowed systematic investigation of spatial structure and dynamics through patch structure manipulation without the potentially confounding effects of variable patch size and patch size dynamics. A fixed initial population size was divided into one, two, four, eight, 16, and 32 patches to result in six separate landscapes. This simulates the effect of habitat fragmentation without habitat loss, or spatial separation of patches. Each simulation was run for the full range of average fire return intervals with both irregular (wildfires) and regular (exact) fire return intervals, following methodology in Regan *et al.* (2010). In different simulations, fires were uncorrelated or correlated between patches, thus allowing a comparison of species responses to one large fire with multiple small uncorrelated fires.

Experiment 2

The second experiment utilized the more realistic spatial structure defined by habitat suitability. To investigate the effect of climate change, simulations were run for all average fire return intervals with seven different climate scenarios: a stable climate, and the 10th, median, and 90th percentiles for both A1FI and A2 scenarios, all for two different habitat suitability thresholds. Patch structure and size in each time step were established with the predicted suitable habitat for the current climate models using a patch separation threshold of 2.5 cells, meaning suitable habitat within a radius of 2.5 cells of a cell were considered part of the same patch. The higher suitability threshold was used to investigate the effects of dispersal and fire refugia on population viability.

Results:

Experiment 1: Changing fire interval and spatial structure

For regular fire return intervals, models predict that 20 years is the optimal fire return for *L. setiger*. The expected minimum abundance (EMA) sharply declines when fire return intervals are small (<10 years) or increase above 20 years (Figure 1.2). However, while extremely short (5-10 years) fire return intervals result in high extirpation risk for a single patch, longer fire intervals do not increase extirpation risk (Figure 1.3). Increasing the number of patches has a negligible impact on the vulnerability of *L. setiger* to fire return interval in this scenario, but when fires are uncorrelated between patches (i.e. have different initial time since last fire), EMAs are slightly increased when the number of patches increases (Figure 1.2).

When fires occur at irregular return intervals (wildfires), an optimal average fire return interval of 15-25 years is maintained across all spatial structures if fires are uncorrelated. EMA gradually declines with longer intervals, and declines more sharply with shorter intervals (Figure 1.2), however extirpation risk only increases as fire return interval reduces (Figure 1.3). Populations are more sensitive to spatial correlation of fires when intervals between fires are variable than if they were of regular length. Correlated fires result in much lower EMAs than for uncorrelated fires. As the number of patches increases the response of the species to shorter fire return intervals worsens, as does EMA overall- likely due to the fact that smaller patches are more susceptible to bad years. For the maximally fragmented landscape with correlated wildfires, EMA increases as fire return interval increases.

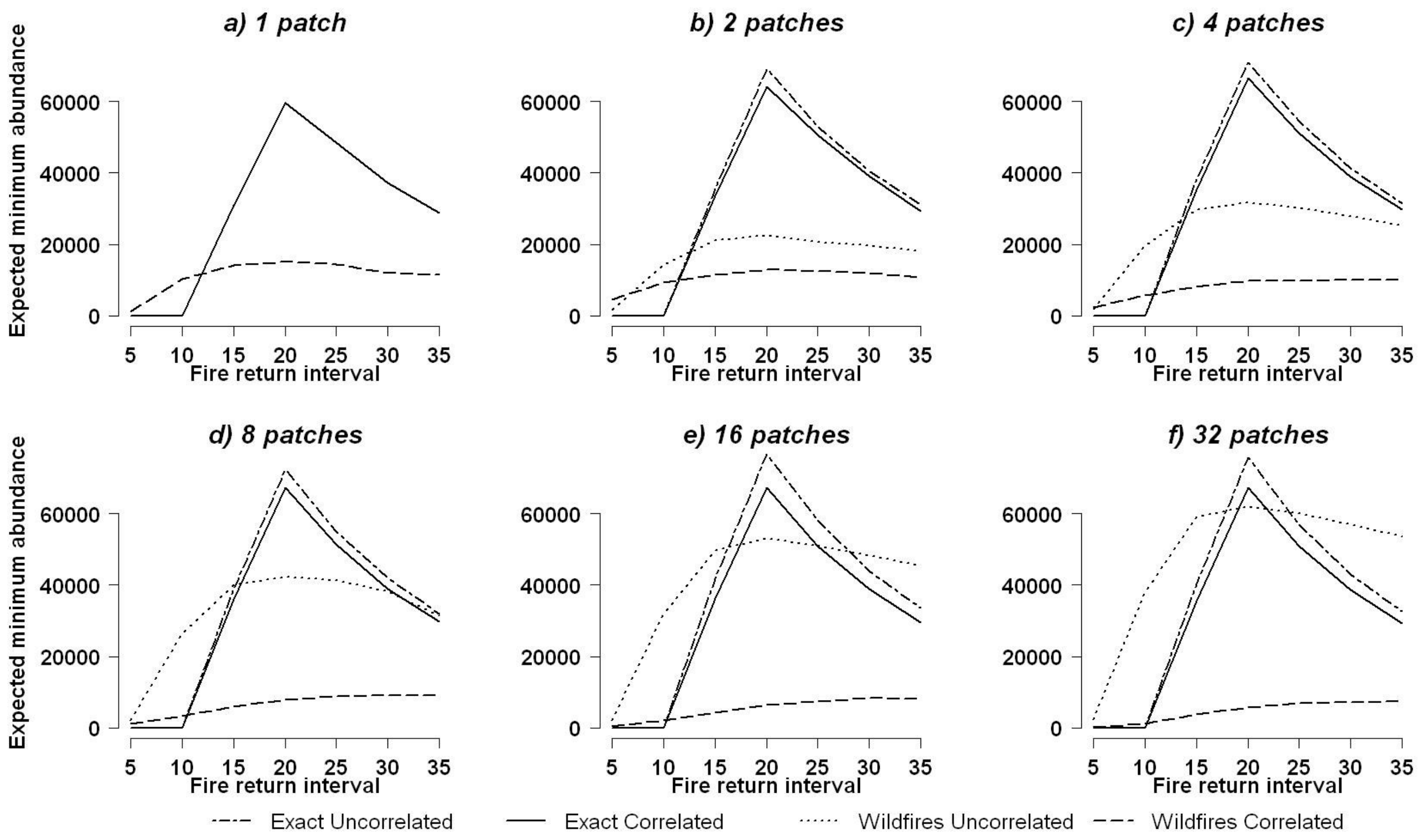

Figure 1.2. Expected minimum abundance (EMA) versus fire return interval (in years) for *Leucopogon setiger* with a range of patch configurations, 1-32 (A-F). Fires occur at either 1) exact intervals, uncorrelated between patches, 2) exact intervals, correlated between patches, 3) average intervals, also referred to as ‘wildfires’, and uncorrelated between patches, or 4) wildfires, correlated between patches.

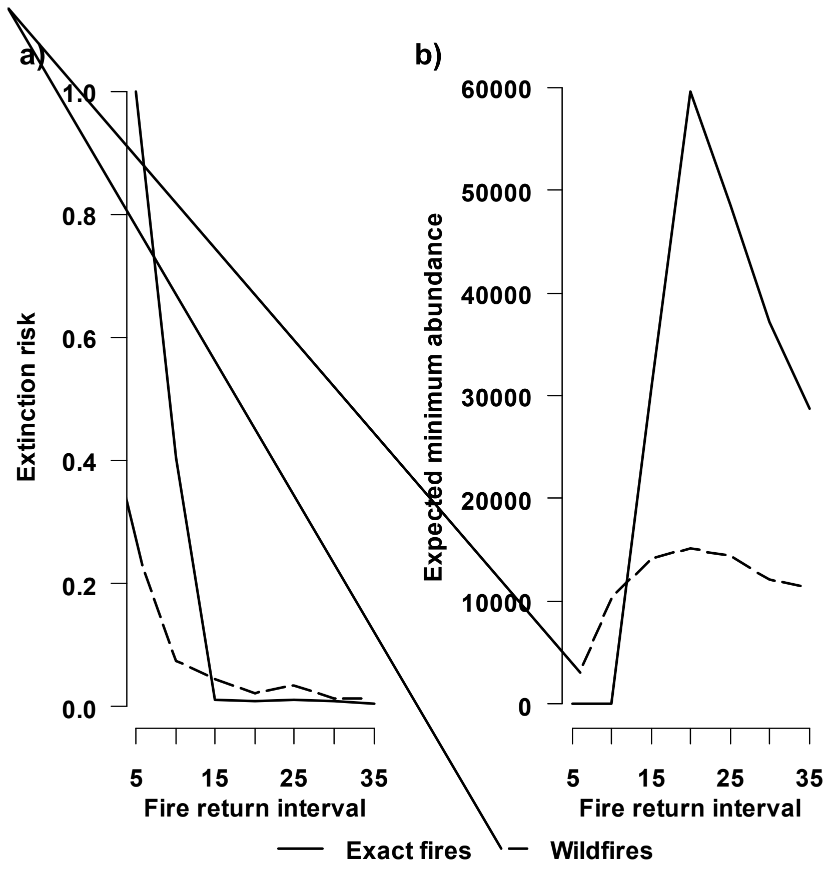

Figure 1.3. A) Exinction risk and B) Expected minimum abundance (EMA) versus fire return interval (in years) for *Leucopogon setiger* in one patch for a stable climate. Fires occur at exact intervals or at irregular intervals as for wildfires.

When comparing EMAs from regular and irregular uncorrelated fire return intervals, increases or decreases in the EMAs are apparent depending on the number of patches and the average fire return intervals tested. EMAs are lower for irregular fire scenarios than they are for exact fire intervals when the average fire return interval is greater than 10 to 15 years for 1, 2, 4, and 8 patches. They are higher for irregular than regular fire intervals for all but the optimal range when there are 16 and 32 patches

(Figure 1.2). Decoupling fires across the landscape by increasing the number of patches while maintaining the same initial abundance, reduces the risk of decline of *L. setiger* for all average fire return intervals except 5 years (Figure 1.2). Thus, spatial decoupling of fire events and longer fire return intervals increase population persistence for *Leucopogon setiger*.

Experiment 2: Climate change and changing fire interval

The optimal average fire return interval remained 15-25 years when the population model was linked to the species distribution model, both with and without climate change and for both climate scenarios tested. This response curve was very similar to the response in experiment one incorporating wildfires. Extreme shortened fire return intervals (5 years) gave the lowest EMAs for the species in every model scenario, in some cases resulting in extinction. *L. setiger* was not sensitive to shifting habitat under the pc50 or pc90 scenarios for both A1FI and A2 climate scenarios (Figure 1.4). However, the pc10 scenario dramatically reduced EMA. These responses to climate are consistent with expectations given the level of changes in habitat suitability, shown as change in carrying capacity (Figure 1.5).

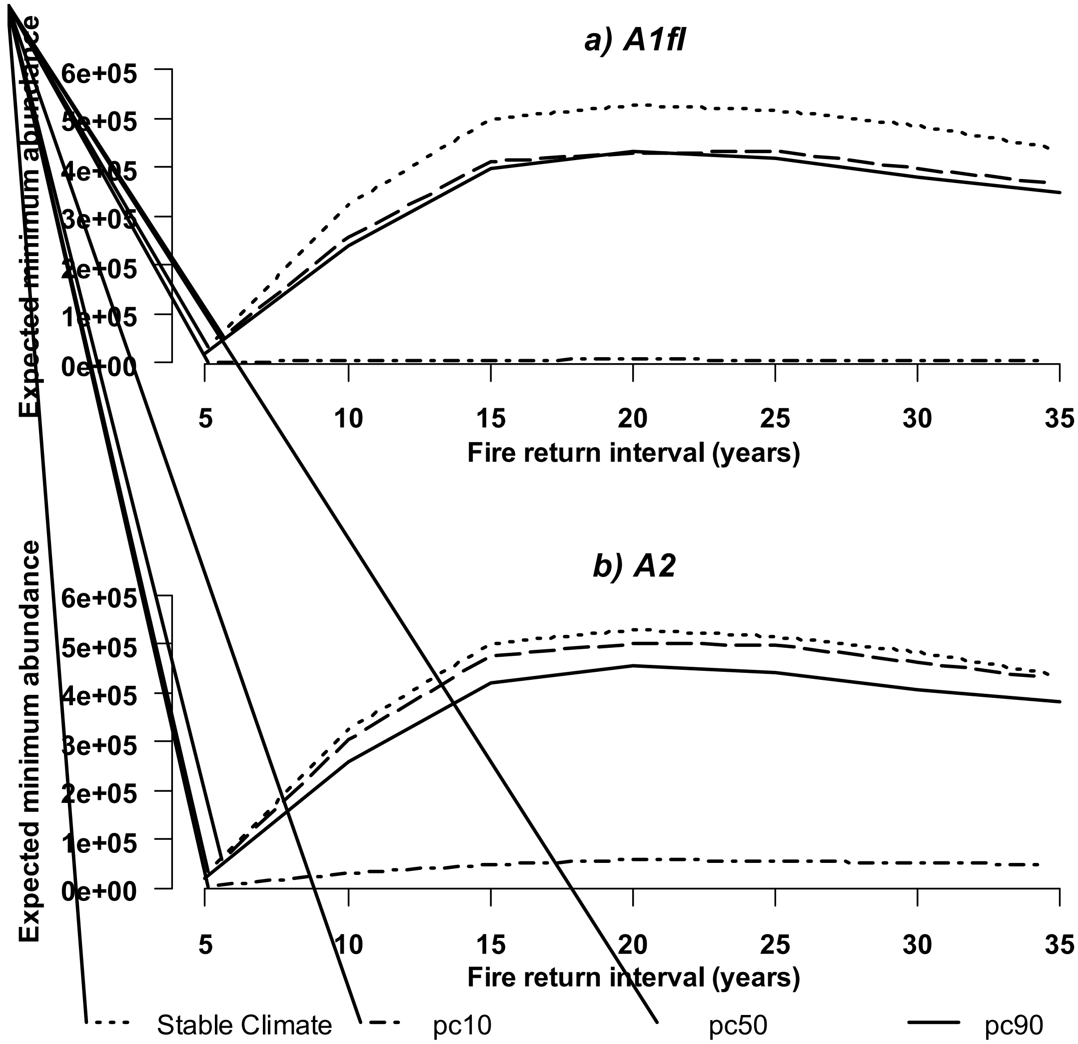

Figure 1.4. Expected minimum abundance (EMA) versus fire return interval (in years) for *Leucopogon setiger* with A1FI and A2 climate scenarios as follows: current climate remaining stable, 10th, median, and 90th percentiles (Stable, pc10, pc50, pc90, respectively) for a composite of various climate models.

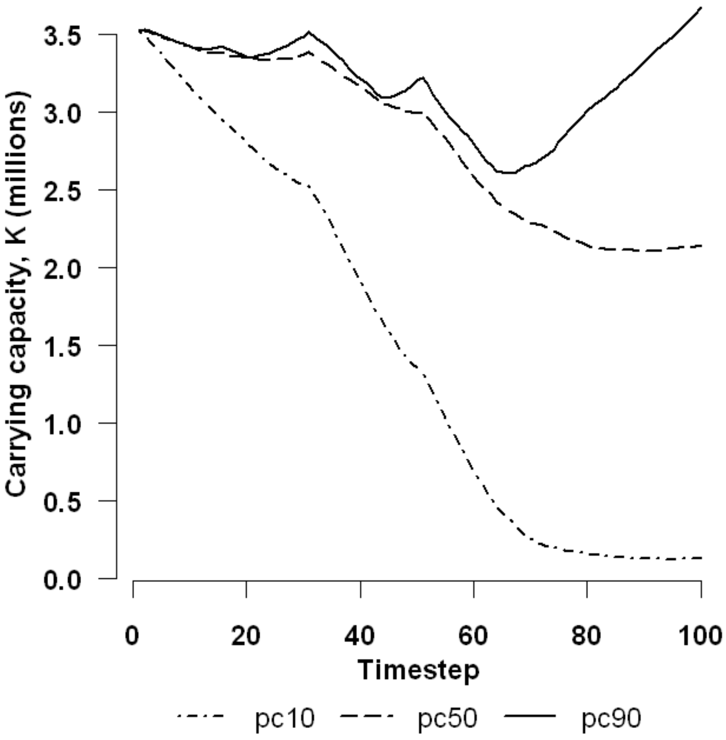

Figure 1.5. Carrying capacity, K for *Leucopogon setiger* by time step. K was calculated using the A2 climate scenario 10th, median, and 90th percentile (pc10, pc50, pc90, respectively) projections for a composite of various climate models.

Dispersal, threshold, and fire refugia

Dispersal of a small portion of seeds produced optimal EMA, but only slightly higher than no dispersal (Figure 1.6a). Dispersal of all seeds from a patch had a negative effects on EMA. This was true whether climate remained stable or changed (not pictured). Including fire refugia within patches by decreasing the percent of standing plants killed in fire increased EMAs, but maintained sensitivity to shortened fire intervals (Figure 1.6b). Lowering the habitat suitability threshold allowed more habitat to be designated as suitable for the species, increasing EMA (Figure 1.7 cf. Figure 1.4). The general response of the species was similar to other scenarios, with fire return interval as the primary influence on EMA and climate change a secondary one. Under a low habitat suitability threshold only the pc10 scenarios impacted the EMA, and the impacts were less severe than scenarios with the higher threshold.

Sensitivity analyses

The shape of the EMA curve (not shown) in response to fire interval was similar for 100 and 200 year scenarios for all climate scenarios (assuming climate change stopped after 100 years). Thus, the duration of the simulation did not affect the general trend of the results. The model was sensitive to changes in most survival parameters, and to changes in percentage of standing plant death during fire, but not sensitive to most changes in fecundity (Supplemental Material). The degree to which the model results were sensitive to changes in vital rates depended on the fire return interval. The model was substantially more sensitive to changes in germination rate, seedbank turnover, and survival rates under the 5 year return interval than any other.

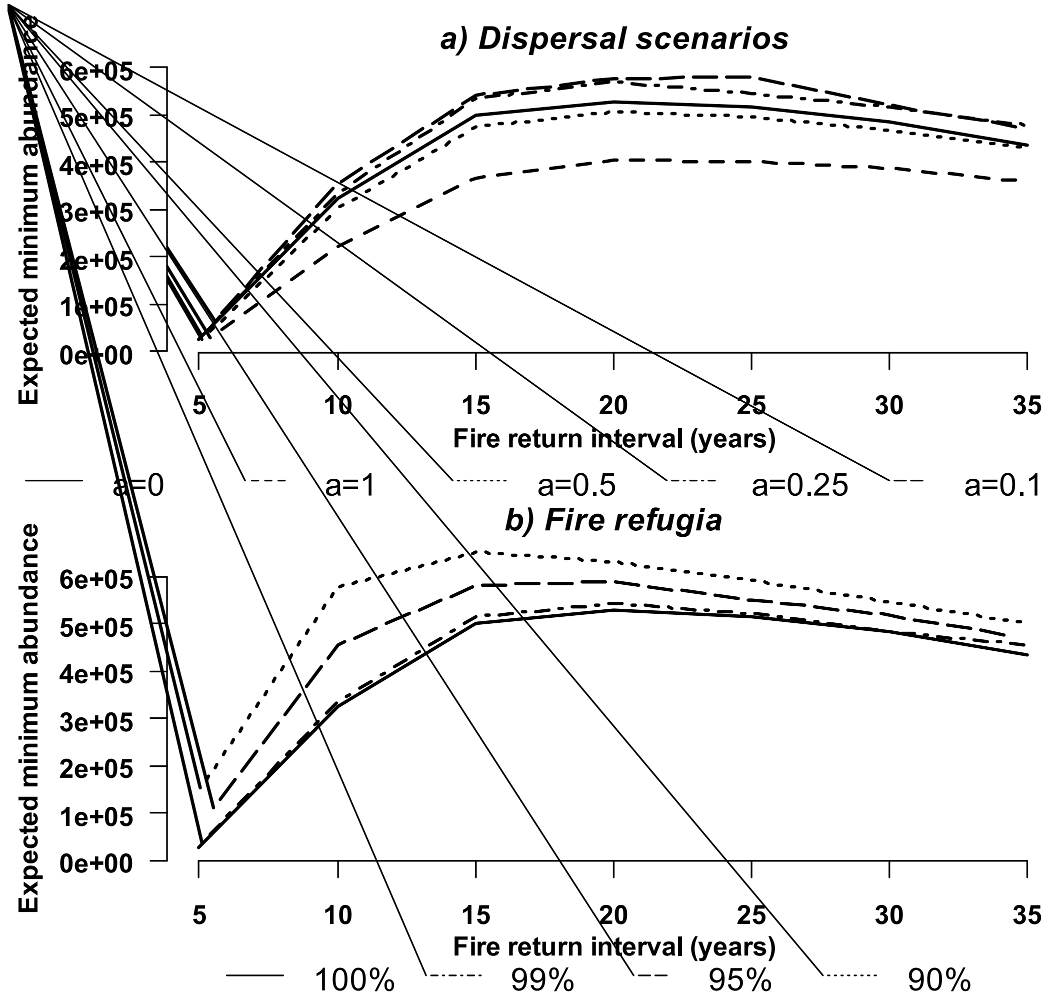

Figure 1.6. Expected minimum abundance (EMA) versus fire return interval (in years) for *Leucopogon setiger.* a) Stable habitat and a variety of dispersal amounts. When a=1, the largest portion of each population's seeds are dispersed. The proportion of seeds dispersing decreases as a decreases. b) Stable habitat and a ranging percent death with fire, allowing for unburned refugia in patches.

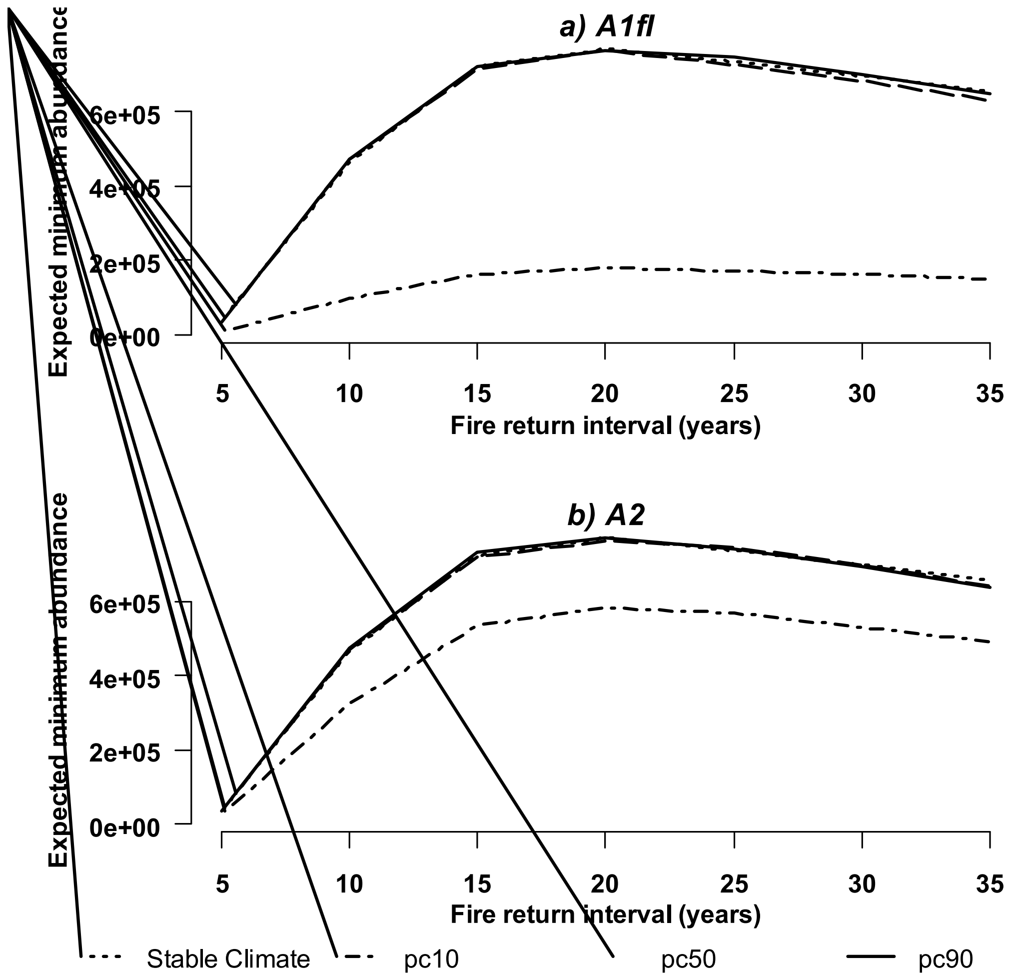

Figure 1.7. Expected minimum abundance (EMA) versus fire return interval (in years) for *Leucopogon setiger* with A1FI and A2 climate scenarios as follows: current climate remaining stable, 10th, median, and 90th percentiles (Stable, pc10, pc50, pc90, respectively) for a composite of various climate models. For these simulations, patch structure was created using minimum training presence value, 0.007, as a threshold for suitable habitat.

Discussion:

The results of this study predict that while obligate seeders may be vulnerable to both altered fire return intervals and climate change, fire is the primary influence. Appropriately timed fires are essential for population persistence; in all scenarios, the worst outcome for *Leucopogon setiger* occurred with the most frequent fires. This is consistent with other studies on fire obligate seeders which experience stand replacing fires. Regan *et al.* (2010) showed comparable results for the Californian obligate seeding shrub *Ceanothus greggii*—the worst scenario, under a variety of fragmentation levels, was the shortest fire return interval (10 years). However, this study used a hypothetical landscape and did not incorporate climate related range shifts. Lawson *et al.* (2010) showed that high fire frequency reduced EMAs for another obligate seeding shrub, *Ceanothus verrocosus*. They concluded that for this species, climate change may overshadow the risk of altered fire regime- though fire was still an important influence. Considering that they tested fire intervals starting at 20 years, the *C. verrocosus* study may not have captured the full vulnerability of the species to extreme shortened (<10 year) fire return intervals. For a third California obligate seeder, *Cupressus forbesii*, model results also indicate vulnerability to short fire return intervals (Regan *et al.,* in press). Keith *et al.* (2008) compared EMA for a number of South African obligate seeders under two different fire return intervals. For all simulations, the 14 year mean fire return interval resulted in higher EMAs than the shorter 8 year return interval. Multiple modelling studies conclude that short fire intervals are detrimental to obligate fire seeding species which experience stand replacing fires.

The impact of climate-related range shifts on obligate seeders are less clear cut. In Keith *et al.* (2008), whether climate impacted obligate seeding species depended on the patterns of distribution change—not surprisingly, for species with widespread contracting suitable habitat, climate was a significant factor, while for species with reduced habitat shifts and contractions, climate had a minimal impact. This aligns with the results for *L. setiger*. Under the pc50 and pc90 climate scenarios, *L. setiger* maintained a core habitat with restricted contractions and shifts (Figure 1.5), resulting in minimal to no (for lower habitat suitability threshold) reductions in EMA. Alternatively, the pc10 scenarios predicted major range contraction, and *L. setiger* was predicted to be extremely vulnerable to climate change in these scenarios. While dispersal ability has been predicted to be an important part of obligate seeders competitive strategy, and may help them respond to climate change (Higgins *et al.,* 2008), in this case dispersal did not appear to have a mitigating effect for the species even under the pc10 scenario, most likely because range contractions rather than shifts were predicted. Keith et al (2008) also found dispersal to be inconsequential to the viability of fynbos shrubs. Thus the plausible bounds of dispersal kernels might be so low that small variations make little difference in model predictions. Overall, climatically induced habitat shifts do not appear to be a significant factor for *Leucopogon setiger.* However, the results predict that even when species are apparently climate winners (Hamer, 2010), that is, their available suitable habitat increases with climate change as in the pc90 climate scenario, they might still be vulnerable to reductions in population size due to habitat shifts

(Figure 4, 5). Thus, results from the niche model incorporated with the metapopulation model provide more nuanced and informed results than from niche models alone.

Fire influences *L. setiger* in a number of ways. The variability in fire return intervals is important; EMA was predicted to be more sensitive to non-optimal fire return intervals when fires returned at an exact interval (Figure 2, 3). Though models predict slight declines in EMA with longer fire intervals, extirpation risk is only increased for shortened intervals (Figure 1.3), indicating that the subpopulations are not vulnerable to long fire intervals. This decline occurs because the population inevitably declines, albeit at slow rates, due to low background mortality as plants age in the absence of fire.

Fire extent is also important. It has previously been shown that spatial and temporal decoupling of fires can be beneficial to another obligate seeder, *Ceanothus greggii* (Regan *et al.,* 2010). This appears to be true for *Leucopogon setiger* as well. Decoupling of fires across a landscape was predicted to reduce vulnerability to reduced fire return intervals; correlated fires across the landscape lowered EMAs dramatically. Thus, conservation strategies which decrease average fire size to produce a heterogeneous mosaic of different aged patches across a landscape might have a beneficial effect on the persistence of *L. setiger*, though there may be a limit to the benefits (Parr & Andersen, 2006), depending on how fire size interacts with dispersal, seedling predation, and recruitment (Bradstock *et al.,* 1996; Regan *et al.,* 2003; Keith, 2012). A lack of data on these interactions in *L. setiger* precluded their inclusion in the model. Fire mosaics may have an additional benefit of increasing fitness; given that obligate seeders tend to create even-aged cohorts (Keeley, 1977), all germinants of a particular patch are selected under the same climatic conditions. If this occurs over very large patches, it potentially increases the chance of maladaptation, particularly under climate change when weather conditions may be changing. When determining management priorities for fire obligate species, it is essential to consider both habitat shifts and fire regimes. However, the primary focus should be on avoiding frequent fires relative to the timing of critical life history events in the species' life cycle.

There are a number of uncertainties involved with a modelling endeavour such as that undertaken here, and thus care should be taken in applying results. First, the modelling process itself highlighted gaps in knowledge, specifically a lack of information about vital rates across geography and through time. While data for the early years of development was plentiful, information on the species at later ages (10-15 years) was sparse, and beyond 15 years information was primarily derived through interpolation. Thus, the predictions incorporating long (over 15 year) fire return intervals are much less certain than those for shorter intervals. The model was robust to uncertainties in adult fecundity, dispersal, and fire refugia, indicating that an increased understanding of adult survival is the most important area for further research. Second, the habitat suitability model assumes equilibrium with the current climate, ignores biotic interactions, and is limited by the accuracy of the climate projections. Third, these types of models assume the influence of climate change will impact a species through changes in habitat suitability, which in turn affect vital rates through density dependent impacts. It is likely that climate change could also have direct effects on demographic rates.

Increased CO_2 could alter growth rate and thus affect maturity, survival, and fecundity. Additionally, plasticity and adaptation may occur and affect the species responses to climate change and fire (Jump & Penuelas, 2005; Keith, 2012). Thus, changing climatic conditions may affect fecundities, germination, or survival rates, or select for more heat or drought tolerance. The model assumed that life history rates were constant under altered fire intervals, yet the results suggest that a five year fire interval was more sensitive to changes in life history parameters than other fire return intervals. This raises questions as to whether frequent fires could select for individuals with earlier maturation, thus offsetting the impact of increased fire frequency. Environmental stochasticity, phenotypic plasticity, and genetic variability may cause greater variability in patterns of survivorship during and after fire (Keith, 2012), allowing for selection to occur. The sensitivity analyses addressed some of these limitations by incorporating small changes in the demographic parameters. While the model is sensitive to changes in germination rate, changes in fecundities had minimal impact, indicating that small changes in fecundity due to increased CO_2 or altered fire regime are unlikely to significantly alter the projections for this species. However, a more detailed investigation of larger changes to these factors, and whether selection could occur at a pace commensurate with climate change or mitigate the species response to shortened fire return intervals might prove insightful.

Despite the uncertainties involved in using spatially dynamic life history models to represent this system, it is a valuable extension which allows a richer and more relevant set of conservation questions to be addressed than with species distribution modelling alone. Incorporating life history parameters and demographic processes into the models allows insights into which factors are most relevant for species responses to stressors. Without a spatially dynamic life history model structure, a projected habitat suitability model would be unable to incorporate the effects of fire regimes on population dynamics. Fire is known to be a crucial process influencing the population dynamics of *L. setiger*, as well as other obligate seeders that have previously been modeled, and this study predicts that frequent fire remains the most serious threat even under future climate change scenarios.

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Chapter 2- The role of demography, intra-species variation, and species distribution models in species' projections under climate change

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Abstract

Organisms are projected to shift their distribution ranges under climate change. The typical way to assess range shifts is by species distribution models (SDMs), which predict species' responses to climate based solely on projected climatic suitability. However, life history traits can impact species' responses to shifting habitat suitability. Additionally, it remains unclear if differences in vital rates across populations within a species can offset or exacerbate the effects of predicted changes in climatic suitability on population viability. In order to obtain a fuller understanding of the response of one species to projected climatic changes, we coupled demographic processes with predicted changes in suitable habitat for the monocarpic thistle *Carlina vulgaris* across northern Europe. We first developed a life history model with species-specific average fecundity and survival rates and linked it to a SDM that predicted changes in habitat suitability through time with changes in climatic variables. We then varied the demographic parameters based upon observed vital rates of local populations from a translocation experiment. Despite the fact that the SDM alone predicted *C. vulgaris* to be a climate "winner" overall, coupling it with a population model incorporating demography at smaller scales resulted in projections of declining populations throughout much of its projected range due to limited dispersal and declining habitat suitability in currently occupied patches. Additionally, results show that altered fecundity and survival rates can reverse projected population trends when compared with trends based on changes in habitat suitability alone.

Introduction

Organisms may respond to climate change in a number of ways including persistence, migration, decline or extinction (Hughes 2000; Davis *et al.* 2005). Increasing understanding of species' responses to climate change can assist in conserving biodiversity as it provides information on the species vulnerable to climate changes and the management strategies that are likely to succeed. Species distribution models (SDMs) have been an influential tool to predict species' responses to climate change as they project distributional changes of species' ranges under various climate scenarios (Guisan & Thuiller 2005; Thuiller *et al.* 2005; Elith & Leathwick 2009; Franklin 2009, Dormann *et al.* 2012). They have been used to ask a number of predictive questions about distributional constraints, and are valuable tools to generate hypotheses (Dormann *et al.* 2012). However, they have a number of limitations, including a failure to incorporate demography (Keith *et al.* 2008; Lavergne *et al.* 2010) and assumptions that a species will respond similarly to climate change across its entire range (Pearson & Dawson 2003; Sinclair *et al.* 2010). Additionally, SDMs typically assume that climate is the only global change acting on a species, while in reality species' responses to other changes might overshadow the impacts of shifting habitat, and life history traits have a strong influence on the magnitude of these impacts (Regan *et al.* 2012; Swab *et al.* 2012). Recent studies integrating life history traits (Keith *et al.* 2008; Fordham *et al.* 2012; Dullinger *et al.* 2012), demography and physiology (Fordham *et al.* 2013a), or intra-specific variability (Morin *et al.* 2008; Bennie *et al.* 2010; Wang *et al.* 2010; Garzón *et al.* 2011, Fordham *et al.* 2013b) with SDMs have shown that increasing the complexity of models can alter predicted responses to climate change, and that populations may react differently to climatic changes in different parts of their range.

There is strong evidence that plant species may have considerable differences in vital rates across populations and have evolved ecotypes in response to environmental variation across broader gradients or even at small scales (Clausen *et al.* 1948, Jain & Bradshaw 1966, Waser & Price 1985, Schmitt & Gamble 1990, Galen *et al.* 1991, Kindell *et al.* 1996; Nagy & Rice 1997). Translocation experiments have shown that offspring fitness may vary among sites (Schmitt & Gable 1990, Galen *et al.* 1991, Kindell *et al.* 1996; Nagy & Rice 1997) and that populations within a species may respond differently to climate. Etterson (2007) used information from translocation experiments as a proxy for the temporal trend of *Chamaecrista fasciculata* (Fabaceae) traits in response to changing climate, and thus projected evolutionary trajectories which suggest that the rate of evolutionary response would be slower than the predicted rate of climate change. Garzón *et al.* (2011) predicted the effect of local adaptation on two *Pinus* species' responses to climate change by incorporating translocation data on survivorship into SDMs. They concluded that SDM results were significantly altered by this information. Thus, there is evidence that integrating demographic information from translocation experiments and spatial information from SDMs can provide a more in-depth evaluation of the response of species to climate change. Demographic response functions have been used to link variation in environment to variation of demographic rates (Schurr *et al.* 2012). However, few studies have incorporated demographic variability into models that predict the vulnerability of species to future climate changes. In this study, we use the observed variation in fecundity and survival across a broad geographical expanse (much of western Europe) to test potential effects of climate change on the demography and consequent population dynamics of a plant.

Spatially explicit metapopulation models can be used to make predictions of population viability under various scenarios (Akçakaya 2000). They have lately been used to incorporate life history dynamics into predictions of species' responses to shifting habitat (Keith *et al.* 2008; Regan *et al.* 2012; Swab *et al.* 2012). This increases the realism of predictions through integrating factors such as fecundity, life span and dispersal with shifting patch structures. Metapopulation models can also incorporate intra-specific variability of life history traits. These advantages make this model type useful for conservation purposes and predicting vulnerabilities of species to global change (Fordham *et al* 2013b). However, models typically assume the same average rates across all populations, thus ignoring differences between populations. Including empirically-based differences in average vital rates across populations adds a further level of realism to spatially-explicit population models that could shed a different light on the effects of global change on population persistence.

Information suitable for generating a spatially explicit metapopulation model was available from a reciprocal transplant experiment using *Carlina vulgaris* (Becker *et al.* 2006), making this species an ideal candidate for studying the effects of intra-specific variation on the response of a species to climate change. *C. vulgaris* is a monocarpic perennial which has been the subject of a number of studies (summarized in Becker 2005). From the translocation experiment, information was available on fecundity and survival at five different provenances, thus providing information on how vital rates changed when individuals (seeds) of each provenance were introduced to new locations. Becker *et al.* (2006) concluded that performance traits and individual fitness decreased with transplant distance, and attributed their findings to regional adaptation. We ask the following questions:

1. How would *Carlina vulgaris* respond to projected changes in habitat suitability due to climate change?
2. How does information on between-population variation in fecundity and survival affect predictions of the response of *Carlina vulgaris* to climate change?
3. Can intra-specific variation in demographic rates offset or exacerbate the effects of predicted changes in habitat suitability on population viability?

Materials and Methods

Study species

Carlina vulgaris L. (Asteraceae) is a monocarpic perennial forb inhabiting sand dunes, dry grasslands, and semi-natural pastures. It is distributed across Europe and western Asia (Meusel, Jäger & Weinert 1992). As a monocarpic perennial, individuals flower most commonly in the second year or later, and die after flowering (Klinkhamer *et al.* 1991). For *C. vulgaris*, there is a tradeoff between reproduction and survival; waiting another year to reproduce increases fecundity, but also increases the probability of death before reproduction (Metcalf *et al.* 2003). Flowering occurs between June and August, and achenes, hereafter called seeds, are dispersed during dry sunny days in late autumn, winter, or spring (Rose *et al.* 2002). Disturbance is important for seedling recruitment and, therefore, population dynamics (Löfgren *et al.* 2000). Grasslands with constant management regimes, such as grazing, have been observed to support stable *C. vulgaris* populations (Löfgren *et al.* 2000; Jakobsson & Eriksson 2005).

Current and future spatial distribution

To answer the question of how *Carlina vulgaris* might respond to projected changes in habitat suitability due to climate change, species distribution models were created for this species across the entire study area, western Europe. For the purpose of this study, habitat suitability refers to climatically suitable cells within areas of suitable land use, e.g. grasslands, pasture, and sand dunes. Current climate layers with a resolution of 10 arc-minutes were obtained from WorldClim (Hijmans *et al.* 2005). Future climate projections with a resolution of 10 arc-minutes were obtained from the International Center for Tropical Agriculture (Ramirez & Jarvis 2008) for A1B CCCMA-CGCM31 and A2 HadCM3 for intervals ranging from 2020 through 2080. The A1B scenario is of an integrated world with rapid economic growth, and thus high energy requirements balanced across a variety of fuel sources. The A2 scenario represents a more divided world with regionally oriented economic development. These two scenarios were chosen as moderate representatives from the range of future climate scenarios still considered plausible.

To evaluate the change in predicted suitable habitat for *Carlina vulgaris* under climate change, current habitat suitability was modeled using Maxent Version 3.3.3f (Phillips *et al.* 2006; Phillips & Dudik, 2008) in the Dismo package for R (Hijmans *et al.* 2011). Maxent has been shown to perform better than most other species distribution modeling methods for predicting suitable habitat with presence only data (Elith *et al.* 2006). Occurrence only data at 24,417 locations were obtained on 7/15/2011 from Global Biodiversity Information Facility (GBIF 2011). Data were cleaned to remove

Table 2.1. The climate factors used for the species distribution model for *Carlina vulgaris.* Factors are ordered by relative contribution to the Maxent model. Percent contribution refers to the increase in regularized gain due to a variable. Permutation importance is the drop in AUC (percentage) when a variable is removed.

Bioclim variable	**Percent contribution**	**Permutation importance**
Temperature seasonality (standard deviation)	50.3	63.2
Max temperature warmest month	18	12.3
Precipitation seasonality	16.9	8.5
Min temperature coldest month	8.9	10.4
Annual mean temperature	4.7	1.8
Mean temperature driest quarter	1.2	3.8

erroneous entries. To reduce geographic bias and match the scale of the climate data, occurrence locations were reduced to one record per 10 arc-minute grid cell, leaving 3,907 occurrences. Pseudo-absences of 1000 random points were drawn from the climate area bounded by land masses within -10 to 38° longitude and 39 to 66° latitude.

Nineteen bioclimatic (bioclim) factors were evaluated for their correlation at presence locations. These factors were evaluated for their suitability to predict the occurrence of *C. vulgaris*. If two factors had correlation coefficients >0.90, one was removed. This left 13 bioclim factors which were used to predict current suitable habitat. Non-influential factors (those with less than 1% contribution to modeled predictions) were removed from the predictive models, leaving six influential climate factors (Table 2.1) with an AUC of 0.822. In particular, sufficient soil moisture (explained by climate factor precipitation seasonality) is considered to be important for seed germination and thus for the distribution of *C. vulgaris (*Klinkhamer *et al.* 1996; Löfgren *et al.* 2000), and dry summers (Max temperature warmest month) should benefit the species (H.H. Bruun, pers. obs). Suitable habitat was projected using 10 degree grid cells for "current" (interpolations of observed data, representative of 1950-2000, Hijmans *et al.* 2005) and future conditions between years 2020 and 2080 using available climate projections (10 year intervals for climate scenario A1B and 30 year intervals for climate scenario A2). Linear interpolation between time periods and projection to the year 2100 created an annual time series of habitat suitability maps for each scenario. Two minimum thresholds of habitat suitability were compared, equal training sensitivity and specificity (ET; threshold = 0.492; Liu *et al.* 2005; Freeman & Moisen 2008) and minimum training presence (MT; threshold = 0.002; Swab *et al.* 2012). The equal training threshold is higher, thus decreasing the amount of available suitable habitat across the landscape. The habitat suitability results were linearly interpolated from 10 arc-minutes into 62500 m^2 sized cells using the ArcMap v. 10.0 interpolation function.

Available suitable habitat in each landscape was identified by using the Corine land-use map from the year 2000, with a resolution of 250m x 250m to only include cells designated as grassland, pasture, or sand dunes, all appropriate habitat types for *Carlina vulgaris.* This land use map was overlaid on the habitat suitability maps. For all cells outside the appropriate land-use types habitat suitability was reduced to zero, otherwise cells were left unchanged.

Table 2.2. Stage matrix with average values and standard deviations for transition between three life stages of *Carlina vulgaris* under averaged home conditions.

	Seeds	**Juveniles**	**Rosettes**
Seeds	0.3 ± 0.03	0	9.941 ± 8.483
Juveniles	0.0685 ± 0.0575	0	2.269 ± 1.937
Rosettes	0	0.632 ± 0.114	0.6109 ± 0.1392

Metapopulation model

A stochastic matrix model with seed, juveniles, and rosettes was developed for *Carlina vulgaris* (Table 2.2). See Supplementary material Appendix 1 for a detailed description of the parameters in the metapopulation model. Survival, fecundity, and transition values were primarily based on data from Becker *et al.* (2006), but amended with additional unpublished data. Fecundity was defined as the average number of offspring per individual in the reproductive stage alive at a given time step (Akçakaya 2005). Survival, germination, and transition values were supplemented with data from the published literature. Standard deviations were calculated from the variation in these data across years. Initial abundances and carrying capacity per cell were estimated using information from Jakobsson & Eriksson (2005). Stages were weighted based upon differences between the maximum observed seedling abundances (Rees *et al.* 2006) and the maximum observed for rosettes (Klinkhamer *et al.* 1996).

Translocation data and region

To study how variation in fecundity and survival could affect projections of the response of *C. vulgaris* to climate change, we used demographic data collected from a translocation experiment that was performed to investigate regional adaptation in

Carlina vulgaris (Becker 2005; Becker *et al.* 2006). In this experiment, individuals were reciprocally transplanted between Sweden, Germany, the Czech Republic, Luxembourg, and Switzerland, resulting in 25 combinations of origin (or home site) and growing site, including 'translocation' to the home site. Each of the 25 combinations are hereafter referred to as "translocation scenario". To evaluate whether variation in vital rates was due to variation in climate conditions, we compared vital rates with climate at the location grown in multiple ways: we regressed (a) average fecundity per translocation scenario with bioclim factors (Figure 2.1) (b) average population growth rate (finite rate of increase, or lambda) per translocation scenario versus habitat suitability value (Supporting Figure 2.1) (c) seed production per reproducing individual versus bioclim factor at the growing site (Supporting Figure 2.2) and (d) seed production per reproducing individuals, separated by origin versus bioclim factor at the growing site (Supporting Figure 2.3). Results from these comparisons showed that subpopulations of *Carlina vulgaris* responded differently to translocation to different sites (Supporting Figure 2.4), but that these differences were not correlated with habitat suitability. Becker (2005) and Becker *et al.* (2006) concluded that differences in lambda and survival rates for this species were due to regional adaptation since rosette size and other traits decreased with distance from the site of origin. However, our analysis of the translocation data indicates that, while there was variation in fecundities in response to translocation across sites, predicted fecundity (which incorporates rosette size and number of reproducing individuals) was only slightly correlated (r^2=0.44) with

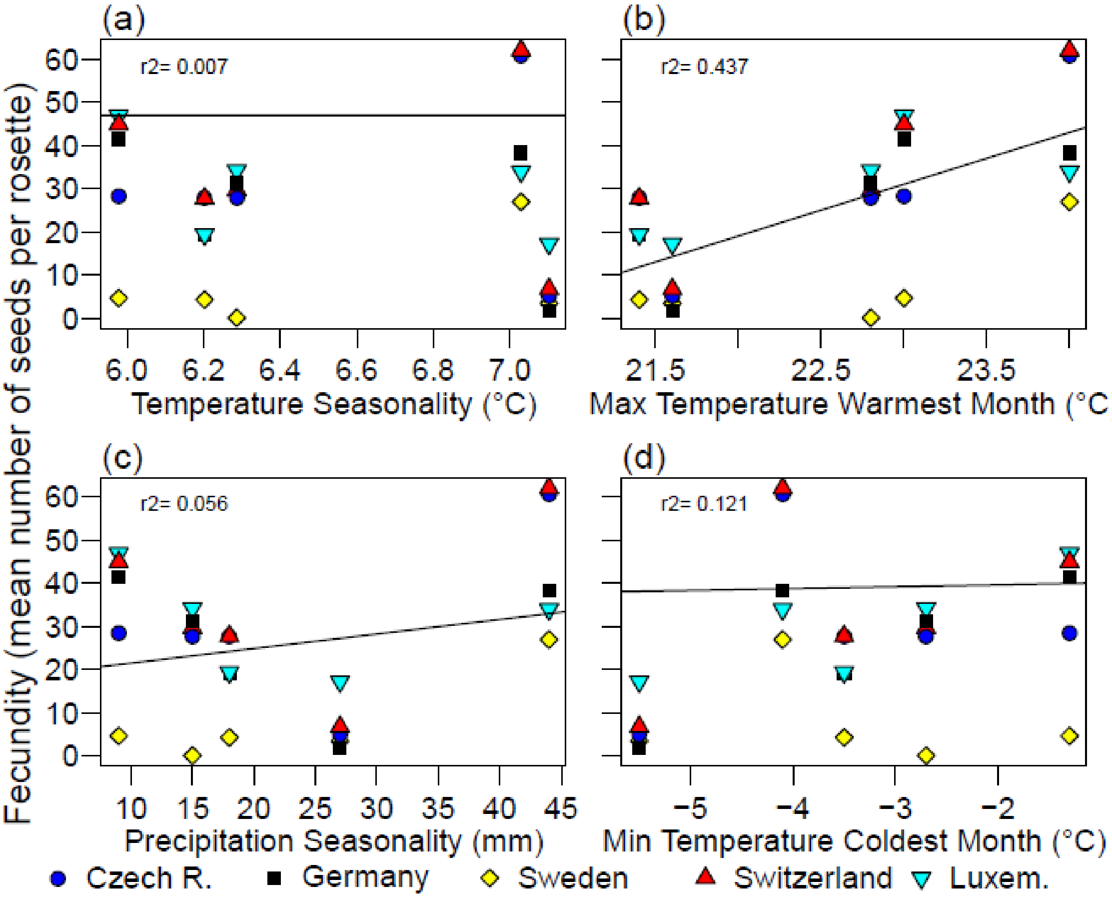


Figure 2.1. Predicted fecundity, *i.e.* mean number of seeds per rosette (average seed production per reproducing individual multiplied by proportion of rosettes flowering annually) per translocation scenario versus bioclim factors at the location grown. Colors and shapes indicate location of origin.

maximum temperature of the warmest month, and not correlated with the other three main climate factors predicted to be important for the species distribution (Figure 2.1). Another translocation experiment using populations within Sweden found no evidence of native superiority, but did find juvenile survival, a component not tested in Becker *et* *al.* (2005), to be 6% higher for natives at their home sites (Jakobsson and Dinnetz 2005). Though there seems to be no adaptation to climate, the translocation experiment data show that life history traits of *C. vulgaris* individuals can vary considerably when moved to different locations. Therefore, there is reason to expect variability of these traits under changing conditions.

Matrix model scenarios were developed to encompass the range of fecundities and survival rates observed in the translocation experiment. The ‘home’ scenario represented fecundity and survival values for *Carlina vulgaris* when individuals were planted in their country of origin, i.e. the location of provenance; metapopulation models would normally have vital rates based on this information alone. Initially, we created 25 different matrix models, one each for plants from each of the five regions when planted in each of the other regions. Given the range of intra-population variability and the lack of correlation of fecundity with climate variables, we tested the entire range of fecundity in all regions.

Results and growth rates associated with matrix models for many translocation scenarios were similar. Thus, we reduced the number of matrix models to fall into categories representative of the range of lambda values observed. Using observed clusters, or breaks, across the 25 lambda values of the matrices, we placed each translocation scenario into a category (Table 2.3). Though in most cases these differences in lambda were due to differences in seed production, for the F5 category differences in survival rates were the main driver instead. Standard deviations were calculated from the variation in individuals from each category across years (Table 2.3).

Table 2.3. Vital rates and their standard deviations for *Carlina vulgaris* rosettes for five fecundity categories. Seed and juvenile production numbers are the average amount of seeds or juveniles produced by any living individual per year, calculated by multiplying the proportion of individuals producing seeds or juveniles by the average number of seeds or juveniles produced by a flowering plant. Categories were delineated by expected minimum abundances.

Fecundity category	**Seed Production**	**Juvenile Production**	**Adult Survival rate**	**Average lambda**
F1	1.17±1.46	0.27±0.33	0.590±0.004	0.88
F2	9.22±0.75	2.11±0.17	0.536±0.051	1.58
F3	11.32±3.69	2.59±0.84	0.566±0.049	1.72
F4	12.81±4.17	2.92±0.95	0.534±0.013	1.78
F5	11.34±4.52	2.59±1.03	0.645±0.147	1.76

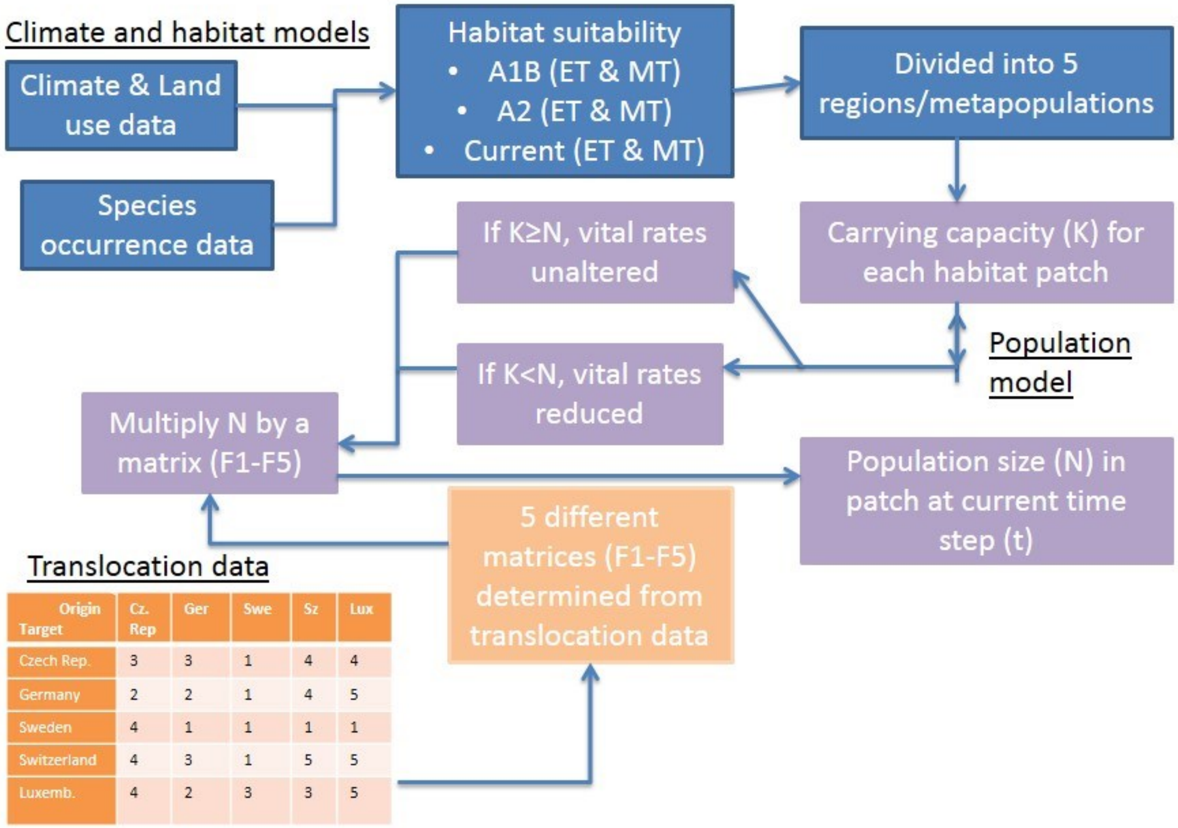
Averaging life history values into these five categories allows for a simpler analysis of the data than comparing 25 matrices, while still allowing for comparison between different values of fecundity and survival across their full range of variability.

The spatial distribution of *Carlina vulgaris* was divided into five separate ‘regions’, Germany, Switzerland, the Czech Republic, Sweden & Denmark, and Luxembourg & France, each representing an area of origin for the translocation study. Some regions included an adjacent sovereign nation in order to ensure comparable amounts of suitable habitat across the regions, e.g. Luxembourg & France. The current habitat suitability for each region was used to develop two patch structures (static ET and MT), thus linking the SDM results with the translocation results, thereby allowing us to run a model with each of the five matrices for each region. Within each region, we also developed dynamic patch structures based on changing climate scenarios: A1B ET, A1B MT, A2 ET, and A2 MT (described above). Changes in habitat suitability (due to climate) were integrated into matrix metapopulation models via a dynamic carrying capacity. As habitat suitability predictions changed through time, the carrying capacity (K) per patch was recalculated. If the abundances were greater than K, vital rates were reduced until abundances were at or below K, in a manner similar to that described by Keith *et al.* (2008) and Swab *et al.* (2012).

Simulations and scenarios

We used RAMAS GIS 5.0 (Akçakaya 2005) to link the metapopulation models with the time series of dynamic habitat suitability maps. Static patch structures, in which habitat suitability of patches remained constant through time, were used as a baseline for comparison. For each region, six habitat suitability scenarios were run with each of the five matrices, for a total of 30 different climate x matrix combinations for each region (Figure 2.2). This enabled us to investigate the impact of dynamic habitat suitability versus altered vital rates, and evaluate how the two changing simultaneously would affect projected population trends.

For each simulation, environmental and demographic stochasticity were incorporated through Monte Carlo simulations for 1500 replications over a 100 year time period. Vital rates were uncorrelated between patches except in a sensitivity analysis. Population viability was assessed using expected minimum abundance (EMA) as a proportion of initial abundance (IA) for consistent comparison across regions. EMA is



Origin Target	Cz. Rep	Ger	Swe	Sz	Lux
Czech Rep.	3	3	1	4	4
Germany	2	2	1	4	5
Sweden	4	1	1	1	1
Switzerland	4	3	1	5	5
Luxemb.	4	2	3	3	5

Figure 2.2. Coupling of habitat suitability model and stochastic population model (which integrates vital rates from translocation data). Each simulation runs for 100 years, with K varying for each patch in each year but other core elements (including matrix) remaining the same. In different simulations, matrices F1 to F5 are substituted. Numbers within the translocation data table indicate matrix category. Each of the 5 regions has a total of 30 simulations, i.e. all combinations of 6 habitat suitability scenarios and 5 different matrices. Modified from Keith *et al.* (2008).

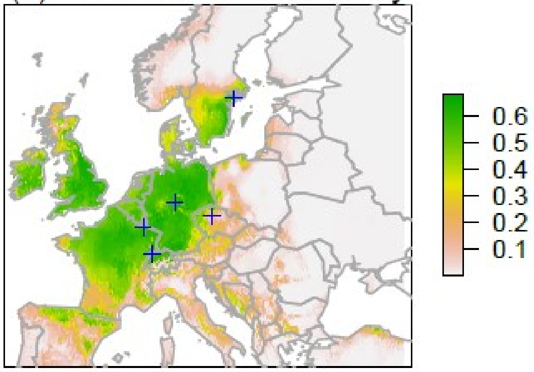
the average of the smallest population size occurring within the 100 year time period across each of the 1500 simulations (McCarthy & Thompson 2001). The initial 10 years of the simulation were excluded from risk calculations to allow stabilization of population dynamics. Sensitivity analyses were performed by separately perturbing initial abundances, germination, transition and survival rates, dispersal, and duration of scenario in order to determine how influential these were on species viability.

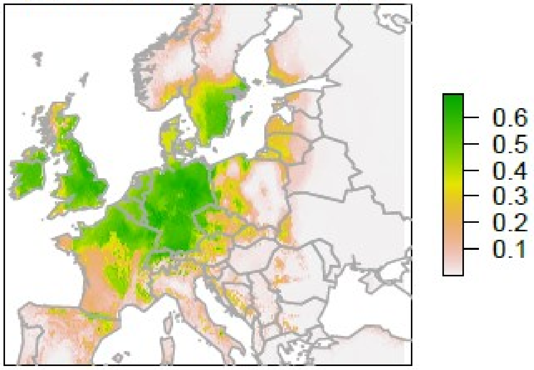
Results

Habitat suitability

Climate change predictions calculated with Species Distribution Models (SDMs) for *Carlina vulgaris* suggest that habitat suitability will shift northward, and might increase overall depending upon the climate scenario (Figure 2.3). However, most of the projected increases are in northern locations currently unsuitable and unoccupied by *C. vulgaris*. For three of the five translocation sites, habitat suitability is predicted to decrease, especially under the more dramatic A2 scenario (Supporting Figure 2.5). Additionally, most of the climate factors considered to be the most influential on the species' distribution (Temperature Seasonality, Max Temperature of the Warmest Month, Precipitation Seasonality) are predicted to change at these locations (Supporting Figure 2.6).

Results from habitat suitability maps show that threshold selection can have a large impact on projections of the amount of suitable habitat, as reflected in changes in carrying capacity (K) through time (Supporting Figure 2.5). Particularly for populations


(a) Current habitat suitability


(b) Habitat suitability 2050

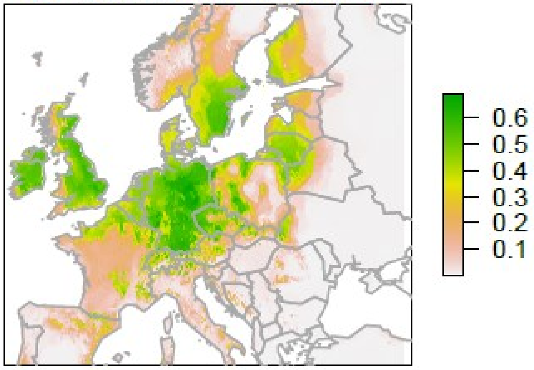

(c) Habitat suitability 2080

Figure 2.3. Predicted habitat suitability for *Carlina vulgaris* with (a) current climate (b) predicted climate in 2050 under scenario A1B (c) predicted climate in 2080 under scenario A1B. Greener colors indicate increasing suitability of habitat. Plus symbols indicate translocation sites.

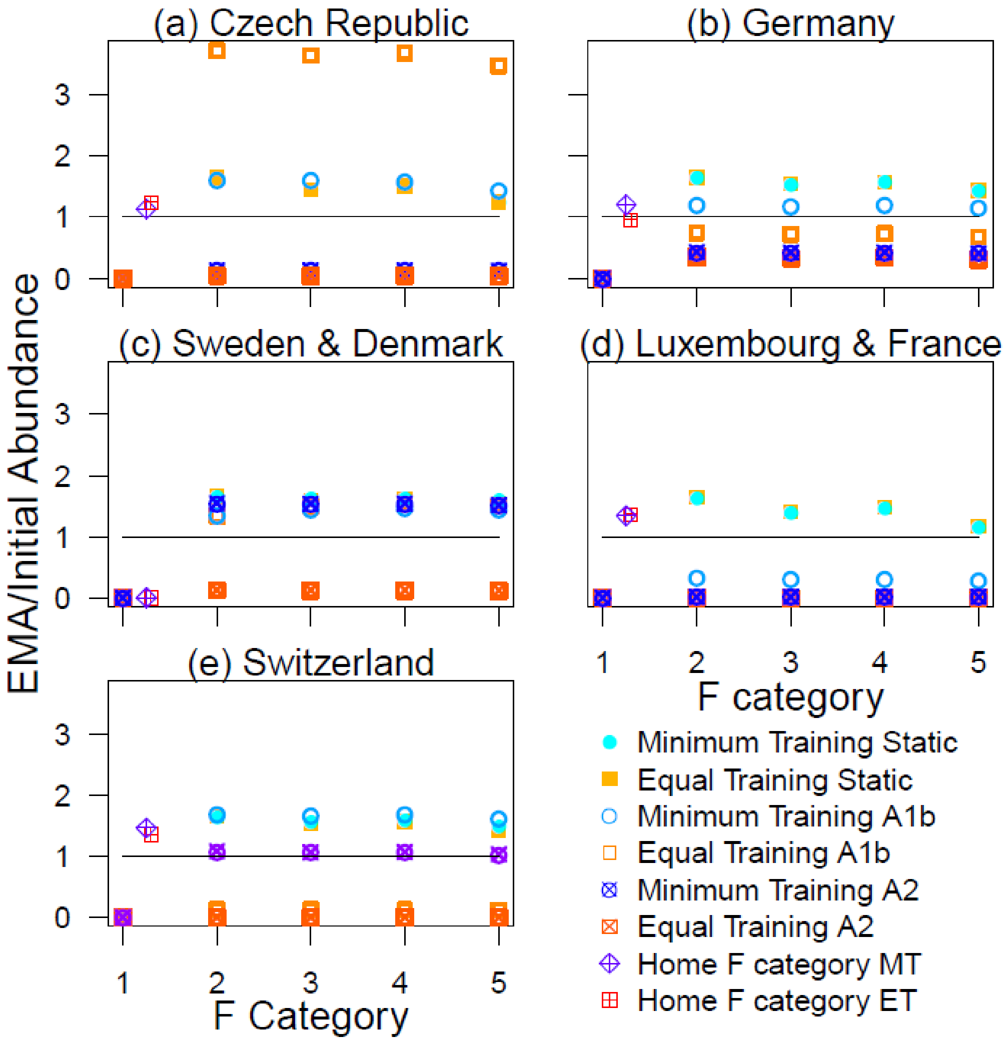


Figure 2.4. Expected minimum abundance (EMA)/Initial abundance for *Carlina vulgaris* metapopulations in (a) the Czech Republic, (b) Germany, (c) Sweden & Denmark, (d) Luxembourg & France, and (e) Switzerland for various threshold selections and under a static climate and changing climate using A1B and A2 predictions. The solid black line indicates the point at which EMA equals initial abundance.

in Sweden and Denmark, suitable initial habitat is significantly lower when the threshold for habitat suitability is based upon the higher Equal Training sensitivity and specificity value.

Intra-specific variability and habitat suitability

As fecundity (and therefore lambda) increases, from category F1 to F4, the expected minimum abundance **(EMA)** relative to initial abundance **(IA)** also increases (Figure 2.4). Populations with the lowest fecundities (F1) are predicted to become extirpated under all climate scenarios. However, fecundity increases above the F2 category do not increase the EMA/IA ratio, and for these categories variability seems to be the main driver of minimum population abundances (Figure 2.4). When comparing results from fecundity categories with the home fecundity (i.e. fecundity of plants when grown in their home location), EMAs can increase or decrease depending on the climate scenario. When both fecundity and habitat suitability decrease, EMAs decrease 100% of the time (Table 2.4). However, even when fecundity and HS both increase, EMA is lower 37.5% of the time. When one factor increases and the other decreases, results are mixed (Table 2.4).

The A2 climate scenario is generally bad for the species, the population model coupled with habitat suitability under the A2 climate scenario predicts declines to, or close to, extirpation for most regions except Sweden and Switzerland under the MT threshold, regardless of the fecundity (Figure 2.4). For the A1B scenario, when habitat declines are proportionally small, as predicted for Germany and Switzerland (Supporting Figure 2.5), or habitat increases are predicted to be in new areas unpopulated currently

Table 2.4. Percentage of scenarios with increases (+) or decreases (-) in EMA for *Carlina vulgaris* metapopulation model results given increases (+) or decreases (-) in fecundity and habitat suitability (HS). Increases or decreases in EMA are as compared with the EMA for a similar scenario, but with stable habitat and home fecundity values.

Fecundity HS	+	-
+	**62.5%+** **37.5%-**	**25%+** **75%-**
-	**57%+** **43%-**	**0%+** **100%-**

by *C. vulgaris,* and unreachable by dispersal as in Sweden, EMA/IA ratios are fairly unaffected by climate scenario or threshold for occupancy (Figure 2.4). However, when habitat declines are predicted to be dramatic, as for Luxembourg and France (Supporting Figure 2.5), we predict population declines under climate change, i.e. decreases in EMA and the proportion of EMA/IA (Figure 2.4). For the Czech Republic, where increases in habitat suitability are predicted in currently occupied patches, climate change is predicted to increase EMAs dramatically under the high threshold A1B scenario.

Sensitivity analysis of life history traits shows that the model is most sensitive to changes in scenario duration, production of juveniles by rosettes, and transition between juvenile and rosette stages (Supporting Table 2.1). It is less sensitive to changes in survival rates for the rosette stage, and insensitive to changes in other parameters such as seed production. Varying the initial abundance to K ratio only affects EMA when the IA is reduced to 10% of the baseline IA, and has a greater impact on models with lower fecundities (Supporting Table 2.1). Seed production for higher fecundity categories is so high that after 10 years there is minimal difference in abundances between scenarios with lower initial abundances and those with higher initial abundances, indicating that this species is limited more by available sites than by seed supply. Dispersal makes no difference for most scenarios, including all minimum threshold models. Five landscape configurations resulted in a positive influence of dispersal (Supporting Figure 2.7). Sweden & Denmark for A1B or A2 ET scenarios, and Switzerland under the A1 ET scenario showed the largest increases in EMA/IA, due to colonization of newly available patches when dispersal occurred. Correlation of environmental stochasticity in vital rates between patches did not affect results.

Discussion

Species Distribution Models (SDMs) project increases, declines, or shifts in suitable habitat for species under climate change (Franklin 2009). For *Carlina vulgaris*, SDMs project an increase in the overall amount of suitable habitat under climate change (Figure 2.3). When this is translated into changes in carrying capacity for specific locations, however, some locations are projected to experience large declines in abundances, while increases are projected for other locations (Supporting Figure 2.5). Incorporating variability of vital rates into predictions of the species´ response to climate change complicates matters even further. When life history variables such as fecundity or survival rates change, this sometimes results in increases in population viability even in the face of decreasing habitat suitability (Table 2.4). Overall, the results of this study indicate that for *Carlina vulgaris*, population models provide different insights into species' responses to climate change than SDMs alone. This is not surprising, because the fact that SDMS ignore life history traits, adaptation, and plasticity of individuals has often been considered a limitation of SDMs (Pearson and Dawson 2003, Dormann 2007, Keith *et al.* 2008, Elith and Leathwick 2009). It is necessary to integrate studies investigating potential plasticity and adaptation of species with SDMs, as in this paper, in order to fully understand the potential responses of species to climate change. Several main findings emerge from the research, discussed in more detail below:

1) Projected increases or decreases in habitat suitability do not always correspond with increases or decreases in expected minimum abundances.
2) Habitat suitability thresholding decisions can affect predictions of species viability.
3) *Carlina vulgaris* is sensitive to extreme declines in fecundity, but not to increases.

Projected increases or decreases in habitat suitability do not always correspond with increases or decreases in expected minimum abundances.

When projected habitat suitability increases, Expected Minimum Abundance (EMA) sometimes increases and sometimes decreases as compared with scenarios with stable habitat (Table 2.4, Figure 2.4). This is sometimes due to changes in fecundity, as the effects of decreased fecundity outweigh the effects of increases in habitat suitability, especially if the increases are in previously unoccupied patches. In some cases (for one, where both fecundity and habitat suitability increase), decreases in EMA are due to low habitat suitability at some point over the hundred year period. These lows are followed by increases in habitat suitability (often in new patches), but due to poor dispersal the population cannot capitalize on these increases. Most studies look at habitat suitability in 30 year intervals (Pearson and Dawson 2003). Results with low EMAs despite overall increases in habitat suitability indicate that simply looking at habitat suitability at a few time periods can be an oversimplification resulting in an underestimate of the vulnerability of the species to climate change. Additionally, increases in fecundity can compensate for decreases in habitat suitability—for example, in 57% of the model scenarios EMA increased when habitat suitability decreased and fecundity increased (Table 2.4). Since the results show that changes in habitat suitability and fecundity interact to affect the species' response to climate change, this indicates that adding complexity by coupling population models with SDMs can change direction and magnitude of predictions.

Habitat suitability thresholding decisions can affect predictions of species viability

Expected Minimum Abundance values were influenced by the choice of threshold for habitat suitability. However, while threshold was important to absolute numbers of projected population declines, it only occasionally affected results when using EMA/Initial Abundance (Figure 2.4). This suggests that habitat suitability threshold decisions can affect predictions of species viability if absolute values of population declines are of interest, whereas the ranking of scenarios (in this case regions and fecundity classes) appear to be robust to training thresholds.

Carlina vulgaris is sensitive to extreme declines in fecundity, but not to increases

In populations with high fecundity (fecundity categories F2-F5), the Expected Minimum Abundance for the focal species seemed to be driven primarily by the coefficient of variation than by average fecundity (Figure 2.4). The most likely explanation for this result is that, for *Carlina vulgaris*, seed production is very high and availability of microsites is the main driver of population size within viable patches. In the model, this was reflected by the fact that for the F2-F5 fecundity categories, average population abundances were at carrying capacity for most simulations. Thus, minimum abundances were driven by years of low seed production and thus lower minimum abundances. The results indicate that variable fecundity will minimally impact this species, typically only if fecundity is low enough that growth rates are below 1.

For the study species, changes in fecundity and survival rates were not correlated with changes in habitat suitability as predicted by SDMs or with changes in environmental variables predicted to be important by SDMs. This indicates that the two evaluations of species' responses to climate change—translocation experiments and SDMs—either are capturing different processes or that the SDMs are incorrect in their predictions. Species distribution models tend to take into account processes affecting species at large scales (Elith and Leathwick 2009), using the entire species distribution to predict changes in habitat suitability (but see Sork *et al.* 2009). Translocation studies generally evaluate life history trait responses to environmental properties at local scales (Bischoff *et al.* 2006, Becker *et al.* 2006), focusing on how individual plants will perform in novel climates within the species range (Becker *et al.* 2006). Thus while predictions of the SDMs provide insight into the effects of climate change on a species' distribution at the larger scale, translocation experiments capture responses of individuals at local scales where plants may respond more directly. This study integrates both scales, and results show that factors at both scales can influence results. Current difficulties in dealing with scale disparities when fitting SDMs (Elith and Leathwick 2009) can potentially be addressed using this methodology.

Because we did not find a strong correlation of fecundity with climate variables, the results of the translocation experiment coupled with the population models merely provide bounds on plausible population responses to novel climate and habitat shifts. However, given that the variability of life history characters influenced results, this study shows that translocation studies can increase understanding of species responses to climate change. If projected future climate conditions at some locations are similar to current climate at translocation sites, information from the translocations can be used to predict how populations will respond to climate change. Even if projected future climatic conditions are novel, information from the translocation experiment can still reveal when, or why, the species might not respond to climate change as a whole. However, given the amount of work required for these experiments, this would best be done for representatives of functional groups to determine which vital rates are most significant and/or most likely to be affected by climate change. Combining these experiments with models as done in this study can be an effective means of determining how and to what extent changes in vital rates will affect populations.

The limitations of species distribution models have been well studied in the literature (Pearson & Dawson 2003; Franklin 2009; Lavergne *et al.* 2010), and the limitations of combining SDMs with metapopulation models have also been addressed (Keith *et al.* 2008; Lawson *et al.* 2010; Regan *et al.* 2012; Swab *et al.* 2012). Adding new components to this modeling platform compounds uncertainty in results. Uncertainty in the model parameters is high given that the translocation experiment followed one cohort for three years in each of the translocation scenarios, and thus year-to-year environmental variability in vital rates is based on only two years for the larger life stages. If the annual environmental variation in survival rates was under-estimated due to the short duration of the experiment, survival rates could have a larger influence on the population viability overall. Fecundity and germination rate, however, are unlikely to affect the species unless they are low enough that population growth rates are below one. Furthermore, the translocation study did not capture viable population dynamics for plants from Sweden, whether at home or away, and therefore in simulations the Swedish-based matrices resulted in extirpation under all scenarios including static habitat suitability. Since there are currently *Carlina vulgaris* populations persisting in Sweden, it is clear that there is a missing factor. Dispersal is another limitation of the model. Since dispersal for this species is thought to be only tens of meters (Rees *et al.* 2006), baseline simulations did not include dispersal despite the fact that rare long distance dispersal is thought to be important to plant population dynamics (Nathan 2006). However, for this species, it is unlikely that new patches will be occupied within a short time and model results including dispersal reflected this.

Overall, the results were fairly robust to perturbations in the demographic parameters as demonstrated in the sensitivity analyses (Supporting Table 2.1), indicating that the general trends of the results are likely to be the same even if there are small changes in life history parameters.

Though the number of climate model scenarios was limited to two, the SDM provided a useful platform for comparing the response of the species to climate changes under various scenarios of decreasing, increasing, and shifting habitat suitability. Land use change will likely also occur with climate change, potentially further reducing habitat availability, resulting in overly optimistic projections of habitat (Thomas *et al.* 2004, Pressey *et al.* 2007). Overall, this study should be taken as an attempt to increase our understanding of species vulnerabilities to climate change rather than one predicting the outcome for *C. vulgaris*.

Species distribution models capture part of the response of species to climate change, but do not reflect all potential responses to climate change (Keith *et al.* 2008, Lawson *et al.* 2010, Swab *et al.* 2012). Coupling life history traits and spatially explicit population dynamics with SDMs allows us to see when changes in habitat suitability will result in changes in abundance across the landscape for the species — not all declines in habitat suitability necessarily lead to declines in populations because they may be accompanied by positive changes in a vital rate. However, if habitat suitability were to continue to decline, it is likely that the beneficial effects of increases in fecundity will ultimately be outweighed by the reduction in suitable habitat in the long run, provided suitable habitat predictions are a good reflection of carrying capacity and hence population survival. Translocation studies often attempt to capture differences between populations in life history traits (Kawecki and Ebert 2004). This study shows these differences may indeed impact species responses to climate. Changes in fecundity, because of plasticity or adaptation, might result in a tempering of the effect of climate change on population predictions if areas with predicted declines in habitat suitability experience increases in fecundity. This is an indication that while species distribution modeling is a valuable tool for predicting species' responses to climate change, integrating these with population models parameterized with information from translocation studies can provide a fuller picture of overall projected trends.

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Chapter 3- The impact of variability on population viability

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Abstract

Population viability is affected by a number of factors, including variability of vital rates, catastrophes, and fluctuations in habitat suitability. Species responses to these factors are rarely captured in field experiments, thus for many species little is known about the impact of variability on population viability. In this study, we focus on a number of sources of change- altered variability in vital rates, directional change in means of vital rates, changes in fire regimes, dispersal, and altered variability in carrying capacity. We used spatially explicit metapopulation models for two different species, a fire obligate seeder *Ceanothus greggii* and a resprouter *Quercus engelmanii* to explore this concept. These species responded differently to change- the obligate fire seeder was more sensitive to changes in fire regime, while the resprouter was more senitive to changes in vital rates, particularly directional changes in means of fecundity. For both species, increased variability in rates caused declines in minimum abundances, while directional changes in means caused similar directional changes in Expected Minimum Abundances (EMAs). Increased variability of carrying capacity of patches, which could

be caused by increasing climatic variability, caused declines in expected minimum abundances. Overall, results show that vulnerability to change depends on functional type, and that viability predictions not including variability could be underestimating species vulnerabilities to global changes.

Introduction

Variability is inherent in natural systems, and resides at all levels of biological organization from genes to individuals to populations, communities, and ecosystems. Population viability, for instance, is dependent upon population size, demographic and environmental stochasticity (Melbourne & Hastings 2008), and random catastrophes (Verboom *et al.* 2010). Climatic variability has been shown to affect fecundity of plants (Davison *et al.* 2010, Evans *et al.* 2010), plant population dynamics (Marrero-Gomez *et al.* 2007), and population growth rates (Buckley *et al.* 2010, Torang *et al.* 2010, Evju *et al.* 2011). Extremes in temperatures and precipitation can decrease survival rates (Saccone *et al.* 2009, Torang *et al.* 2010, Andrello *et al.* 2012) and fecundity (Herrera 1991, Andrello *et al.* 2012). But variation in the environment (hereafter termed environmental variability) can also lead to episodes of high recruitment (Higgins *et al.* 2000), promoting coexistence by benefiting some species over others (Levine and Rees 2004, Adler *et al.* 2006). Environmental variability can cause fluctuations in the means of vital rates (increased variability of these rates) or directional changes in means. Understanding how vital rate changes affect populations is fundamental to predicting species', and ultimately community, responses to environmental changes (Gotelli &

Ellison 2006, Morris *et al.* 2008, Buckley *et al.* 2010). The effect of environmental and demographic variability on population growth rates and persistence has been well studied (Boyce *et al.* 2006, Melbourne & Hastings 2008), yet the direct effects of abiotic or biotic factors on plant demography and population dynamics have been rarely examined (Dahlgren & Ehrlen 2009). Additionally, few studies compare and contrast the impact of environmental variability on population dynamics between species (Forcada *et al.* 2008, Morris *et al.* 2008, Dalgleish *et al.* 2010).

Historical evidence indicates that fluctuations in climate contribute to changes in vital rates. For example, tree ring studies show that species have responded historically to climate variability with changes in the rate of biomass growth (Jackson *et al.* 2009). Under climate change projections, environmental fluctuations are expected to increase (Katz and Brown 1992, Morris *et al.* 2006). Temperatures in particular are projected to have more extremes- particularly higher highs (Easterling *et al.* 2000, Schär *et al.* 2004, IPCC 2007, Wigley 2009). These extremes are predicted to drive species responses to climatic trends (Parmesan *et al.* 2000), affect species' fitness and population dynamics (Easterling *et al.* 2000), and select for species with wider physiological tolerances (Compton *et al.* 2007). Environmental fluctuations, if large enough, can lead to subpopulation extirpation or recolonization (Jackson *et al.* 2009).

Plants in particular are exposed to a wider range of climatic variability than mobile animals which can burrow or migrate to avoid climatic extremes (Hirzel & Le Lay 2008). While plants tend to be adapted to a certain amount of climatic variability, fecundity, survival rates, and germination rates vary about a mean from year to year, often in correlation with variation in climate (Evans *et al.* 2010). Even short term variations in vital rates can increase extinction risk (Chirakkal & Gerber 2010), and weak associations of environmental factors with vital rates can have long term effects on population growth (Dahlgren & Ehrlen 2009). Despite this fact, in studies of the effects of climate change on population persistence thus far, ecologists have paid more attention to the responses of plant populations to changes in climatic averages than changes in variability (Parmesan & Yohe 2003, Thomas *et al.* 2004, Morris *et al.* 2006), though some studies have considered the effect of altered climatic variability (Knapp *et al.* 2002, Adler *et al.* 2006, Dagleish *et al.* 2010). Ideally, ecologists would predict population response to climate change using knowledge of the relationship between vital rates and climate (Morris *et al.* 2006). However, a lack of data on this relationship for most species makes this difficult. For this study we instead analyze the impact of changes in vital rates, dispersal, and disturbance on species viability.

Simulating population dynamics through modeling is a central tool for evaluating species viability in dynamically changing environments (McKelvey 1996). Matrix population models are a common method of linking vital rates to metapopulation dynamics, and they have been widely used to quantify population dynamics across species with different functional types (Silvertown *et al.* 1993, 1996, Buckley *et al.* 2010). A variety of techniques exist to incorporate changes in vital rates into population growth rate estimates (Caswell 2000, Fieberg & Ellner 2001, Kaye & Pyke 2003, Tuljapurkar *et al.* 2003, Doak *et al.* 2005, Dahlgren & Ehrlen 2009). Variability, as an inherent feature of dynamic systems, is typically represented in population modeling simulations through probability distributions encompassing a range of plausible values (Regan *et al.* 2003). Since models for plants tend to be based on a few years of data across only a few subpopulations (Menges 2000, Crone *et al.* 2011), changes in future demographic rates are likely to be underestimated, leading to a potential overestimate in the viability of populations with models that ignore projections of increased climatic variability (Verboom *et al.* 2010).

Catastrophes are another source of variability in vital rates, however species' responses to catastrophes differ from their response to year-to-year environmental variation—catastrophes are defined as small probability events that cause large changes in vital rates beyond the scope of environmental variation. As with annual variation in abiotic and biotic factors, many species have adaptations to catastrophes. For instance, many plant functional types are characterized according to their life history responses to fire (Syphard & Franklin 2009). Some projections show resprouting shrubs to benefit from more frequent fires, increasing in abundances over other functional groups (Syphard *et al.* 2006), though for specific species, models project abundances to decrease given more frequent fires (Conlisk *et al.* 2012). Obligate fire seeding species are particularly at risk from shortened fire return intervals (Syphard *et al.* 2007) and in many cases more frequent fires are a more significant threat than range shifts due to climate change (Keith *et al.* 2008, Lawson *et al.* 2010, Swab *et al.* 2012, Syphard *et al.* 2013). Changes in precipitation and maximum temperatures, as well as anthropogenic changes such as increased ignitions or fire suppression, are all predicted to alter fire regimes, i.e. the intensity, frequency and size of fires (Whelan 1995). Overall, shortened fire return intervals are projected to negatively impact population persistence, negatively impact vital rates, and cause extinctions. Therefore, incorporating these into projections of fire adapted species responses to global changes is essential for accurate assessments of these species viabilities.

Given the likelihood of increased environmental variability under global change, a fuller understanding of the vulnerabilities of species with different life history traits will inform prioritization of species and actions for conservation management. In this study we look at two different types of changes in vital rates- changes in means and changes in the amount of variability. We analyze the impact of these changes in vital rates as well as alterations in dispersal, carrying capacity, or fire size and frequency on species viability in an extensive sensitivity analysis for two species with two different responses to fire. *Ceanothus greggii* is an obligate seeding shrub which is projected to be vulnerable to shortened fire return intervals (Regan *et al.* 2010, Syphard *et al.* 2011). *Quercus engelmenii* is a resprouting tree species which is projected to have a lesser response to altered fire regime (Conlisk *et al.* 2012). Our overall research questions were:

1) What source of change had the greatest impact on EMAs?
2) Were changes in means or changes in variability more important?
3) How might differences in responses across the plant functional types highlight how different life history traits could mitigate or exacerbate increased environmental variability?

We use spatially explicit metapopulation models for this task, as they include detailed life history characteristics such as fecundity, survival rates, germination rates, and response to fire events while allowing for manipulation of these characteristics and incorporation of global changes such as climate change, habitat fragmentation, or altered fire regimes. Comparison of results between simulations allows for analysis of the impact of various scenarios on population viability (Regan *et al.* 2010). Investigating the vulnerabilities of these species to various changes is a start to understanding vulnerabilities of other species in these functional types. In particular, we are interested in shedding light on whether one plant functional type (long-lived resprouters or long-lived obligate seeding shrubs) is more vulnerable to changes in vital rates (increased variability or directional changes) and which sources of change each functional type is most sensitive to. The contribution of survival rate and fecundity to population growth rates can differ by functional type (de Kroon *et al.* 2000, Buckley *et al.* 2010), and thus comparative analyses across different types of plant species can use life history theory to help predict which species will be most vulnerable to increased climatic variability (Dalgleish *et al.* 2010), and how they are vulnerable. As climate parameters increase in means **and** become more variable, which change will have the biggest effect on population viability?

Methods

Ceanothus greggii- *Ceanothus greggii* var perplexans (Trel.) Jepson is a fire obligate seeding evergreen shrub that occurs in the chaparral of the California Floristic

Province (Hickman 1993). The species requires fire to stimulate germination; in fire events, standing plants die and germination occurs, resulting in even-aged cohorts with rare germination between fires (Keeley 1992). A metapopulation model for this species was described in detail in Regan *et al.* (2010) and updated in Syphard *et al.* (2013). These studies modeled the species using RAMAS Metapop (Akçakaya & Root 2005). For the present study, the model described in Syphard *et al.* (2013) was used as the baseline model.

Quercus engelmanii- *Quercus engelmanii* Greene is a small tree native to California and Baja California. It typically occurs in chaparral, grasslands, or foothill woodlands. It is classified as vulnerable on the IUCN Red list (IUCN 2011). This species responds to fire by resprouting from canopy or basal root crowns (Conlisk *et al.* 2012). Germination from acorns is the primary means of reproduction for the species. A metapopulation model for this species created in RAMAS Metapop was described in detail in Conlisk *et al.* (2012). This model was used as the baseline model for this study.

Scenarios

For both species, sequential changes, or treatments, were made to the baseline models to understand how changes in vital rates and processes affect species viability and how this might change as some sources of variability increase with climate change. The parameters targeted for sensitivity analysis in this study were survival rates, germination rates, fecundities, fire frequency and spread, environmental correlation between populations, dispersal, and carrying capacity (Supplemental Table 3.1). These parameters were chosen because they are likely to be affected by climate change.

Survival rates (Young *et al.*1981), germination rates (Levine & Rees 2004), fecundity (Herrera 1991), and spread of fire (Flannigan *et al.* 2000) have already been shown to be altered by climatic variability for some species. Environmental correlation between populations may increase or decrease with climate change. Although dispersal is not likely to be directly altered by climate change, it is considered to be an important factor in facilitating species' distribution shifts (Thomas *et al.* 2004). Therefore, understanding the influence of dispersal on population persistence is a key component of understanding how species might respond to climate change. Changes in carrying capacity have been used as a proxy for changes in habitat suitability due to climate change for a number of metapopulation models (Larson *et al.* 2003, Keith *et al.* 2008, Anderson *et al.* 2009, Swab *et al.* 2012). Though many studies only focus on climate-induced changes in habitat suitability, all of the above factors could influence a species' response to climate change. Therefore, understanding species responses to variability and shifts in these characteristics is paramount in understanding species' responses to climate change.

In order to evaluate the importance of the above parameters to species' viability under climate change, we perturbed the mean values of these parameters and/or their coefficients of variation (CV) across scenarios and gauged the effect on expected minimum abundances (EMAs). The spatial arrangement of patches for our models was generated via species distribution models (SDMs) constructed with MaxEnt. The SDMs incorporated presence data, current climate layers, and environmental predictors such as soil and terrain variables (Conlisk *et al.* 2012, Syphard *et al.* 2013). Occupied patches were identified using maps of current distribution.

Survival rates

For this study, we changed the CVs for survival rates (described in Syphard *et al.* 2013 and Conlisk *et al. 2*012) to evaluate the impact of increased or decreased variability in these rates on the species viability. We investigated CVs between 0.001 and 0.75 (Supplemental Table 3.1). A previous sensitivity analysis by Conlisk *et al.* (2012) found *Quercus engelmanii* to be sensitive to changes in mean sapling and adult survival rates, but not to changes in other survival or transition variables. For *Ceanothus greggii,* a sensitivity analysis by Regan *et al.* (2010) found the species to be slightly sensitive to changes in mean survival rate of individuals up to 26 years of age. Since changes in the survival rates were analyzed for both species in sensitivity analyses in the previous studies, we did not include these in our study.

Germination rates

Ceanothus greggii- Baseline germination rate (GR) in the event of a fire was set to 1.8%, which includes first year seedling mortality, in keeping with the 2-year time step established for this model (Syphard *et al. 2*013). However, germination is uncertain and could be affected by climate change. Therefore, for this study we also changed the GR by 20% to 300% of the baseline value at specified intervals (Supplemental Table 3.1).

Quercus engelmanii- The annual germination rate (GR) for *Q. engelmanii* was set at 1.6% with a standard deviation of 2.6%. This included seed predation and first year seedling mortality, since, like *C. greggii*, the stages in the matrix model were based on a 2-year time step (Conlisk *et al. 2*012). For this study, separate scenarios changed the germination rate by 20% to 300% of the baseline value at specified intervals (Supplemental Table 3.1).

Fecundity

The average values and coefficients of variation of fecundity (described in Syphard *et al.* 2013 and Conlisk *et al. 2*012) were decreased by 50% and increased by 150% to 350% of the baseline values at 50% intervals for both species. The primary objectives of this were to determine whether increased fecundity could mitigate the impact of more frequent fire intervals and to ascertain whether population viability (as measured via EMA) is sensitive to variability in fecundity. Three different types of scenarios were implemented: a) average fecundity only was increased, b) both the average and the standard deviation were increased, and c) only the standard deviation of the fecundity was increased. This enabled us to separate the impacts of changes in average fecundity from changes in variation in fecundity.

Fire

Hazard functions based on Wiebull distributions specified the probability of an unplanned fire under a range of fire regimes; these probabilities were identical to those used in Syphard *et al.* (2013). We examined the impacts of eight different average fire return intervals (10, 20, 30, 40, 50, 60, 70, and 80 years) on species viability. We also investigated a variety of fire spread scenarios. Baseline scenarios assumed fires could not spread between distinct patches. Other scenarios compared different amounts of fire spread scenarios. For these scenarios, fire spread was modeled using the following dispersal equation:

$$\mathrm{M}_{ij} = \mathrm{a}\exp\left(-\mathrm{D}_{ij}{}^{\frac{c}{b}}\right), \qquad \text{if } \mathrm{D}_{ij} < \mathrm{D}_{max} \text{ or } \mathrm{D}_{ij} = \mathrm{D}_{max}$$

where M_{ij} is the probability of fire spread from populations i to j, D_{ij} is the distance between the two populations, b=0.88, c=0.34, D_{max}=600, and a varied by fire spread scenario between 0.05, 0.1, 0.25, and 1. For comparison, we also included scenarios with regional fires (fires occur in all patches simultaneously) and with exact fire intervals (for each patch a fire occurs exactly once every x years, as opposed to using a random fire occurrence averaging an x-year fire return interval).

Dispersal

Ceanothus greggii: *C. greggii* has been shown to have highly restricted dispersal with rare recolonization of extirpated patches (Holl *et al.* 2000). Therefore, inter-patch seed dispersal was not included in the baseline models (Regan *et al.* 2010; Syphard *et al.* 2013). However, given that dispersal might be a key component of population persistence under shifting ranges in response to climate change, and long distance dispersal events can be difficult to document, we compared scenarios with various rates of dispersal, in part to gauge the amount of dispersal necessary to establish viable populations. Dispersal was modeled using the following equation (identical to the fire dispersal equation, above):

$$\mathrm{M}_{ij} = \mathrm{a}\exp\left(-\mathrm{D}_{ij}{}^{\frac{c}{b}}\right), \qquad \text{if } \mathrm{D}_{ij} < \mathrm{D}_{max} \text{ or } \mathrm{D}_{ij} = \mathrm{D}_{max}$$

where M_{ij} is the dispersal rate between populations i and j, D_{ij} is the distance between the two populations, b=0.88, c=0.34, D_{max}=600, and a varied by dispersal scenario between 0.05, 0.1, and 0.25 (Supplemental Table 3.1). Total dispersal from a patch averaged 0.4%, 0.8%, and 2.5% for the three *a* scenarios, respectively; dispersal amounts varied by patch depending on its distance from other patches. These parameters were chosen to be identical to those in the fire spread equation because they exhibit a curved dispersal function that allows for larger amounts of short distance dispersal and minimal long distance dispersal (Swab *et al. 2*012), and the varied *a* values present a variety of scenarios. These scenarios allow us to determine if a small level of seed dispersal might mitigate the impacts of variability for this species.

Quercus engelmanii: Dispersal of acorns between patches is primarily attributed to birds, in particular jays (Gomez 2003, Conlisk *et al. 2*012). In baseline models, dispersal was incorporated using the above equation, where a=0.01, b=4, c=1, and D_{max}=10. This resulted in a dispersal rate averaging 6.9% of seeds from each patch. Although this dispersal rate is realistic, we wanted to determine if higher amounts of dispersal increase species viability. Therefore, different dispersal scenarios were evaluated by increasing dispersal rates using the above equation and b=0.88, c=0.34, and D_{max}=10. The parameter *a* was varied across the values 0.05, 0.1, and 0.25 (Supplemental Table 3.1). Total dispersal from a patch averaged 17.8%, 35.6%, and 76.8% for these three *a* scenarios, respectively. Maximum dispersal was limited by patch size; less seeds dispersed to smaller patches.

Carrying capacity variation

We set the annual coefficient of variation of *K* to 10%, 25%, 50%, and 75% of the average carrying capacity for each patch (Supplemental Table 3.1). Carrying capacity reflected the maximum density of plants in the largest-sized/older stages, and were specific to a particular patch (sum of habitat suitability for all cells in the patch multiplied by the carrying capacity for one cell). Carrying capacity was scaled for younger/smaller sized stages with weights based on the sizes of these stages relative to the largest-sized stage (see Conlisk *et al.* 2012 and Syphard *et al.* 2013 for details). Conlisk *et al.* (2012) and Syphard *et al.* (2013) allowed carrying capacity to change deterministically in response to climate projections. We use the same patches as in the initial timestep for those studies, but vary *K* around a stable mean. Allowing *K* to fluctuate annually provides one mechanism for studying how the population persistence might be affected by variation in climate, as it pertains to habitat suitability.

Correlation of environmental stochasticity

For *Ceanothus greggii,* Regan *et al.* (2010) found no impact of spatial correlation in variability of environmental stochasticity in fecundities and survival rates (environmental correlation) on the viability of the species. No similar analyses were performed for *Q. engelmanii.* However, there is the potential for spatial environmental correlation of vital rates, in concert with variability in carrying capacity or dispersal, to have cumulative effects on population persistence. Climate change could potentially impact species on micro or macro scales (Adger *et al.* 2005), and therefore it is worthwhile to determine the effect of aligned changes in variability. We ran a number of scenarios with 100%, 50%, and 25% spatial correlation of environmental stochasticity (Supplemental Table 3.1). These percentages represent the similarity of environmental fluctuations of fecundity, survival rates, and carrying capacity between patches within a year. For all scenarios, environmental stochasticity was positively correlated to the same degree across all patches regardless of distance. Different scenarios evaluated the impact of spatial correlation in environmental stochasticity alone, and correlated with with variation in dispersal and carrying capacity (Supplemental Table 3.1).

Simulations and scenarios

We used RAMAS GIS 5.0 (Akçakaya 2005) to link the metapopulation models with the habitat suitability maps for current species distribution. For each simulation, environmental and demographic stochasticity were incorporated through Monte Carlo simulations for 1500 replications over a 100 year time period. Vital rates were uncorrelated between patches except when noted. Population viability was assessed using expected minimum abundance (EMA) as a proportion of initial abundance (IA) for consistent comparison across regions. EMA is the average of the smallest population size occurring within the 100 year time period across each of the 1500 simulations (McCarthy & Thompson 2001).

Results:

Survival, Germination, and Fecundity

Ceanothus greggii: Increasing variability in survival rates results in decreased in EMA (Figure 3.1a, Supplemental Table 3.1). Interestingly, the EMA reduced substantially (to between 48 and 75% of baseline values) when the coefficient of variation for survival rates increased by 0.5%. Further decreases in EMA as the CV increased did not go beyond 36%. Changes in EMA as a function of germination rate were small until post-fire germination rate decreased to around 40% of the baseline rate (Figure 3.1c). This resulted in decreased EMA; this effect was greater for optimal fire return intervals (FRI) of 30 to 50 years, with EMAs decreasing to 20-38% of the baseline for the 10% germination rate, as compared with 44-53% for longer fire intervals, for example. Increases in germination rate did not impact EMA.

EMA increased as fecundity increased (Figure 3.2a), irrespective of whether the coefficient of variation (CV) in fecundity increases as well (Figure 3.2c); differences in EMA with and without increases in CV of fecundity alone are negligible, varying 96-106% for most scenarios (Figure 3.2e). Increases in EMA were larger for shorter fire return intervals with the largest range of EMAs (varying 113-121% from baseline) observed for 20 year fire return intervals and smaller differences (between 102 and 107%) for 70-80 year fire return intervals. Increased variability in fecundity (in the absence of a concomitant increase in average fecundity) resulted in a slight decrease in EMA for all average fire return intervals, with a slightly larger range of EMAs when FRIs were 20-40 years. Changes were similar for all fire return intervals except 10 year intervals, which was dominated by extinction.

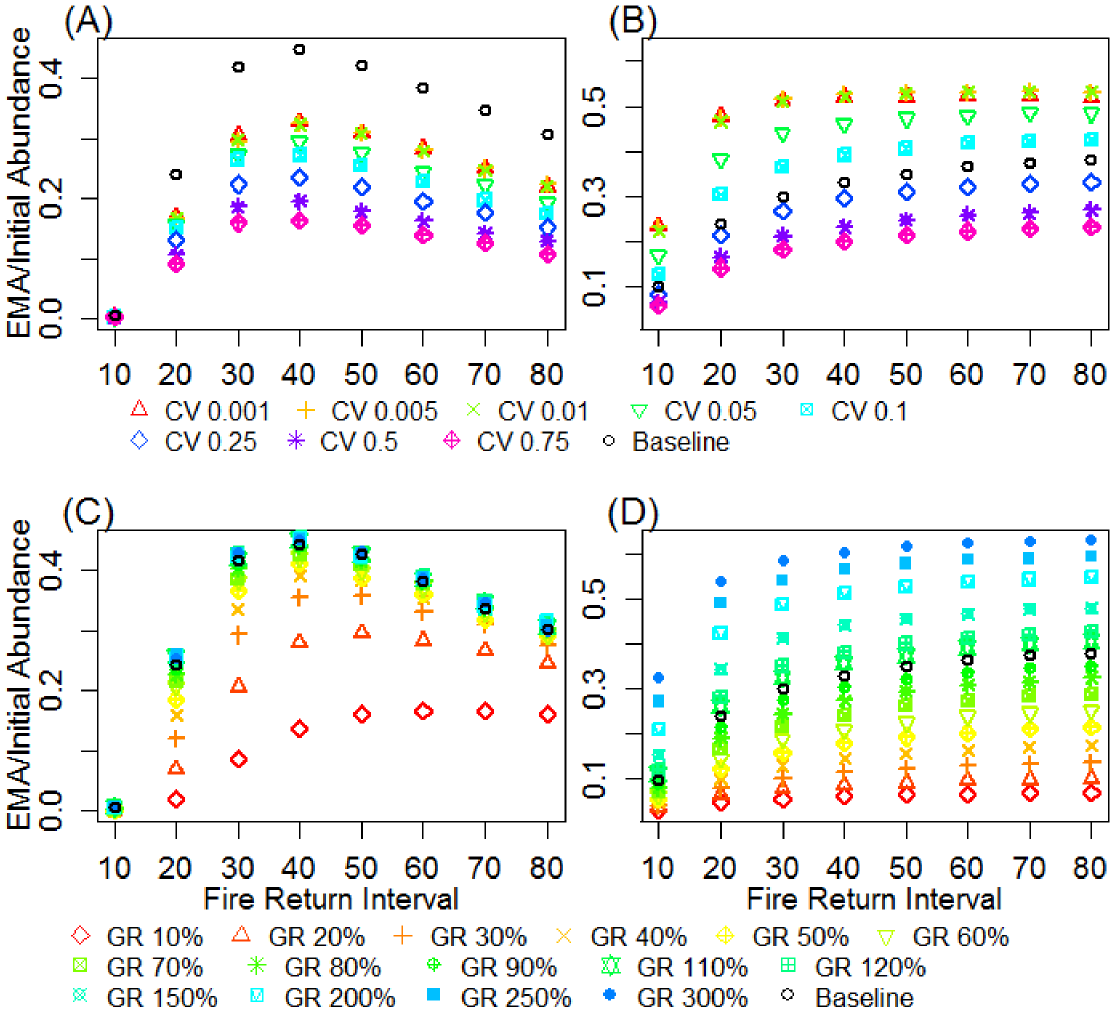

Figure 3.1 Expected minimum abundance (EMA)/Initial abundance for *Ceanothus greggi* (first column) and *Quercus engelmannii* (second column) scenarios for fire return intervals ranging from 10 to 80 years. Initial abundances is the number of individuals at the beginning of the scenarios. **A & B-** Varied coefficient of variation for survival rates. Treatment labels "CV #" refer to the set coefficient of variation, ranging from 0.001 to 0.75. **C & D-** Varied germination rate. Treatment labels "GR #" refer to the amount the germination rate is varied by in each simulation. This varies from 10% to 300% of the original value.

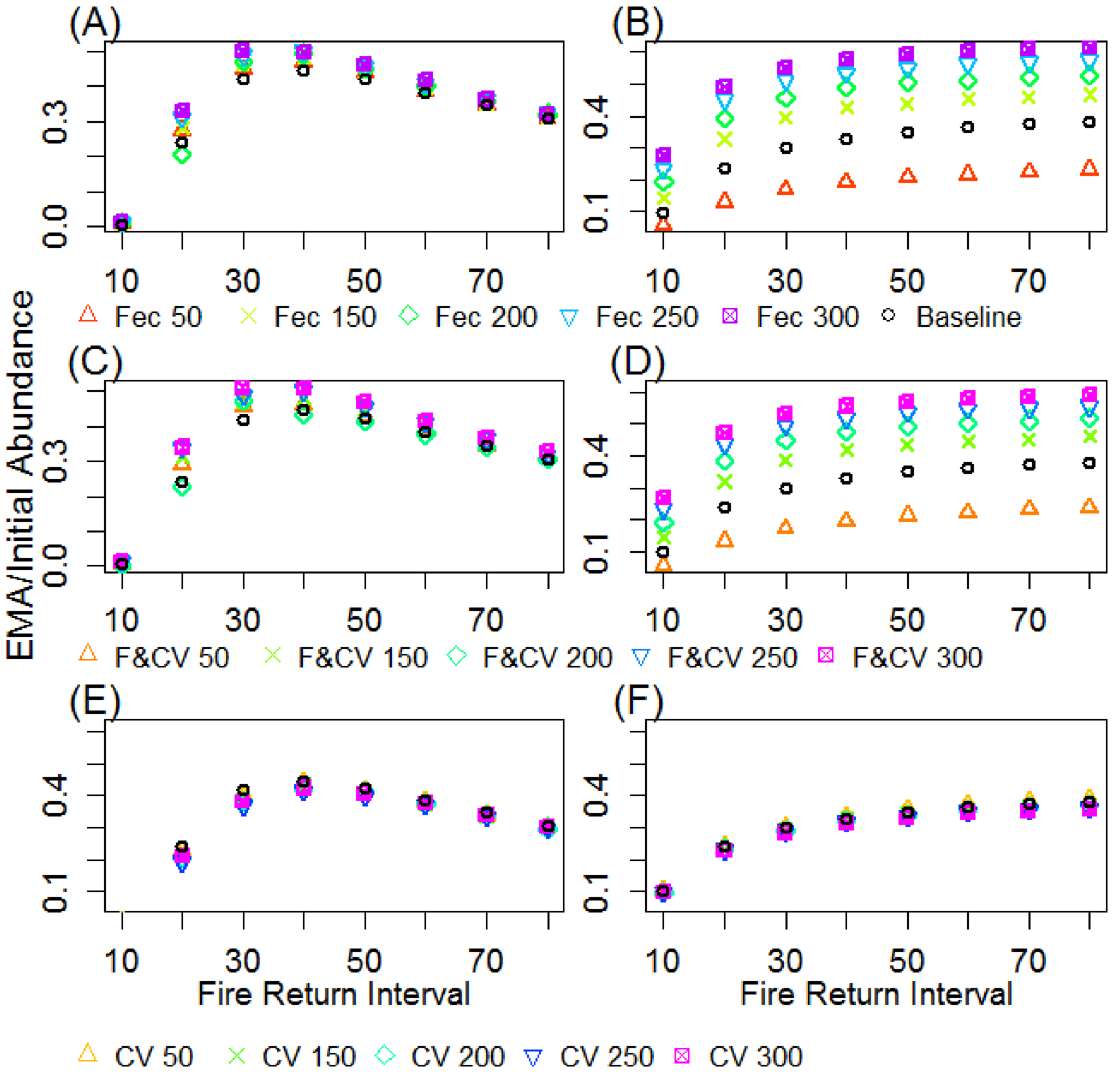

Figure 3.2 Expected minimum abundance (EMA)/Initial abundance for *Ceanothus greggii* (first column) and *Quercus engelmanii* (second column) scenarios for fire return intervals ranging from 10 to 80 years. **A & B**- Increased fecundity scenarios. **C& D**- Increased fecundity and annual variation in fecundity. **E & F**- Increased annual variation in fecundity. Treatment labels “Fec #”, “F&CV #”, and “CV #” refer to the percentage from baseline fecundity or the coefficient of variation was altered, 50% to 300%.

Quercus engelmanii: For *Quercus engelmanii*, lower CV's in survival rates (from baseline conditions) resulted in higher EMAs; as CV's increased the EMA decreased (Figure 3.1b). Changes in the germination rate resulted in substantial increases (165 to 327% for germination rates increasing by 300%) and decreases (17.9 to 28% for germination rates decreasing to 10% of the baseline) in EMAs following the direction of change in the average rate *(*Figure 3.1d). Fire return interval influenced the species response to altered germination rate; scenarios with 10 year FRIs were less negatively influenced by reductions in germination rate with a maximum of 29% of baseline as compared with 18% of baseline for most other intervals. Ten year FRIs were also more positively influenced by increases when compared with longer intervals (with a max of 328% increase in EMA as compared with 166-225% increases for the other FRIs).

Unlike *C. greggii*, changes in average fecundity for *Q. engelmannii* had dramatic effects on EMAs with EMA increasing to 162-281% or decreasing to 54-51%with increases or decreases in average fecundity, respectively (Figure 3.2b). Changes in the coefficient of variation in fecundity had negligible effects on EMAs (Figure 3.2d, 3.2f), EMAs were between 94-102% of baseline EMAs. The amount of change in EMA observed with changes in fecundity was similar for all fire return intervals.

Fire, Environmental Correlation

Ceanothus greggii: For all *C. greggii* scenarios, EMA was nearly zero for the 10 year fire return interval (FRI), irrespective of any changes in parameter values. Thus, the results reported here are limited to 20-80 year FRI. Results for all scenarios except exact fire intervals and the lowest germination rates had the same shape of curve in response to fire, with 10 year intervals resulting in extinction and optimal intervals between 30-50 years.

Expected minimum abundance (EMA) decreased (Figure 3.3a) as the spatial correlation of fires increased (i.e. as the spatial arrangement of fires transitioned from patchy spatially-independent fires to very large regional fires with high fire spread across patches). Exact, or uniform, fire return intervals resulted in higher EMAs for the 20-40 year FRIs than scenarios with stochastic fires (e.g. wildfires or unplanned fires). There was minimal (90-113%) difference in EMAs between scenarios with wildfires or exact fire intervals when intervals were longer than 40 years. Changes in correlation rates of environmental stochasticity of survival, fecundity, and *K* caused EMAs to vary only between 98-103% of baseline values (Supplemental Table 3.1).

Quercus engelmanii: Changes in fire interval affected *Q. engelmanii* similarly for all scenarios—longer FRIs resulted in higher EMAs. When fire was strongly spatially correlated (fire dispersion rates of 1.0 or 0.5) EMAs were lower than when fires were patchy (i.e. spatially independent or with dispersion rates of 0.25 or 0.1) (Figures 3b). Unlike *C. greggii,* exact, or uniform, fire return intervals made little (81-100% of baseline) difference to EMA compared with stochastic fire return intervals, for all average FRIs. Increasing correlation of environmental stochasticity of survival, fecundity and carrying capacity, had a larger affect on EMAs, with lower EMAs (to 65% of baseline) exhibited as spatial correlation of environmental stochasticity in demographic rates increased (Supplemental Table 1). Increasing spread of fire between).

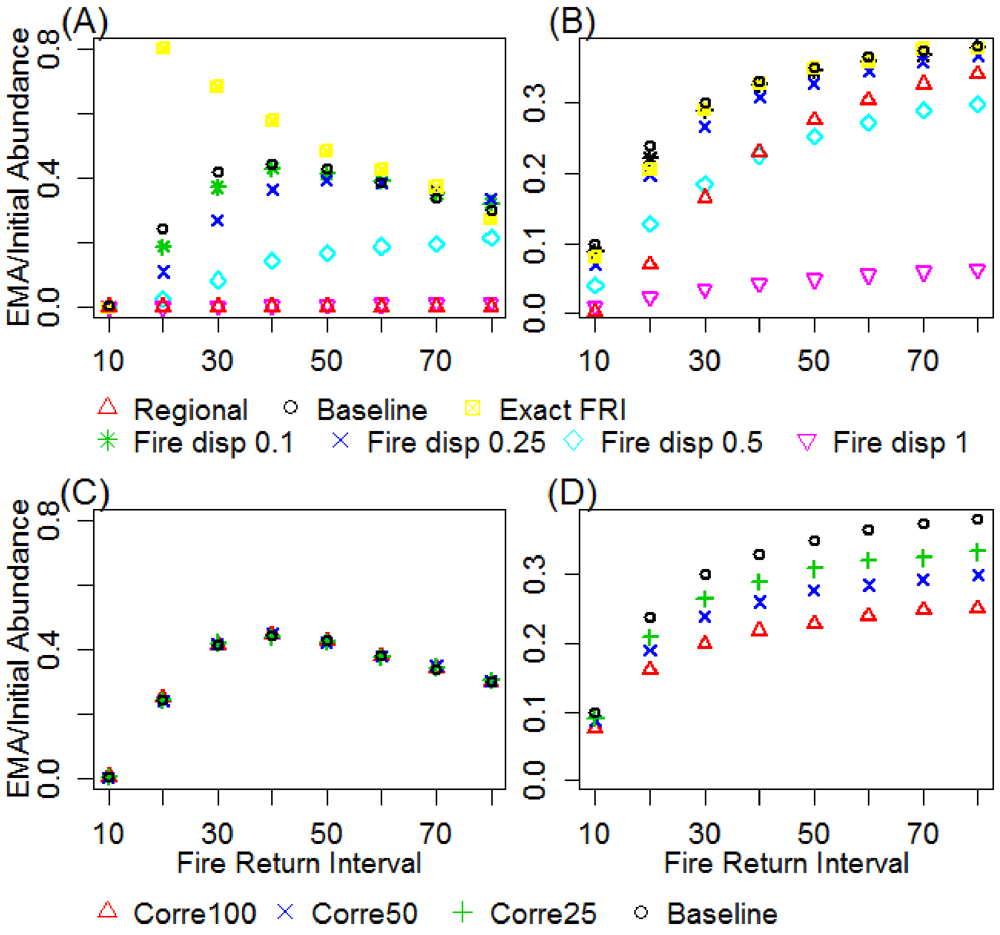

Figure 3.3 Expected minimum abundance (EMA)/Initial abundance for *Ceanothus greggii* (first column) and *Quercus engelmanii* (second column) scenarios for fire return intervals ranging from 10 to 80 years. **A & B**- Varied fire scenarios. Treatment labels "Fires disp #" refer to the a value from equation 1, determining the dispersal of fire between patches. A higher value means a larger spread of fire. **C & D**- Varied amounts of correlation of environmental stochasticity of fecundity, survival rates, and carrying capacity between patches. All patches have equal correlation within each scenario. Treatment labels "Corre #" refer to the amount of correlation between patches.

patches minimally impacted EMAs (to 71-97% of baseline) until spread was larger (Disp=0.5 or 1, Figure 3.3b

Dispersal, Environmental correlation, and varying carrying capacity

Ceanothus greggii: Correlation in environmental stochasticity of fecundity, survival rates, and carrying capacity had no effect (to 99-103% of baseline) on EMA (Figure 3.3c). Since the species is considered to have no long distance dispersal, we only included small amounts of dispersal in the dispersal scenarios. Increasing seed dispersal increased EMAs up to 131%, but most were only increased to 104-113% (Figure 3.4). This species benefitted more from dispersal when experiencing shorter FRIs (20-40 years, EMAs were 109-131% as compared with baseline) than longer intervals (EMAs were 104-113%). Spatial correlation in fecundity across patches did not affect these results (Supplemental Figure 3.1)

Annual variability in carrying capacity had a large impact on results (Figure 3.5a). Even including a 10% annual variation in carrying capacity resulted in declines to between 95-82% when compared with baseline EMA. 25% or higher variation resulted in EMAs of 64-72% of baseline EMAs. Spatial correlation in variability in carrying capacity (indicating synchronous fluctuations in K across patches) did not affect these results (Supplemental Figure 3.3). When carrying capacity was set with a ceiling density dependence function instead of a density dependence function where population size gradually decreased to *K* whenever *K* was exceeded, the impact of variability in carrying capacity was increased (Figure 3.5c), but correlated fluctuations in *K* still had no impact on results (Supplemental Figure 3.4).

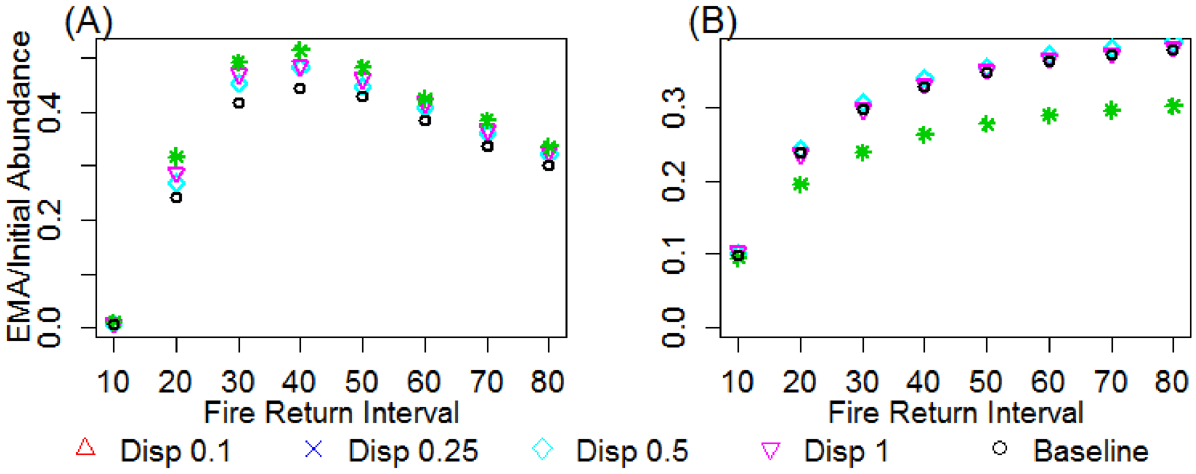

Figure 3.4 Expected minimum abundance (EMA)/Initial abundance for A) *Ceanothus greggii* and B) *Quercus engelmanii* scenarios for fire return intervals ranging from 10 to 80 years Treatment labels "Disp #" refer to the *a* value from the seed dispersal equation. A higher value means a larger amount of seed dispersal between populations. "Baseline" has a small amount of dispersal for *Quercus engelmanii*, and no dispersal for *Ceanothus greggii*.

Quercus engelmanii: Increasing correlation of environmental stochasticity lowered EMAs up to 65% of baseline EMAs (Figure 3.3d, Supplemental Table 3.1), and dispersal seemed to have little impact on this (Supplemental Figure 3.2). Dispersal is considered to be part of the life cycle for *Q. engelmanii,* and so was included in all models. However, for the dispersal scenarios the amount of dispersal was increased. Increasing dispersal appeared to have no impact on EMAs (with EMAs between 99-103% of baseline) until *a* was set to 0.25 in the equation governing dispersal rates, resulting in lower EMAs (79-96% of baseline EMAs, Figure 3.4). This impact increased with increasing fire return interval.

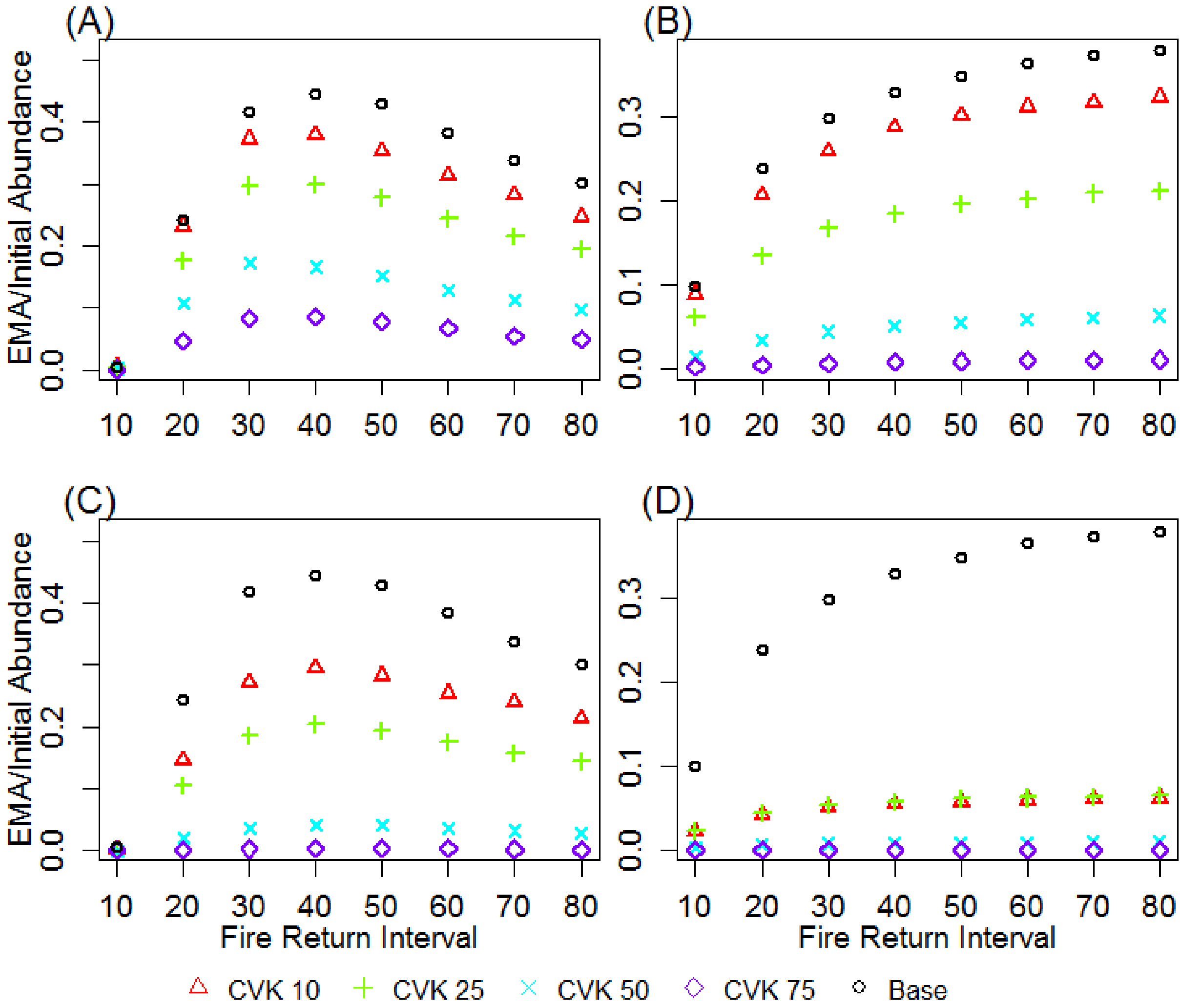

Figure 3.5 Expected minimum abundance (EMA)/Initial abundance for *Ceanothus greggii* (first column) and *Quercus engelmanii* (second column) scenarios for fire return intervals ranging from 10 to 80 years. **A & B**- with user defined density dependence. **C & D**- with ceiling carrying capacity. Treatment labels 'CVK #" refer to the percentage of variation designated for the carrying capacities of the scenarios. The "Base" scenario has no environmental correlation or CVK.

Table 3.1 Summary of results for *Ceanothus greggii* (CEGR) and *Quercus engelmanii* (QUEN) for various scenarios. (+) indicates an increase in expected minimum abundances given changes in the parameter, (-) indicates a decrease, and (0) indicates no change in EMAs.

Change	**CEGR**	**QUEN**
Survival variability	-	-
Germination change	0/-	+/-
Fecundity change	0	+
Fecundity variability	0	0
Fire spread	-	0/-
Env Corr	0	-
Carrying capacity variability	-	-

When annual variability in carrying capacity increased, EMAs declined; larger increases in variability in *K* resulted in larger decreases in EMA up to 0.02-003% of baseline EMAs (Figure 3.5b, Supplemental Table 1). Even a 10% annual variation in carrying capacity (*K*) reduced EMAs to 85-90% of baseline, while 50 and 75% variation in K resulted in near extinction. The impact of variability in *K* was increased when a ceiling density dependence function was used instead of a density dependence function where population size gradually decreased to *K* whenever *K* was exceeded (Figure 3.5d). With a ceiling carrying capacity, even 10% variability in K resulted in dramatic declines in

EMA (to 16-23%) over scenarios without variability. Spatial correlation in variability in carrying capacity had no impact on these results, whether a user defined density dependence function was used (Supplemental Figure 3.5) or ceiling (Supplemental Figure 3.6).

Discussion

What source of change had the greatest impact on EMAs?

The results of this study provided insights into the response of the species to change in life history traits, carrying capacity, dispersal, and fire (Table 3.1). Overall, the influence of change on the species depended on the source of variation; for instance changes in spatial correlation of environmental stochasticity had little to no impact on expected minimum abundances (EMAs), while variability in carrying capacity had a large impact for both species.

Vital rates (survival, germination rate, fecundity):

As expected, both species experience declines in EMA when averages of vital rates decline or variability increases. For *C. greggii* in particular, changes in vital rate parameters did not have a large impact on expected minimum abundances. Since the baseline model for *C. greggii* has high seed production, the species was robust to changes in mean and variation of fecundity. Regan *et al.* (2010) showed *C. greggii* to be sensitive to changes in survival rates of individuals up to 26 years of age. In this study, the low variability in survival rates of the baseline *Ceanothus greggii* model meant that changes in survival rate variability were all increases in variability and thus resulted in lower EMAs. Given the high rates of survival and fecundity for this species, plasticity of vital rates is unlikely to mitigate the impact of more frequent fires for this species

Changes in vital rates, particularly changes in averages of germination rate and fecundity, had a greater impact on the *Q. engelmanii.* indicating that plasticity in fecundity could potentially mitigate the negative influence of stressors such as climate change or altered fire regimes. Conlisk *et.al* (2012) showed that *Q. engelmanii* was sensitive to changes in sapling survival rates, but not to changes in other survival rates. However, results from this study show the oak to be affected by variability in survival rate, which is likely in part due to the stage based model- for instance, variability in the survival rate of all adults affects more individuals than variability in survival rate of individuals of one age.

Processes (Fire, Environmental correlation, dispersal, carrying capacity):

Changes in average fire interval and spread had a greater impact on *Ceanothus greggii,* though *Quercus engelmanii* was affected by changes in fire return interval as well. For both species, EMAs were lower with increased spread of fire, i.e. larger fires. Despite differences in response to fire, for both species EMAs are reduced when fires are larger. This corroborates results for *C. greggii* on an artificial spatial arrangement of patches on a smaller scale (Regan *et al.* 2010). This finding could be important to conservation efforts, as extreme fire weather is the dominant influence on area burned and fire severity (McKenzie *et al. 2*004). Larger and more frequent fires are also increasingly likely given increases in invasive grasses (Keane *et al. 2*008) and climate change (Driscoll *et al. 2*010). However, reductions in EMA from larger fires only occur when fire spread occurs at a high degree across the landscape. Therefore, average fire return interval is likely to be the primary influence of fire because fires are unlikely to reach the size that triggered declines in EMA in our models.

. Overall, results suggest changes in vital rates and fire regime can have a large influence on both of these species. The type of change with the greatest impact on expected minimum abundances differs between species, with vital rate changes having a larger impact on the resprouter and changes in fire regime having a larger impact on the obligate seeder.

Were changes in means or changes in variability more important?

Both directional changes in means and changes in the amount of variability impacted the species, and neither had a clearly more significant impact on species viability. However, it was clear that variability of fire and carrying capacity impacted both species, and therefore variability of processes has the potential to be more important than direct changes in vital rates. Variability is inherent in the environment, and understanding and predicting fluctuations in populations is a central focus of many ecology studies (Morris and Doak 2004, Evans *et al. 2*010). Climate change is predicted to increase environmental variability (Katz and Brown 1992) and may also result in selection for different vital rates, although this prospect is unlikely given the rapid pace of current climate change (Davis and Shaw 2001). If environmental variability translates into changes in variability or means of life history parameters, carrying capacity, or altered fire return intervals, viability analyses ignoring the variability of population responses could seriously underestimate species vulnerabilities to climate change. Predictions of species responses to climate change for conservation purposes typically use associations between current climate and spatial distribution to predict future distributions (Thomas *et al. 2*004, Elith *et al. 2*006). More detailed models link life history characteristics with bioclimatic habitat models, and include other global changes such as fire and urban growth (Keith *et al. 2*008, Lawson *et al. 2*010, Swab *et al. 2*012, Fordham *et al. 2*012, Syphard *et al.* 2013). Though these studies often include directional changes in carrying capacity (*K*) based on predicted changes in habitat suitability, annual variability in *K* is typically ignored. Our results show that even for populations with no directional trend in carrying capacity, annual variability in *K* can be a driver affecting EMAs (Figure 3.5), with bad years adversely affecting overall species viability (Roughgarden 1974). Longer lived species are generally thought to be less sensitive to increasing interannual variation in vital rates (Morris *et al. 2*006, Dalgleish *et al. 2*010). Long lived species also tend to have lower maximum growth rates and thus may take longer to recover from bad years. This could be somewhat mitigated by a slower response to declines in *K*; scenarios with a ceiling carrying capacity and thus an immediate drastic response to decreases in carrying capacity resulted in lower expected minimum abundances than scenarios with a tempered response to population exceedance of *K* (Figure 3.5). However, in this study even in simulations without directional changes in carrying capacity in response to climate change, large annual variability in carrying capacity caused near extinction for some scenarios, and reduced expected minimum abundances for both species (Figure 3.5). Changes in means also impacted the species, though it was increases variability which tended to cause more dramatic reductions, with EMAs as low as 2-12% of baseline scenarios (Supplemental Table 1). Thus, increased variability should be considered a bigger threat in most situations.

How might differences in responses across the plant functional types highlight how different life history traits could mitigate or exacerbate increased variability?

Much of the difference in responses of the two species to changes in variability and means can be attributed to differences in functional type, based here on response to fire. For all scenarios tested in this study, fire return interval was the most significant factor for the obligate seeder, *Ceanothus greggii*. This corroborates with other studies indicating that fire return interval is a key component to long-lived obligate seeders' viability (Regan *et al. 2*010, Lawson *et al. 2*012, Syphard *et al. 2*013). The main concern for this species (and other obligate seeders) under global changes is frequent fire (Regan *et al. 2*010, Swab *et al. 2*012, Syphard *et al. 2*013). The obligate seeder was only affected by changes in mean germination rate when they were dramatically reduced, and was not greatly impacted by changes in fecundity. *C. greggii* tends to have large underground seedbanks of up to 2000 seeds per m^2 (Zammit & Zedler 1988), and thus it is likely more limited by carrying capacity after emergence than by germination rate or fecundity itself, especially since germination tends to occur directly post fire. Developing a large seedbank is an essential characteristic for obligate seeders who experience germination only in fire years. Obligate seeders therefore are unlikely to be mitigated from the impacts of fire or climate change through adaptive differentiation of vital rates across a changing landscape, even if time scales of such environmental changes were congruent with the time scale that adaptation occurs on. Increases in fecundity in particular are unlikely to bolster species viability in response to frequent fire. Even increasing mean fecundity by 350% did not increase EMA for *C. greggii* when average fire return intervals were 10 years (Figure 3.2). Increased mean fecundity did improve results for the 20 year fire return intervals somewhat, however increases were relatively small.

Viability of the resprouter, *Quercus engelmanii,* is more robust to fire frequency than it is for *C. greggii*—the 10 year fire return interval does not always cause extinction, and though EMAs increase with fire return interval, differences between average fire return interval length is often negligible. The resprouter responded more negatively to high levels of fire spread than regional fires, indicating that fire frequency has more of an impact than spatial correlation of fires. *Quercus engelmanii* was more sensitive to changes in life history parameters than the obligate seeder. Futhermore, its population vital rates exhibit greater variation than those of *C. greggii* (Conlisk *et al.* 2012, Syphard *et al.* 2013). In particular, oaks are known for masting events which dramatically increase fecundity in some years (Espelta *et al.* 2008). Conlisk *et al.* (2012) modeled the response of the species to various masting scenarios, and found that increased masting when coupled with decreased predation of seeds resulted in higher expected minimum abundances. This aligns with our results, indicating that EMA is raised by increases in the amounts of seedlings through any route—increased fecundity, germination, or reduced predation. Since EMAs of *Q. engelmanii* were particularly sensitive to changes in germination rates, studies on the effect of climate change and other threats on the germination rate of this species would provide insight into the species' overall response to climate change. Changes in germination rate might allow the species to mitigate other negative impacts of climate change or altered fire regimes.

Conclusions

Typically, the impact of global change processes on species viability is considered on large scales. At local scales, however, population dynamics are influenced by vital rates. Therefore, it is important to consider how changes in vital rates and changes in processes affect species. For instance, species might be threatened by climate even if the spatial distribution of the species does not change.. Additionally, functional type can impact species responses to global changes, and species could be vulnerable to other threats alongside climate change. This has implications for conservation planning- if different functional types have different vulnerabilities to global changes, then plans must adapt accordingly. Focusing on the development of reserves to protect land projected to have suitable habitat under climate change while ignoring the potential threat of altered fire regimes could result in species loss. Thus in order to conserve species, it is necessary to incorporate multiple threats, life history traits, and potential responses of vital rates and processes to climate changes in projections of species responses to climate change.

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Supplemental Material from Chapter 1

Appendix A- Table of sensitivity analyses results

Supplemental Table 1.1 Results of sensitivity analyses for a spatially explicit demographic metapopulation model for the Australian shrub *Leucopogon setiger.* Numbers indicate proportion of change from baseline (the vital rates used for the model in all other simulations) for parameters that induced a greater than 0.10 proportional change in expected minimum abundance (EMA), when the parameter was perturbed by 10%. No value indicates that the proportional change in EMA was less than the change in the parameter. A "+" sign indicates that the parameter was increased by 10%, "-" sign indicates it was decreased by 10%. "Survival" refers to the diagonal within the matrix, when individuals stay in the same stage. "Transition" refers to sub diagonals within the matrix, when individuals are transitioning between stages. "Fecundity" refers to seed production. For example Stage 3 Transition Stage 5+ means that the transition rate from stage 3 to stage 5 was increased by 10%.

Parameter change	Fire return interval						
	5	10	15	20	25	30	35
Seed Survival+	1.834	0.825	0.420	0.371	0.359	0.356	0.429
Seed Survival-	0.625	0.542	0.447	0.393	0.376	0.371	0.345
Year1 Transition+	0.642	0.347	0.189	0.159	0.129	0.120	0.159
Year1 Transition -	0.478	0.315	0.223	0.169	0.150	0.170	0.130
Year2 Transition -	0.491	0.319	0.209	0.184	0.177	0.165	0.135
Year2 Transition +	0.341	0.234	0.135				0.115
Year3 Transition -	0.451	0.307	0.216	0.178	0.169	0.175	0.121
Year3 Transition +	0.369	0.246	0.127				
Year4 Transition Stage 1+							
Year4 Transition Stage 2+	0.118						
Year4 Transition Stage 3+	0.154	0.123					

Year4 Transition Stage 1-	0.171						
Year4 Transition Stage 2-	0.216	0.108					
Year4 Transition Stage 3-	0.290	0.117					
Stage1 Survival-	0.313	0.279	0.267	0.270	0.278	0.297	0.277
Stage1 Transition Stage 2-							
Stage1 Transition Stage 3-		0.129					
Stage1 Survival+	0.199	0.210	0.195	0.216	0.211	0.225	0.301
Stage1 Transition Stage 2+							
Stage1 Transition Stage 3+							
Stage2 Survival-	0.482	0.463	0.421	0.401	0.416	0.422	0.407
Stage2 Transition Stage 3-	0.229	0.130	0.122	0.111	0.114	0.111	
Stage2 Transition Stage 4-	0.110						
Stage2 Survival +	0.383	0.430	0.378	0.372	0.387	0.400	0.459
Stage2 Transition Stage 3+	0.105	0.127					0.133
Stage2 Transition Stage 4+							
Stage3 Survival -	0.341	0.196	0.163	0.135	0.131	0.141	0.120
Stage3 Transition Stage 4-	0.722	0.673	0.630	0.601	0.609	0.619	0.609
Stage3 Transition Stage 5-							
Stage3 Survival +	0.722	0.626	0.480	0.461	0.470	0.519	0.627
Stage3 Transition Stage 4+	0.262	0.206	0.143	0.120			0.136
Stage3 Transition Stage 5+							
Stage4 Survival -	0.678	0.700	0.699	0.705	0.716	0.730	0.740
Stage4 Transition Stage 5-							
Stage4 Survival +	0.611	0.627	0.420	0.406	0.435	0.508	0.677
Stage4 Transition Stage 5+							
Stage5 Survival +	0.112	0.247	0.167	0.149	0.183	0.209	0.313
Stage5 Survival -	0.210	0.209	0.195	0.201	0.221	0.242	0.251
Stage1 Fecundity+							
Stage1 Fecundity -	0.184						
Stage2 Fecundity +							
Stage2 Fecundity -							
Stage3 Fecundity +	0.205						
Stage3 Fecundity -	0.184						
Stage4 Fecundity+	0.276	0.153					
Stage4 Fecundity-	0.247	0.172	0.118				
Stage5 Fecundity+							
Stage5 Fecundity-							

Supplemental Material from Chapter 2

Appendix B-Metapopulation model methods

Survival rates

A stochastic matrix model with seed, juveniles, and rosettes was developed for *Carlina vulgaris.* Probability of flowering is generally a function of the size of the individual rosette in the previous year (Klinkhamer *et al.* 1991, 1996; de Jong *et al.* 2000; Rose *et al.* 2002). Within one year, seeds are integrated into the seedbank or emerge as seedlings and become juveniles, which do not produce seeds (Klinkhamer *et al.* 1996; de Jong *et al.* 2000). Survival of juveniles (first-year, non-flowering plants) was calculated by averaging the survival probabilities reported in Klinkhamer *et al.* (1996), who provided data for seedling survival over a number of years for Dutch populations. At the onset of the second year, juveniles become adult rosettes, hereafter termed "rosettes". In subsequent years, rosettes may flower and die or stay as rosettes. Rosette survival and transition values were based on data from Becker *et al.* (2006) and additional unpublished data from Becker (pers. comm.). Standard deviations were calculated from the variation in these data across years.

Disturbance, typically in the form of grazing, is associated with increased growth of *Carlina vulgaris* populations (Löfgren *et al.* 2000); without disturbance, population growth rates tend to be less than one. Several studies found declining populations of *C. vulgaris* in the landscape (Klinkhamer *et al.* 1991, 1996; Löfgren *et al.* 2000; Rose *et al.* 2002). However, they also found persisting or increasing populations, and the formation of new populations. Since disturbance is required to achieve positive population growth, it is thought that *C. vulgaris* is characterized by short term dispersal and frequent new establishment of populations rather than stable population dynamics (Klinkhamer *et al.* 1996). For our model, patches (clusters of adjacent cells of suitable habitat, described above) are at least one kilometer square; thus, local extinction, short-distance dispersal and local recolonization events all take place within the patch. However, using a metapopulation model with multiple patches allows us to evaluate how changing habitat suitability due to climate change impacts the species at the landscape scale.

Juvenile survival differed among studies. In Sweden, juveniles were found to have >95% survival during their first season (Löfgren *et al.* 2000). However, Klinkhamer *et al.* (1996) found that in the Netherlands 30-80% of juveniles survived to June of the year after germination. Since survival rate seems to depend on characteristics within microsites and the cell size for the matrix model will encompass a variety of microsites, we averaged these values to determine a transition rate of (0.63±0.11, Table 3) for juveniles to rosettes, which encompasses survival of juveniles. A survival rate for rosettes (0.61±0.14, Table 3) was determined using data on individuals from 5 locations across Europe (unpublished data, Becker, pers. comm).

Seed Production and Emergence

Carlina vulgaris generally does not flower or produce seeds in the first year after germination, and many plants will delay flowering to a third or later year (Klinkhamer *et al.* 1991, 1996; Rose *et al.* 2002). Mean age at flowering in a British study was 3.04 years with a maximum of 8 years (Rees *et al.* 2006). Optimal size for flowering is a tradeoff between increase in seed production and mortality risk (de Jong *et al.* 2000). Probability of flowering increases with rosette diameter and weight, and seed production is proportional to plant biomass (Klinkhamer *et al.* 1991, 1996; de Jong *et al.* 2000; Rees *et al.* 2006). Individuals generally die after producing seed. Thus, the effect of age is indirect: older plants are larger and, thus, more likely to flower. Since the matrix model uses stages rather than ages, this results in a high annual mortality rate for the rosette stage with fecundity averaged between non reproducing and reproducing individuals on a yearly basis.

In the matrix model, fecundity was represented using unpublished data from Becker. Rather than have a separate stage for flowering plants, this model averaged seed production across all living individuals. The average number of seeds produced by a flowering individual was multiplied by the proportion of reproductive rosettes, and divided by the total number of rosettes. This resulted in average fecundity per individual per year of 33.13. Seeds of *C. vulgaris* are produced in September to December, and seedlings emerge from April to June (Klinkhammer *et al.* 1996; de Jong 2000; Rose *et al.* 2002). *Carlina vulgaris* tends to accrue only small and transient seedbanks (van Tooren and Pons 1988; Eriksson and Eriksson 1997; Thompson *et al.* 1997; de Jong *et al.* 2000; Rees *et al.* 2006), with disappearance of seeds from the seedbank mainly due to germination (Pons 1991). De Jong *et al.* (2000) retrieved 15% of seeds sown as juveniles the first year after sowing, and 2% the second and third year after sowing. Therefore, within a year some seeds will enter the seedbank while others will emerge as juveniles.

Establishment of seedlings can be limited by available microsites (Klinkhamer *et al.* 1996; Löfgren *et al.* 2000; Rose *et al.* 2002), or by seed availability (Greig-Smith and Sagar 1981; Löfgren *et al.* 2000). The percentage of seeds that germinate varied among studies. In lab trials, 60-100% of *Carlina vulgaris* seeds germinated (van Tooren and Pons 1988). Greig-Smith and Sagar (1981) found 10-17% emergence in open plots, and 63-65% in plots protected from predators (survival March-June). Few seedlings survive to the end of the first year. Klinkhamer *et al.* (1996) found that 9.4 ±1.9% of seeds survived to seedling establishment one year later in a stable population in good habitat, while a declining population had 0.5±0.3% survival. De Jong *et al.* (2000) found 15% of seeds survived as seedlings the following year. Becker (2005) found that 2.5% of sown seeds produced seedlings which survived until summer. Since the model incorporated both declining and growing areas within each patch and included survival through the first year, we used an average of the four values which included seed and seedling mortality over a year (6.85% ± 0.57485, Table 3), and multiplied this by the number of seeds produced to estimate the transition rate between rosettes and juveniles (2.269±1.937, Table 3).

Transition from rosettes to seeds in the seedbank included 30% of the fecundity (9.941±8.483 seeds per individual per year, Table 3). In subsequent years, seeds in the seed bank had a 0.3±0.03 annual survival rate. Seedbank survival combined with a 6.85% germination rate results in 2% emergence of the original seedbank in the second year and less than 1% of the seed cohort remaining by the 5th year. This aligns with results from de Jong *et al.* (2000).

Most seed dispersal occurs within a 10 m radius of the parent plant (Greig-Smith & Sagar 1981; Löfgren *et al.* 2000), and is generally limited to tens of meters (Rees *et al.* 2006). Seeds are equipped with a pappus and may be dispersed by wind, but the pappus easily detaches and seeds are heavy, so few seeds are dispersed over long distances (Greig-Smith and Sagar 1981; Rees *et al.* 2006). Thus dispersal was excluded except in a sensitivity analysis as the distance between patches is beyond 1 km.

Initial abundance

Initial abundance was estimated using information from Jakobsson & Eriksson (2005), who found the number of flowering individuals in a 3.14 km^2 circle to average 1029.28 (or 327.8 per km^2) over two different Swedish counties. The percentage of individuals flowering per year averaged 20% (Klinkhamer *et al.* 1996), so after including non-flowering individuals the density per 1 km^2 would be 1639 individuals. Since the cell size used for the models was 0.0625km^2, the actual density per cell was set at 102. The number of flowering individuals varied greatly between 2 km^2 circles (Jakobsson & Eriksson 2005), so for comparison we ran simulations with a range of initial abundances: 10%, 50%, 150%, and 170% of the above density (spanning the minimum and maximum densities found by Jakobsson & Eriksson 2005). In some places abundances may be much higher than this (Matthies personal observation), so these numbers are likely not an accurate estimation of total population size. However, since the numbers are kept the same between simulations, comparing results from different scenarios reflects relative performance of the scenarios. The total initial population was distributed across stages in the model according to the stable stage distribution.

Carrying capacity and density dependence

Limitation by carrying capacity, *K*, means that all suitable habitats in the landscape are occupied (Münzbergová & Herben 2005). At a local scale (e.g. within each patch), the population is limited by microsite availability (Münzbergová & Herben 2005). Thus, while each patch in the model is climatically suitable for *Carlina vulgaris,* in reality within each patch the distribution would be limited to recently disturbed grasslands. To provide a plausible estimate for carrying capacity the maximum observed density (1710 flowering individuals per 3.14 km^2 circle) was scaled to account for the availability of suitable microsites; *K* was set at 2723 rosettes per km^2, or 170 individuals per cell. Total *K* for each patch is the sum of *K* across all cells within the patch.

The carrying capacity (defined here as the maximum number of individuals that can be accommodated per habitat patch) was based on available space and thus depends on the size of plants. Carrying capacity could potentially be greater for smaller plants than for larger plants. Since juveniles take up proportionally less space per plant than rosettes, the carrying capacity for juveniles could reasonably be expected to be larger than the carrying capacity for rosettes; thus we set the carrying capacity for rosettes to be 9.5% the carrying capacity for juveniles. In this way the plants in each stage are weighted, relative to the largest-sized rosette stage, to calculate a "stage equivalent" total abundance for comparison to the rosette-specific carrying capacity. These calculations were based upon the difference between the maximum observed seedling abundance per 1 m^2, (400, Rees *et al.* 2006) and the maximum observed for rosettes (34, Klinkhamer *et al.* 1996). Density dependence is primarily exhibited during recruitment (Rees *et al.* 2000; Rose *et al.* 2002); however, adult density can impact plant growth (Rose *et al.* 2002). When populations exceed carrying capacity, it is likely that mortality would be increased as well. Within the model, a ceiling density dependence function reduced the population to K by the following time step whenever the population exceeded K.

Additional References

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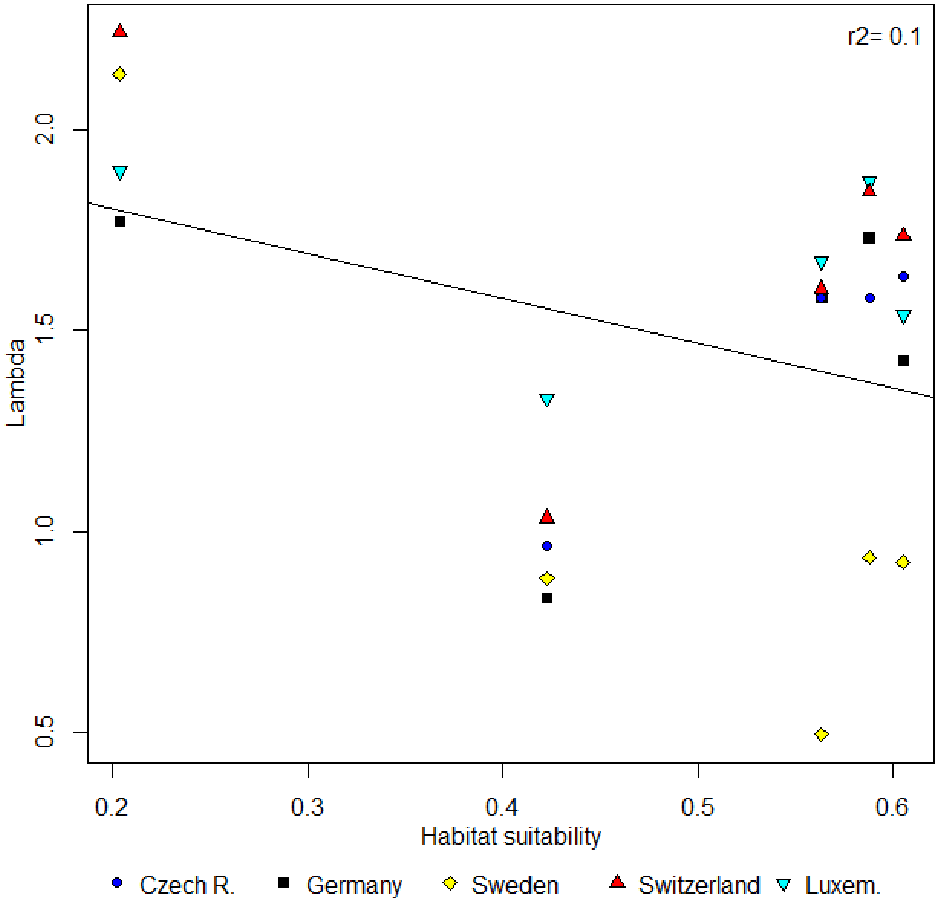
Appendix C- Table of Sensitivity analysis results

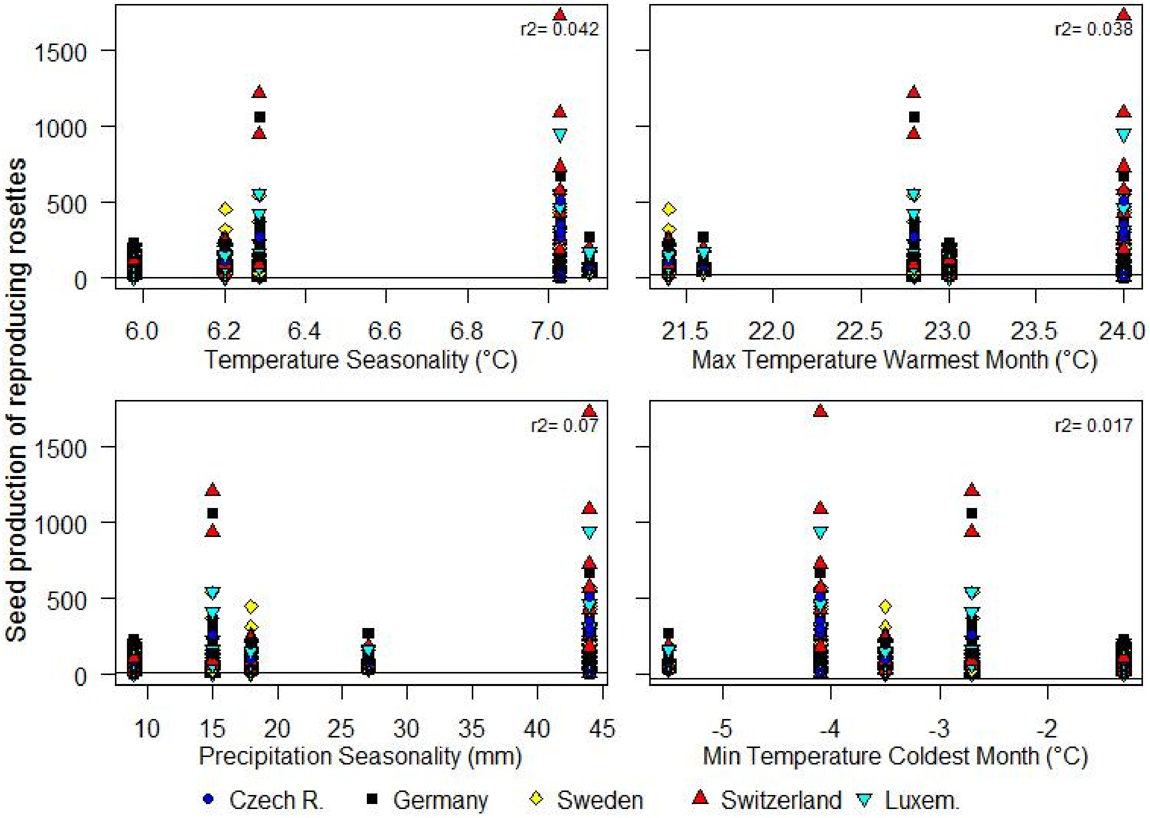
Supporting Table 2.1. Sensitivity analysis for life history parameters. Each matrix parameter was perturbed by + or – 10%. The resulting expected minimum abundance (EMA) was compared with the 'baseline' EMA (home matrix with no changes in parameters). A positive change in transition values between stages is indicated by "Stage1+Stage2", with three possible stages: seeds, juveniles, and rosettes. When the change in the resulting EMA is more than 10%, the model is considered to be sensitive to that parameter. The model is somewhat sensitive to those parameters highlighted in light orange, and more sensitive to those highlighted in darker orange.

Scenario	Percent change from Baseline
Duration 50	0.249
Duration 250	0.228
Juvenile+Rosettes	0.131
Duration 150	0.125
Rosette+Juvenile	0.115
Rosette-Juvenile	0.108
Juvenile-Rosette	0.104
Rosette-	0.074
Rosette+	0.060
Seeds+Juveniles	0.039
Seeds-Juveniles	0.034
Rosette+Seeds	0.031
IA -70%	0.017
IA -10%	0.014
Juvenile-	0.010
IA -90%	0.010
IA +90%	0.008
IA -50%	0.008
Rosette-Seeds	0.005
Initial abundance +10	0.004
Juvenile+	0.003
IA +70%	0.002
IA +50%	0.001

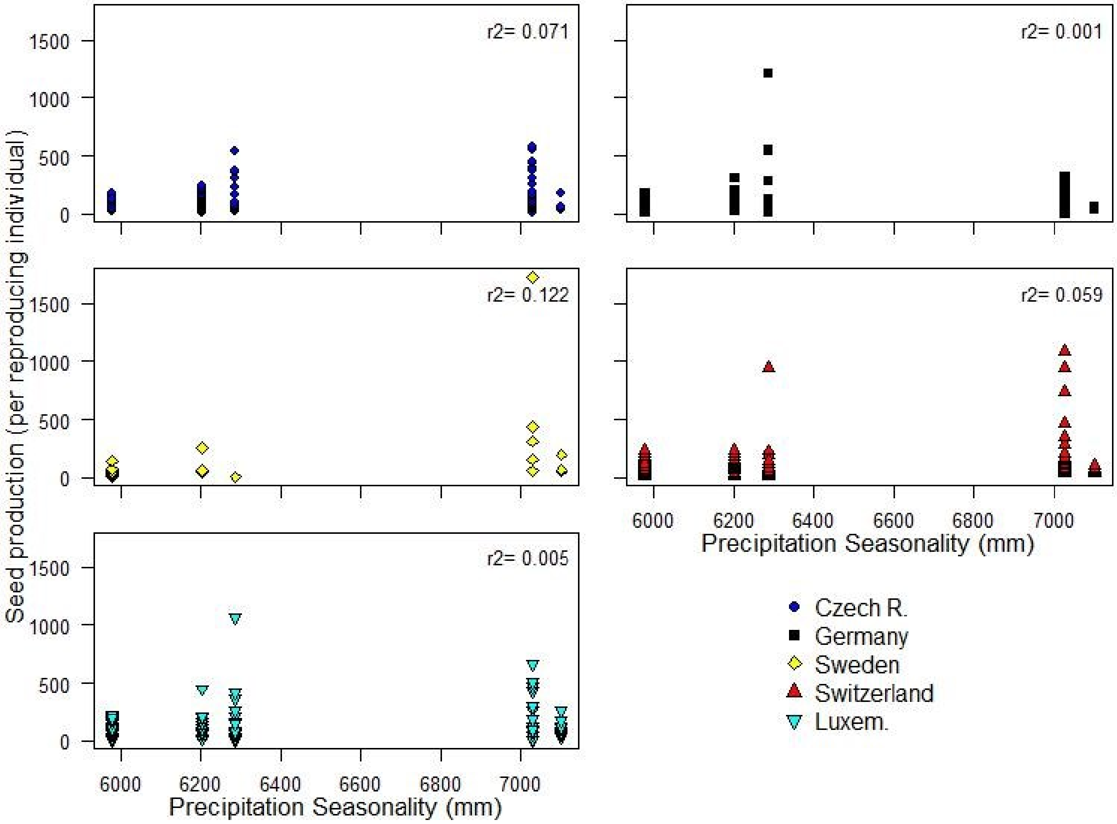
Appendix D- Supplemental Figures



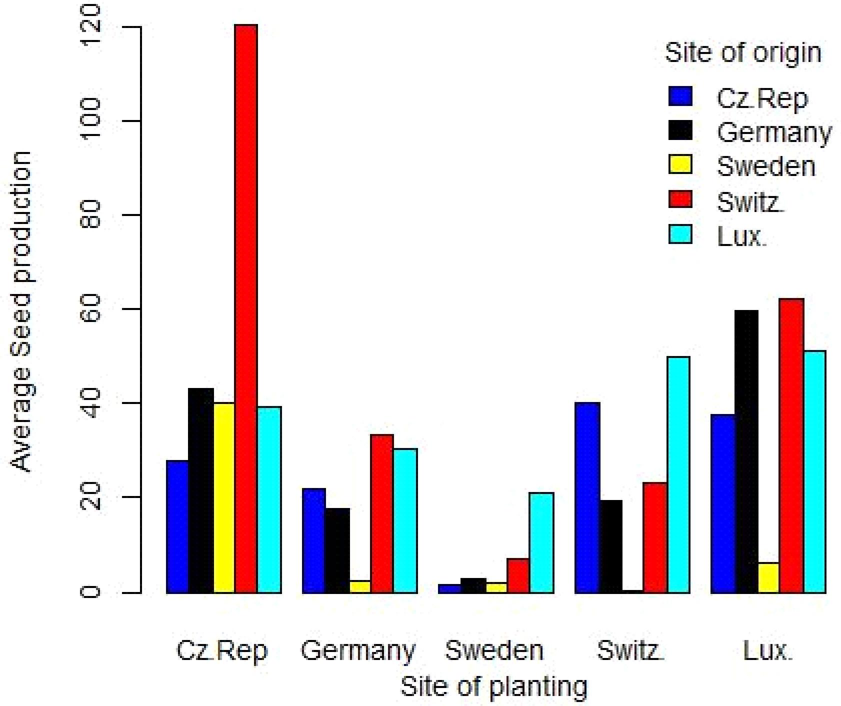
Supporting Figure 2.1. Habitat suitability factor versus lambda (average population growth rate) for the 25 various translocations performed on *Carlina vulgaris* individuals. Colors and shapes indicate origin of the individuals. Lambda values are the dominant eigenvalues of matrices developed for each translocation scenario with survival rates, fecundity, and transition values calculated using data from the translocation experiment.



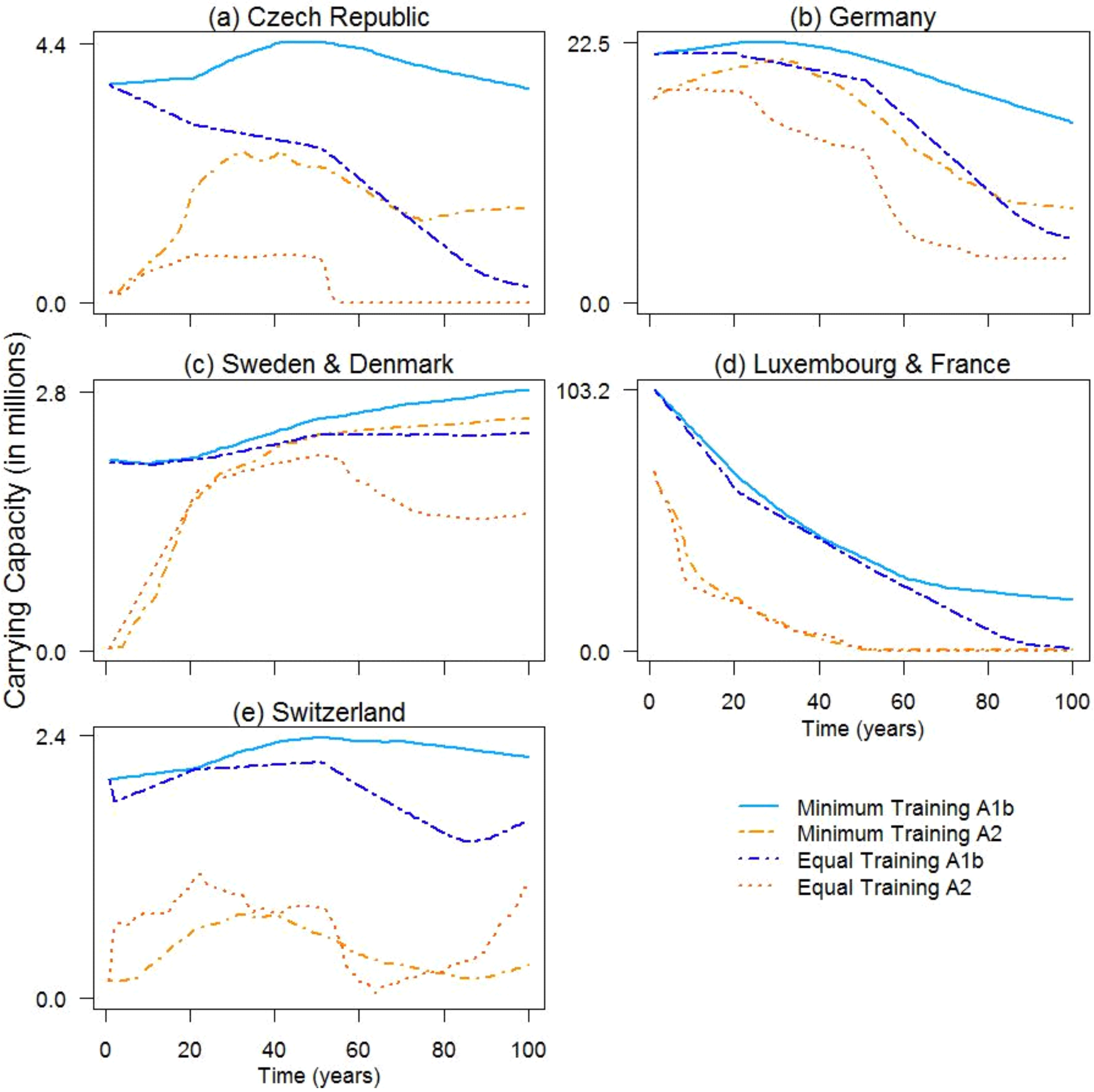
Supporting Figure 2.2. Seed production of reproducing individuals (based on rosette size) versus bioclim factors at the location grown (colors and shapes indicate location of origin).



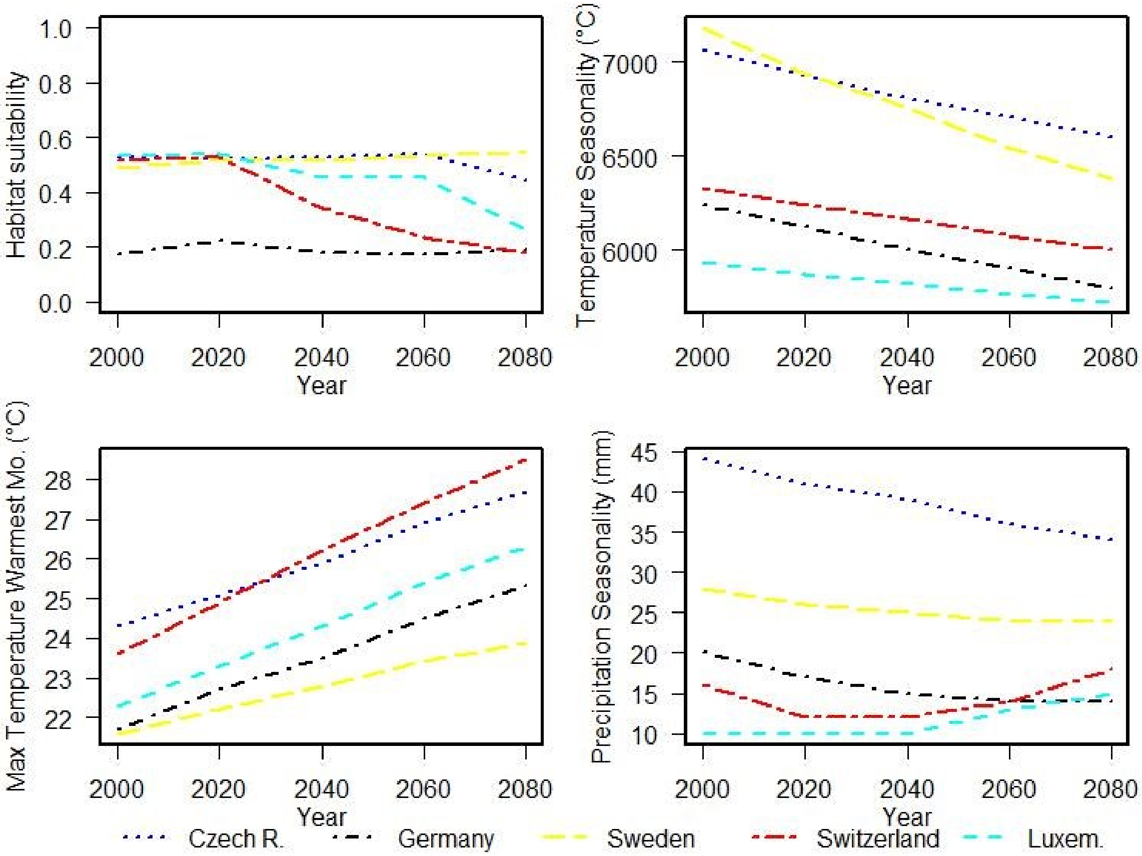
Supporting Figure 2.3. Climate factor Bio 4, precipitation seasonality versus predicted seed production (based on rosette size) for reproducing *Carlina vugaris* individuals. Each Figure shows individuals originating at each of the five different translocation sources.



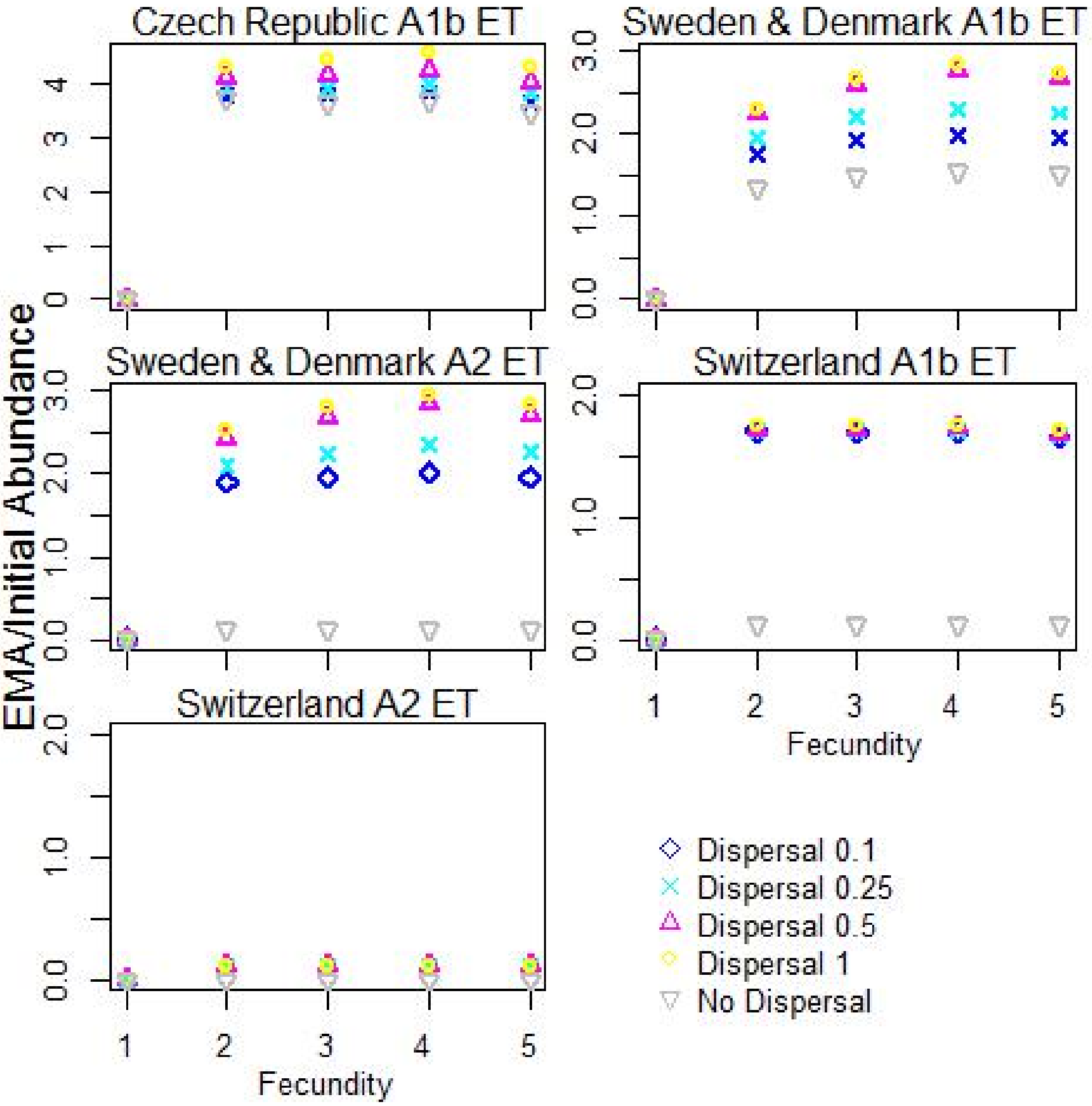
Supporting Figure 2.4. Expected average seed production per reproducing individual of *Carlina vulgaris* (grouped by site of planting), when planted at home and translocated to other sites.



Supporting Figure 2.5. Carrying capacity through time for *Carlina vulgaris* metapopulations based on habitat suitability in (a) the Czech Republic, (b) Germany, (c) Sweden & Denmark, (d) Luxembourg & France, and (e) Switzerland



Supporting Figure 2.6. Predictions of a) Habitat suitability for *Carlina vulgaris* through time b) Temperature Seasonality c) Max Temperature of the Warmest month and d) Precipitation Seasonality. Values are taken from the grid cell containing the translocation site within each country.



Supporting Figure 2.7. EMA/IA and fecundity category for scenarios with increasing proportions of seed dispersal. Only scenarios in which dispersal affected EMAs are shown.

Supplemental Material from Chapter 3

Appendix E-Table of Scenarios and Results

Supporting Table 3.1 Scenarios implemented and the impact of the scenario on expected minimum abundances (EMA) for a) *Ceanothus greggii* (CEGR) and b) *Quercus engelmanii* (QUEN) when compared with baseline results. Numbers above one represent increases above baseline, numbers below one represent decreases. CV stands for coefficient of variation.

a) *Ceanothus greggii*

Scenario	**Fire Return Interval**							
Varied CV of survival	10	20	30	40	50	60	70	80
CV 0.001	0.71	0.70	0.73	0.74	0.72	0.74	0.74	0.73
CV 0.005	0.55	0.69	0.71	0.73	0.73	0.73	0.74	0.75
CV 0.01	0.56	0.69	0.72	0.73	0.72	0.73	0.74	0.73
CV 0.05	0.48	0.64	0.66	0.66	0.65	0.63	0.66	0.64
CV 0.1	0.51	0.62	0.63	0.61	0.60	0.60	0.59	0.58
CV 0.25	0.47	0.54	0.54	0.53	0.51	0.51	0.53	0.50
CV 0.5	0.40	0.44	0.45	0.44	0.42	0.42	0.42	0.43
CV 0.75	0.37	0.38	0.38	0.37	0.36	0.36	0.38	0.36
Germination Rate								
GR 10%	0.00	0.08	0.20	0.31	0.38	0.44	0.49	0.53
GR 20%	0.03	0.29	0.50	0.63	0.69	0.74	0.79	0.81
GR 30%	0.12	0.50	0.70	0.80	0.83	0.87	0.92	0.92
GR 40%	0.16	0.66	0.81	0.88	0.90	0.93	0.95	0.96
GR 50%	0.34	0.77	0.88	0.93	0.90	0.95	0.95	0.97
GR 60%	0.60	0.86	0.92	0.95	0.93	0.97	0.98	0.97
GR 70%	0.56	0.89	0.93	0.96	0.96	0.99	1.02	1.01
GR 80%	0.68	0.94	0.97	1.00	0.97	1.00	1.01	1.01

GR 90%	0.65	0.97	0.98	1.00	0.98	0.99	1.00	1.00
GR 110%	1.11	1.06	1.01	1.01	0.99	1.01	1.03	1.02
GR 120%	0.76	1.03	1.03	1.03	0.99	1.02	1.04	1.04
GR 150%	1.09	1.07	1.03	1.02	0.98	1.01	1.00	1.01
GR 200%	1.02	1.05	1.02	1.02	0.99	1.01	1.01	1.05
GR 250%	1.30	1.07	1.03	1.02	1.00	1.02	1.03	1.02
GR 300%	1.11	1.05	1.03	1.02	1.01	1.02	1.04	1.00
Fecundity								
Fec 50	1.12	1.13	1.07	1.05	1.02	1.01	1.03	1.02
Fec 150	1.55	1.15	1.11	1.09	1.02	1.04	1.03	1.04
Fec 200	1.55	0.85	1.13	1.11	1.05	1.05	1.06	1.06
Fec 250	1.82	1.27	1.17	1.13	1.07	1.06	1.08	1.07
Fec 300	1.98	1.37	1.21	1.12	1.08	1.09	1.08	1.07
Fec 50, CV	1.20	1.20	1.10	1.04	0.99	1.02	1.02	1.02
Fec 150, CV	1.62	1.28	1.13	1.09	1.04	1.05	1.04	1.06
Fec 200, CV	0.54	0.93	1.14	0.97	0.96	0.98	1.01	1.01
Fec 250, CV	2.25	1.39	1.17	1.13	1.06	1.07	1.08	1.05
Fec 300, CV	2.18	1.40	1.23	1.15	1.10	1.09	1.09	1.09
CV Fec 50	0.74	0.93	0.96	0.99	0.97	0.99	1.01	1.01
CV Fec 150	0.53	0.87	0.93	0.98	0.95	0.97	1.00	0.99
CV Fec 200	0.56	0.83	0.91	0.95	0.96	0.98	1.01	0.99
CV Fec 250	0.44	0.79	0.89	0.93	0.93	0.97	0.99	0.98
CV Fec 300	0.33	0.86	0.92	0.95	0.95	0.98	1.01	1.01
Fire								
Regional	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Exact	0.00	3.30	1.64	1.30	1.13	1.11	1.10	0.90
Disp 0.1	0.51	0.77	0.89	0.96	0.96	1.02	1.04	1.06
Disp 0.25	0.13	0.45	0.64	0.82	0.91	1.00	1.08	1.11
Disp 0.5	0.00	0.10	0.20	0.32	0.39	0.49	0.58	0.71
Disp 1	0.00	0.00	0.01	0.01	0.02	0.02	0.03	0.04
Environmental Correlation								
Corre 100	1.07	1.03	0.99	1.00	1.00	0.99	1.01	0.99

Corre 50	0.86	0.99	1.00	1.02	0.99	0.98	1.03	1.00
Corre 25	0.97	1.00	1.01	0.99	0.99	0.99	1.03	1.02
Seed Dispersal								
Disp 0.1	1.08	1.11	1.08	1.09	1.04	1.06	1.07	1.06
Disp 0.25	1.44	1.18	1.13	1.09	1.08	1.09	1.09	1.08
Disp 0.5	1.81	1.31	1.18	1.16	1.13	1.11	1.14	1.11
CV Carrying capacity (K)								
CVK 10	0.86	0.95	0.89	0.85	0.82	0.82	0.84	0.82
CVK 25	0.82	0.72	0.71	0.67	0.65	0.64	0.64	0.65
CVK 50	0.34	0.44	0.42	0.37	0.36	0.34	0.34	0.32
CVK 75	0.12	0.19	0.20	0.19	0.18	0.17	0.16	0.16
CVK 10, cdd	0.47	0.60	0.65	0.66	0.66	0.66	0.71	0.71
CVK 25, cdd	0.32	0.43	0.45	0.46	0.45	0.46	0.47	0.48
CVK 50, cdd	0.05	0.08	0.09	0.09	0.09	0.10	0.10	0.09
CVK 75, cdd	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01

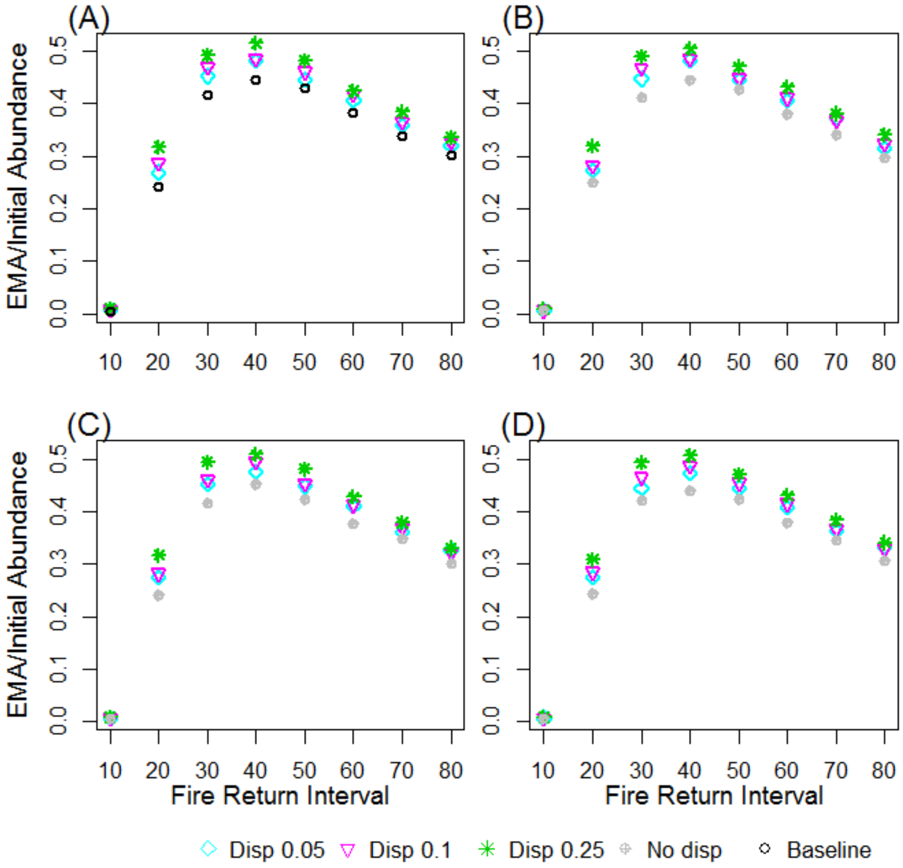
b) *Quercus engelmanii*

Scenario	**Fire Return Interval**							
	10	20	30	40	50	60	70	80
Varied CV of survival								
CV 0.001	2.37	2.00	1.72	1.58	1.49	1.43	1.39	1.27
CV 0.005	2.34	1.98	1.72	1.59	1.52	1.45	1.43	1.12
CV 0.01	2.26	1.96	1.70	1.58	1.51	1.46	1.42	0.88
CV 0.05	1.71	1.60	1.47	1.40	1.35	1.31	1.30	0.71
CV 0.1	1.29	1.28	1.22	1.19	1.16	1.14	1.13	0.18
CV 0.25	0.83	0.90	0.90	0.89	0.89	0.88	0.87	0.27
CV 0.5	0.66	0.69	0.71	0.70	0.71	0.71	0.70	0.36
CV 0.75	0.57	0.59	0.61	0.61	0.61	0.61	0.61	0.61
Germination Rate								
GR 10%	0.29	0.20	0.18	0.18	0.18	0.18	0.18	0.18
GR 20%	0.35	0.27	0.26	0.26	0.26	0.26	0.26	0.27
GR 30%	0.41	0.34	0.34	0.34	0.35	0.35	0.35	0.36

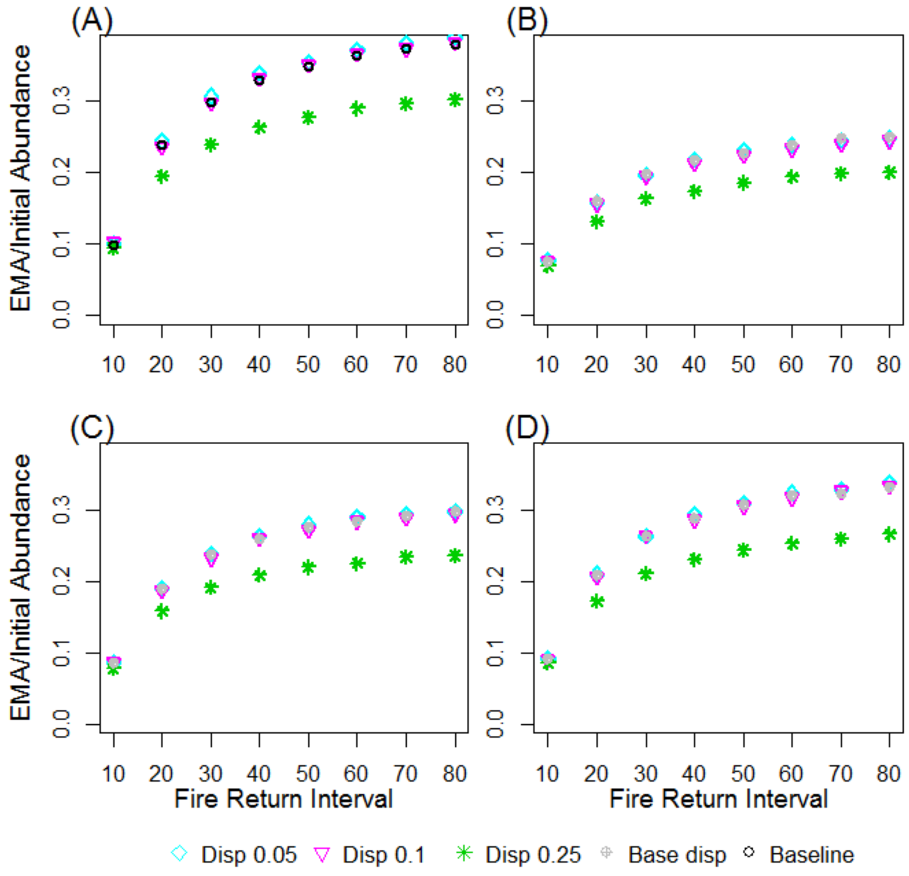
GR 40%	0.49	0.42	0.43	0.44	0.45	0.45	0.46	0.46
GR 50%	0.56	0.51	0.52	0.54	0.55	0.55	0.56	0.56
GR 60%	0.64	0.60	0.62	0.63	0.64	0.65	0.66	0.66
GR 70%	0.72	0.70	0.72	0.73	0.75	0.75	0.76	0.76
GR 80%	0.81	0.80	0.82	0.83	0.84	0.84	0.84	0.86
GR 90%	0.90	0.90	0.92	0.92	0.92	0.92	0.92	0.92
GR 110%	1.11	1.09	1.09	1.08	1.07	1.07	1.07	1.07
GR 120%	1.21	1.18	1.17	1.16	1.14	1.13	1.12	1.12
GR 150%	1.55	1.44	1.38	1.34	1.30	1.28	1.27	1.26
GR 200%	2.13	1.78	1.63	1.55	1.51	1.47	1.45	1.44
GR 250%	2.75	2.05	1.81	1.71	1.65	1.61	1.57	1.56
GR 300%	3.28	2.25	1.95	1.83	1.77	1.70	1.68	1.66
Fecundity								
Fec 50	0.58	0.55	0.56	0.58	0.59	0.59	0.60	0.61
Fec 150	1.46	1.38	1.32	1.29	1.26	1.24	1.23	1.23
Fec 200	1.95	1.65	1.53	1.48	1.45	1.41	1.40	1.39
Fec 250	2.36	1.89	1.71	1.63	1.58	1.55	1.52	1.52
Fec 300	2.81	2.06	1.84	1.75	1.70	1.66	1.63	1.62
Fec 50, CV	1.02	1.01	1.02	1.02	1.02	1.02	1.02	1.02
Fec 150, CV	0.99	0.98	0.99	0.99	0.99	0.98	0.98	0.99
Fec 200, CV	0.98	0.98	0.97	0.98	0.97	0.96	0.97	0.97
Fec 250, CV	0.98	0.96	0.96	0.97	0.95	0.96	0.95	0.96
Fec 300, CV	0.98	0.95	0.95	0.96	0.95	0.94	0.94	0.94
CV Fec 50	0.58	0.55	0.57	0.59	0.61	0.61	0.61	0.62
CV Fec 150	1.46	1.34	1.29	1.27	1.24	1.23	1.21	1.22
CV Fec 200	1.93	1.62	1.50	1.45	1.41	1.38	1.36	1.37
CV Fec 250	2.36	1.84	1.65	1.57	1.54	1.50	1.47	1.46
CV Fec 300	2.73	1.99	1.78	1.69	1.63	1.59	1.57	1.56
Fire								
Exact	0.81	0.86	0.97	0.99	1.00	0.98	1.01	0.99
Disp 0.1	0.88	0.93	0.97	0.99	0.99	0.98	0.98	1.00
Disp 0.25	0.71	0.82	0.89	0.93	0.94	0.94	0.96	0.97
Disp 0.5	0.40	0.53	0.61	0.68	0.72	0.74	0.77	0.79
Disp 1	0.09	0.10	0.12	0.13	0.14	0.15	0.16	0.17

Environmental Correlation								
Corre 100	0.76	0.68	0.66	0.66	0.65	0.65	0.66	0.66
Corre 50	0.87	0.80	0.80	0.79	0.79	0.78	0.78	0.79
Corre 25	0.92	0.88	0.88	0.88	0.88	0.88	0.87	0.88
Seed dispersal								
Disp 0.1	1.02	1.02	1.03	1.03	1.02	1.02	1.02	1.03
Disp 0.25	1.04	0.99	1.00	1.01	1.01	1.00	1.00	1.01
Disp 0.5	0.96	0.82	0.80	0.80	0.80	0.80	0.79	0.80
CV Carrying capacity (K)								
CVK 10	0.90	0.87	0.87	0.87	0.86	0.86	0.85	0.85
CVK 25	0.63	0.56	0.56	0.56	0.56	0.55	0.56	0.56
CVK 50	0.15	0.14	0.15	0.16	0.16	0.16	0.16	0.17
CVK 75	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03
CVK 10, cdd	0.23	0.18	0.17	0.16	0.16	0.16	0.16	0.16
CVK 25, cdd	0.23	0.19	0.18	0.17	0.17	0.17	0.17	0.17
CVK 50, cdd	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CVK 75, cdd	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

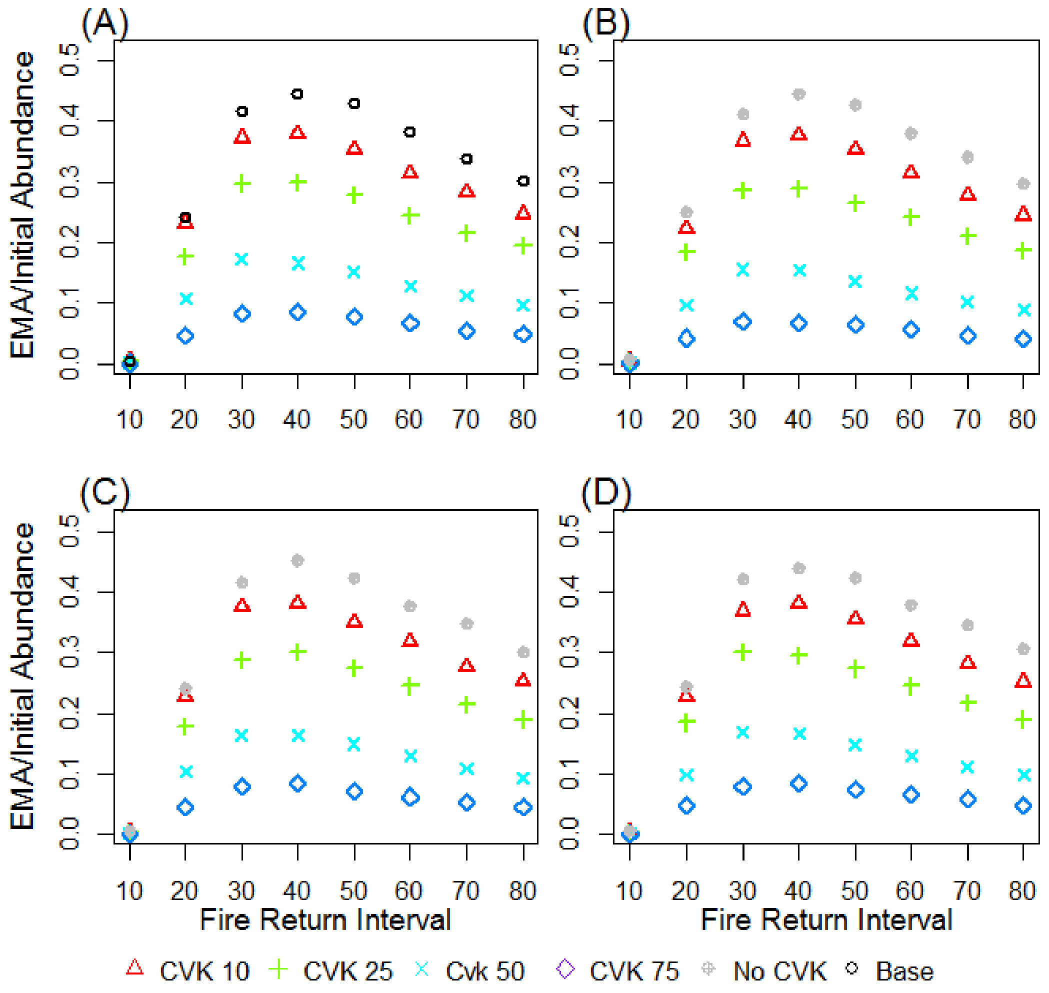
Appendix F-Supplemental Figures



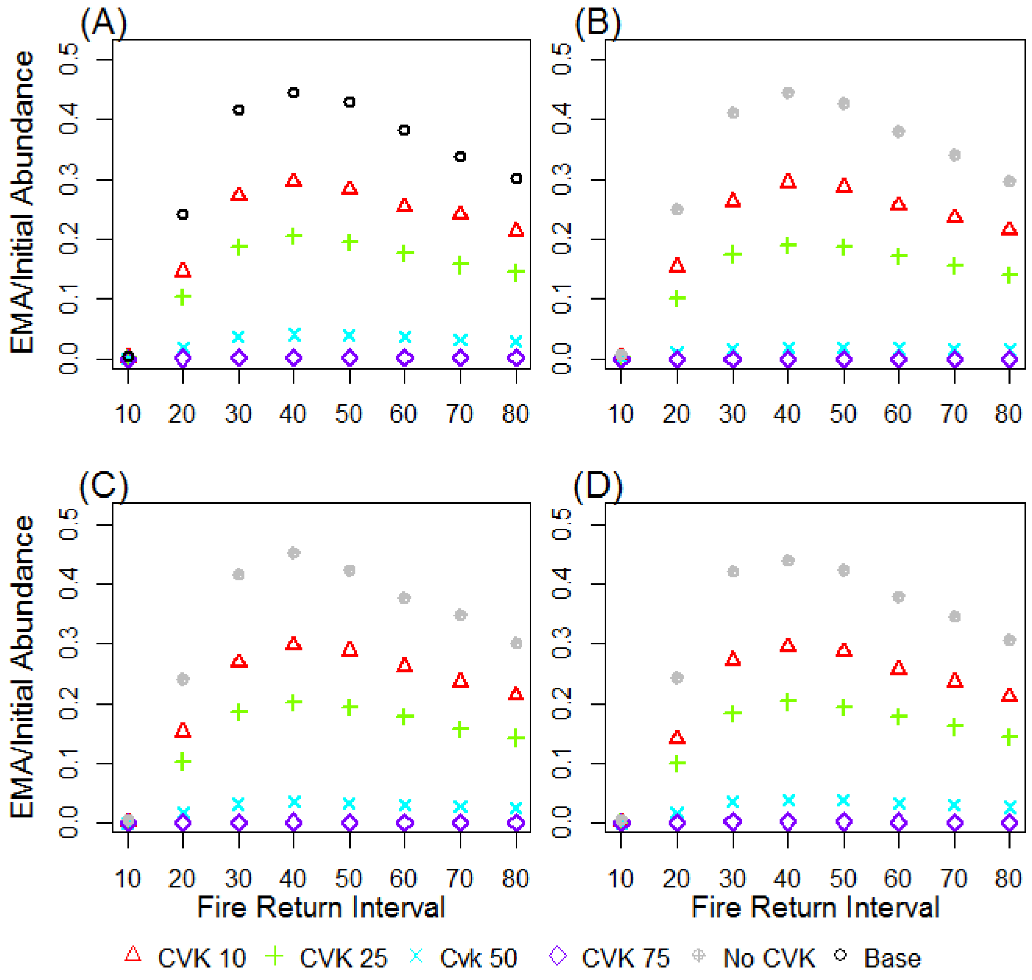
Supplemental Figure 3.1. Expected minimum abundance (EMA)/Initial abundance for *Ceanothus greggii* for fire return intervals ranging from 10 to 80 years. A) Varied amounts of seed dispersal. B) 100% Correlation of environmental stochasticity of fecundity, survival rates, and variation in carrying capacity and varied seed dispersal. C) 50% Correlation of environmental stochasticity and varied seed dispersal. D) 25% Correlation of environmental stochasticity and varied seed dispersal. Treatment labels "Disp #" refer to the a value from equation #.#. A higher value means a larger amount of seed dispersal between populations. "No disp" has no dispersal, and correlation of environmental stochasticity matching the other scenarios in the Figure. "Baseline" has no correlation of environmental stochasticity.



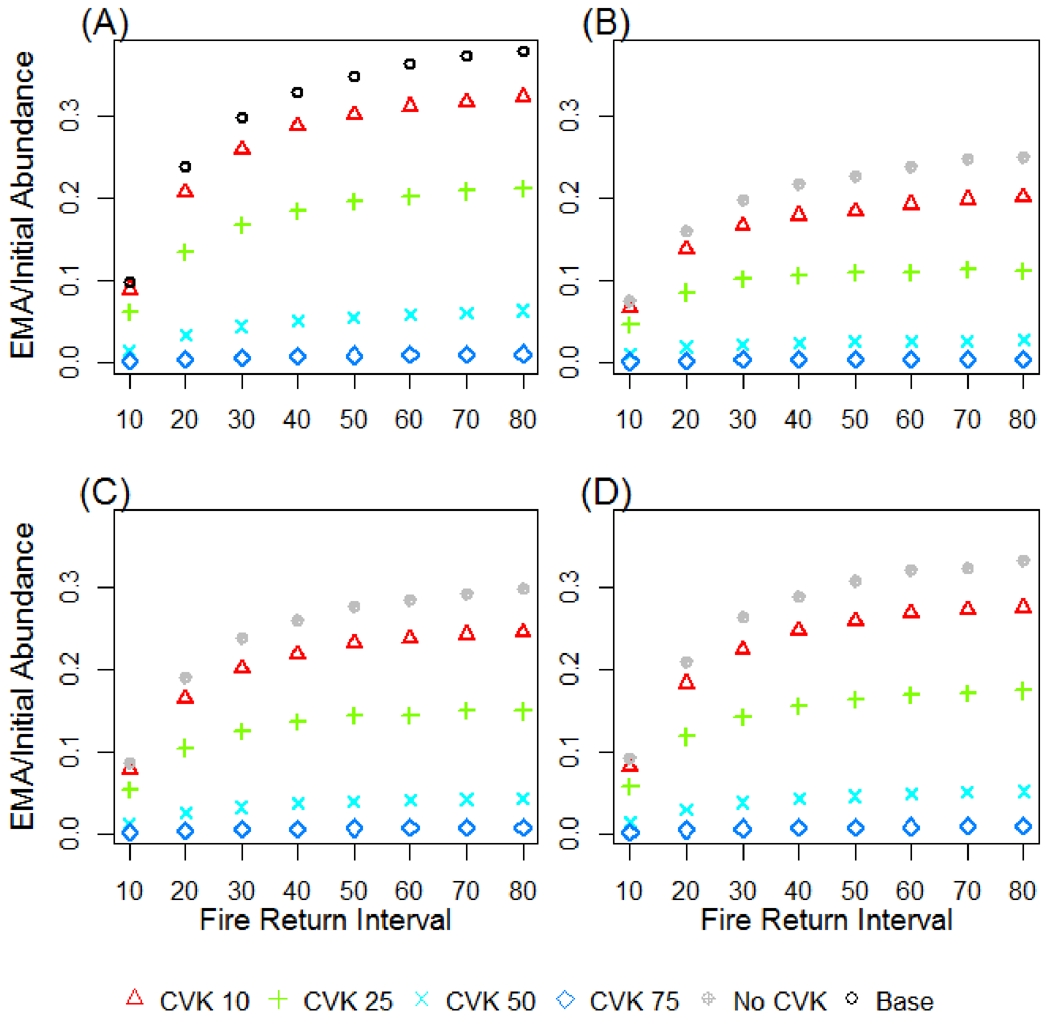
Supplemental Figure 3.2. Expected minimum abundance (EMA)/Initial abundance for *Quercus engelmanii* scenarios for fire return intervals ranging from 10 to 80 years. A) Varied amounts of seed dispersal. B) 100% Correlation of environmental stochasticity of fecundity, survival rates, and variation in carrying capacity and varied seed dispersal. C) 50% Correlation of environmental stochasticity and varied seed dispersal. D) 25% Correlation of environmental stochasticity and varied seed dispersal. Treatment labels "Disp #" refer to the a value from equation #.#. A higher value means a larger amount of seed dispersal between populations. "Base disp" has the baseline dispersal equation for *Quercus engelmanii* and correlation of environmental stochasticity matching the other scenarios in the Figure. "Baseline" has no correlation of environmental stochasticity.



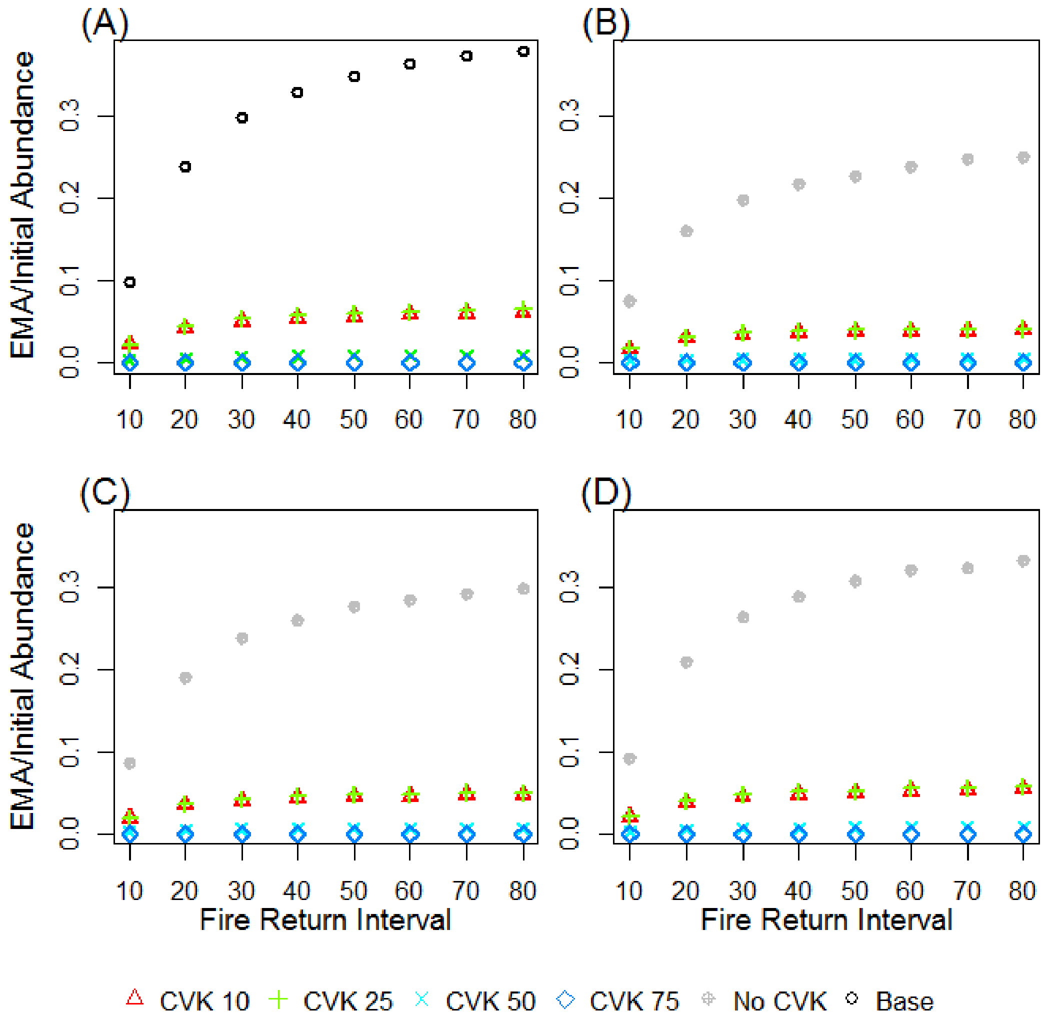
Supplemental Figure 3.3. Expected minimum abundance (EMA)/Initial abundance for *Ceanothus greggii* scenarios for fire return intervals ranging from 10 to 80 years with user defined density dependence. A) Annual variation in carrying capacity (K). B) 100% Correlation of annual variation in K between patches. C) 50% Correlation of annual variation in K between patches. D) 25 Correlation of annual variation in K between patches. Treatment labels ‘CVK #” refer to the percentage of variation designated for the carrying capacities of the scenarios. Scenario “No CVK” had the specified amount of correlation of environmental stochasticity, but no variability in carrying capacity.



Supplemental Figure 3.4. Expected minimum abundance (EMA)/Initial abundance for *Ceanothus greggii* scenarios for fire return intervals ranging from 10 to 80 years with ceiling carrying capacity. A) Annual variation in carrying capacity (K). B) 100% Correlation of annual variation in K between patches. C) 50% Correlation of annual variation in K between patches. D) 25 Correlation of annual variation in K between patches. Treatment labels 'CVK #" refer to the percentage of variation designated for the carrying capacities of the scenarios. Scenario "No CVK" had the specified amount of correlation of environmental stochasticity, but no variability in carrying capacity.



Supplemental Figure 3.5. Expected minimum abundance (EMA)/Initial abundance for *Quercus engelmanii* scenarios for fire return intervals ranging from 10 to 80 years with user defined density dependence. A) Annual variation in carrying capacity (K). B) 100% Correlation of annual variation in K between patches. C) 50% Correlation of annual variation in K between patches. D) 25 Correlation of annual variation in K between patches. Treatment labels 'CVK #" refer to the percentage of variation designated for the carrying capacities of the scenarios. Scenario "No CVK" had the specified amount of correlation of environmental stochasticity, but no variability in carrying capacity.



Supplemental Figure 3.6. Expected minimum abundance (EMA)/Initial abundance for *Quercus engelmanii* scenarios for fire return intervals ranging from 10 to 80 years with ceiling carrying capacity. A) Annual variation in carrying capacity (K). B) 100% Correlation of annual variation in K between patches. C) 50% Correlation of annual variation in K between patches. D) 25 Correlation of annual variation in K between patches. Treatment labels ‘CVK #” refer to the percentage of variation designated for the carrying capacities of the scenarios. Scenario “No CVK” had the specified amount of correlation of environmental stochasticity, but no variability in carrying capacity.