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# 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 the vulnerability of species 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.

**Location** Australian sclerophyll woodland and heathland.

**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** *Leucopogon 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 historical regime, was predicted to be a strong 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 the impacts of global change 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.

## Keywords

Altered fire regimes, Australia, bioclimate envelope model, *Leucopogon setiger*, metapopulation model, niche model, obligate seeders, population viability, range shifts.

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## INTRODUCTION

Anthropogenic climate change is projected to shift, fragment, contract or increase the distributions of many species and probably lead to redistributions (Peterson *et al.*, 1997; Pearson & Dawson, 2003) and, for some species, extinction (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 such as: 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 the vulnerability of species 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 the vulnerabilities of species 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.*, 2008). 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 (Hennessy *et al.*, 2005). 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 – long-lived obligate seeding shrubs – that is dominant in many fire-prone ecosystems and is sensitive to changes in fire regime.

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 the viability of obligate seeders (Keith *et al.*, 2008), another concludes that climate plays a larger role (Lawson *et al.*, 2010), although each study shows that both fire and climate are likely to be important. There is also evidence that the spatial structure of populations plays a large part in determining the vulnerability of obligate seeders to changing fire return intervals (Regan *et al.*, 2010). Furthermore, dispersal defines a species' ability to reach a suitable habitat, and thus can mitigate a species' response to shifting habitat (Engler *et al.*, 2009; Regan *et al.*, 2012). Overall, it is uncertain how fire regime changes or range shifts will interact, and whether one will exert a 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 as 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 affect 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* R. Br. (Ericaceae). This species has been the subject of a number of field studies devoted to understanding and quantifying demography and responses to fire (Ooi *et al.*, 2004, 2006a,b, 2007; Ooi, 2007, 2010). 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 when 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<sub>2</sub> levels, may affect plant allocation

and thus feed back into demographic function by having an impact on 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; Henle *et al.*, 2004; Isaac & Cowlshaw, 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 & Zavaleta, 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. What impact do altered fire regimes have on this species and what role does spatial structure play in the 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?

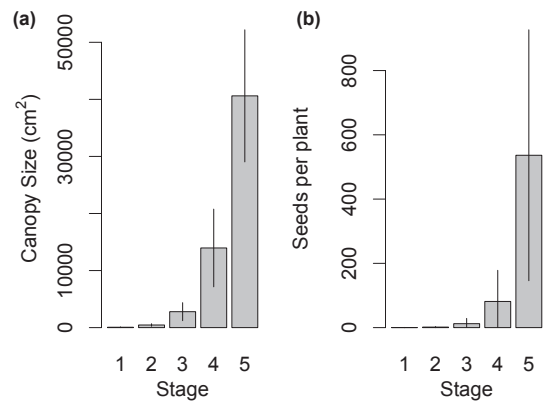
## MATERIALS AND METHODS

### Study species

*Leucopogon setiger* is a fleshy fruited endemic of New South Wales (NSW), in south-eastern Australia. Its core habitat is fire-prone dry sclerophyll forest (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 (Ooi *et al.*, 2004, 2006a,b, 2007; Ooi, 2007, 2010) to estimate survival rates and from additional field data on canopy size, fecundity and post-fire response, collected for the purpose of this current study. Field data were collected in the Royal National Park, NSW, in June 2009 at sites originally described by Ooi (2007) and are summarized in Fig. 1.

### 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



**Figure 1** (a) Canopy size distribution, i.e. length by width, and (b) seed production per individual by stage for 73 *Leucopogon setiger* individuals from four different populations within Royal National Park, NSW, Australia, June–July 2009. Bud counts per plant were made for all individuals, and these numbers were reduced by known rates of predation and seed viability, using the methodology explained in the methods, to give the values in (b). Stage was defined by size and bud production, as outlined in the Materials and Methods.

Intergovernmental Panel on Climate Change (IPCC, 2007), and derived for the years 1990, 2030, 2050 and 2070 using projected climate scenarios interpolated using ANUCLIM 5.1 (Houlder *et al.*, 2003) for two emissions scenarios: A1FI, rapid economic growth, fossil fuel intensive, and A2, regionally oriented economic growth and less severe warming than A1FI. For each scenario, climate predictions were generated for 10th percentile, median and 90th percentile climate values (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, 27 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/research/publications/software-datasets/anuclim>). The environmental data were rescaled to 30'' grid cells (*c.* 1 km) 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 modelled using MAXENT 3.3.3e (Phillips *et al.*, 2006; Phillips & Dudík, 2008). MAXENT has proved to be 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 and Heritage), current suitable habitat was predicted using MAXENT and then projected for future conditions in the years 2030, 2050 and 2070. MAXENT was used to determine which climatic, topographic and substrate variables were the best predictors of species presence. The contribution of non-influential factors (those below 2%) to modelled predictions, including multiple climate factors, was 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 because 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 operating 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 5.0 (Akçakaya, 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 (Fig. 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 4 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, levelling off to around 95% annual survival thereafter (Ooi, 2010). Thus our survival rate was set at 35% for the first year and 94–95% thereafter (Table 1). The 94–95% survival rate beyond 4 years of age 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 10%, based on variability recorded by Ooi (2007), but lowered for most simulations to prevent overflow errors.

#### 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 7 and 15 years were sampled. Bud counts were recorded for 20–25 shrubs per stand, and used to determine seed production by stage (Fig. 1). Previous work found that *c.* 11% of flowers developed into mature fruits (M.K.J.O., unpublished 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 means and standard deviations based on bud counts above. The seed bank was estimated to decay exponentially at a rate of 0.156 ( $\pm$  0.070) annually (Ooi *et al.*, 2006a), and an additional 6% of those remaining failed to germinate. Thus, annual seed survival was set at 79.3% with an estimated half-life of 2.99 years.

#### Post-fire recruitment

During a fire event 76.8% of seeds in the seed bank are killed by indirect heat or burning (M.K.J.O., unpublished data). When fire mortality and predation are accounted for, germination of the stored pre-fire seed bank occurs at a rate of 0.068.

**Table 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



Seedling 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. The carrying capacity ( $K$ ) was determined by calculating the maximum number of *L. setiger* individuals in a monospecific stand (size of one 30'' 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 1–4 and stages 1–5, respectively. Seeds were not subject to carrying capacity. The carrying capacity ( $K$ ) per cell (300 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 and 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 the 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):

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

where  $h = 1/\text{mean fire interval}$ ,  $c$  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

*Leucopogon setiger* is dispersed by ants and birds (Keighery, 1996; Stansbury, 2001; Ooi, 2007). Potential dispersal rates of seeds from *L. setiger*, as calculated based upon the average daily distance travelled by dispersers of the seeds, predict that only 0.6% of seeds were estimated to reach a distance of over 300 m, 7% over 50 m, 17% over 15 m and 95% less than 15 m. 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 movement of the species to new habitats (Higgins *et al.*, 2003; Engler *et al.*, 2009), we modelled extreme dispersal at 10 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

$$M_{ij} = a \exp\left(-D_{ij}^{c/b}\right)$$

where  $a$ ,  $b$  and  $c$  are function parameters and  $D_{ij}$  is the distance between the two populations (Akçakaya, 2005). For the simulations including dispersal,  $b$  was set to 0.88 and  $c$  to 0.34. These values best simulate the 10 times extended estimated dispersal kernel for this species. As 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 number 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. 2000–99). 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 1, 2, 4, 8, 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 the 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

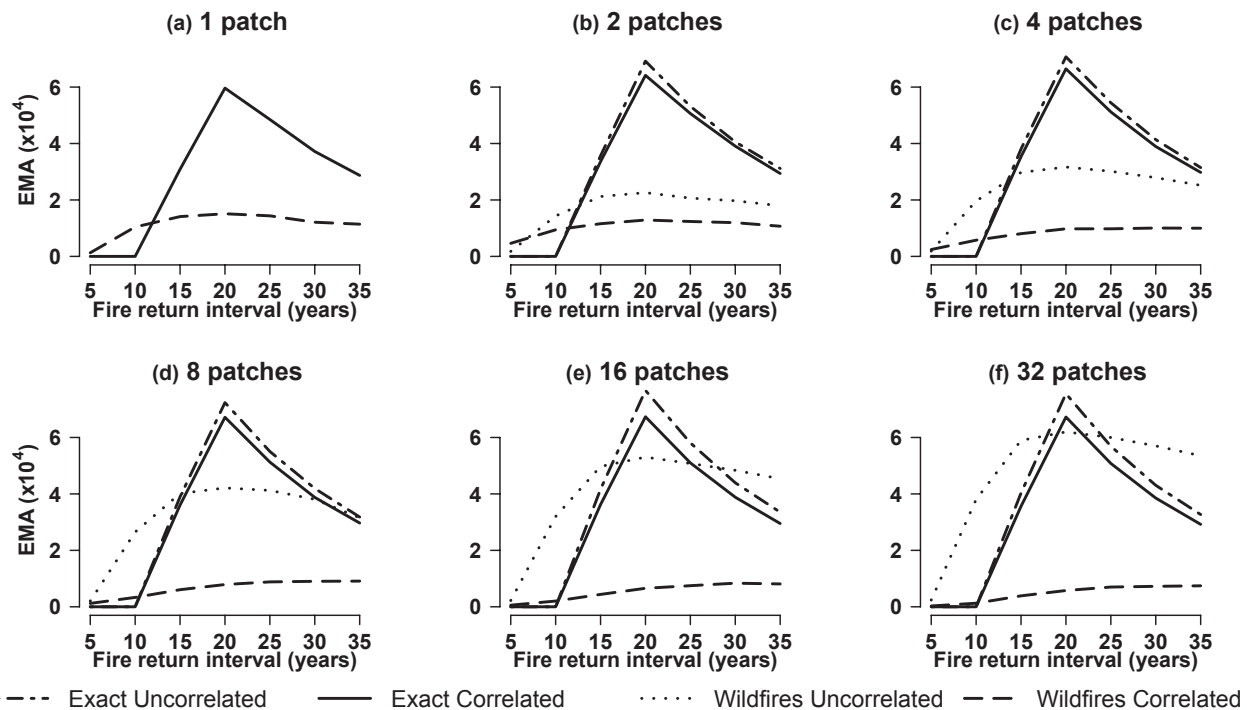
The second experiment utilized the more realistic spatial structure defined by habitat suitability. To investigate the effect of climate change, simulations were run for all average fire return intervals with seven different climate scenarios: a stable climate, and pc10, pc50 and pc90 for both A1FI and 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 that suitable habitat within a radius of 2.5 cells of a cell was 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

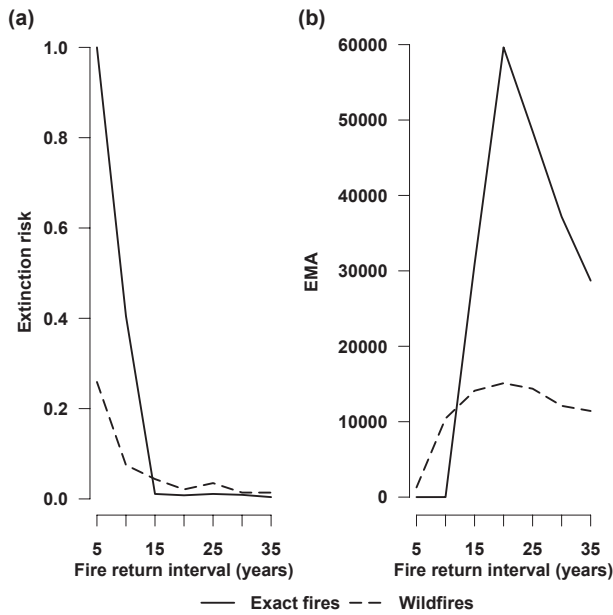
### Experiment 1: Changing fire interval and spatial structure

For regular fire return intervals, models predicted that 20 years is the optimal fire return for *L. setiger*. The EMA sharply declined when fire return intervals were small (< 10 years) or increased above 20 years (Fig. 2). However, while extremely short (5–10 years) fire return intervals resulted in high extirpation risk for a single patch, longer fire intervals did not increase extirpation risk (Fig. 3). Increasing the number of patches had a negligible impact on the vulnerability of *L. setiger* to fire return interval in this scenario, but when fires were uncorrelated between patches (i.e. have a different initial time since the last fire), EMAs were slightly increased when the number of patches increased (Fig. 2).

When fires occurred at irregular return intervals (wildfires), an optimal average fire return interval of 15–25 years was maintained across all spatial structures if fires were uncorrelated. The EMA gradually declined with longer intervals, and declined more sharply with shorter intervals (Fig. 2); however, extirpation risk only increased as the fire return interval reduced (Fig. 3). Populations were more sensitive to spatial correlation of fires when intervals between fires were variable than if they were of regular length. Correlated fires resulted in much lower EMAs than uncorrelated fires. With correlated fires, EMA decreased as the number of patches increased,



**Figure 2** Expected minimum abundance (EMA) versus fire return interval (in years) for the Australian shrub *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) irregular intervals, also referred to as ‘wildfires’, and uncorrelated between patches; or (4) wildfires, correlated between patches.



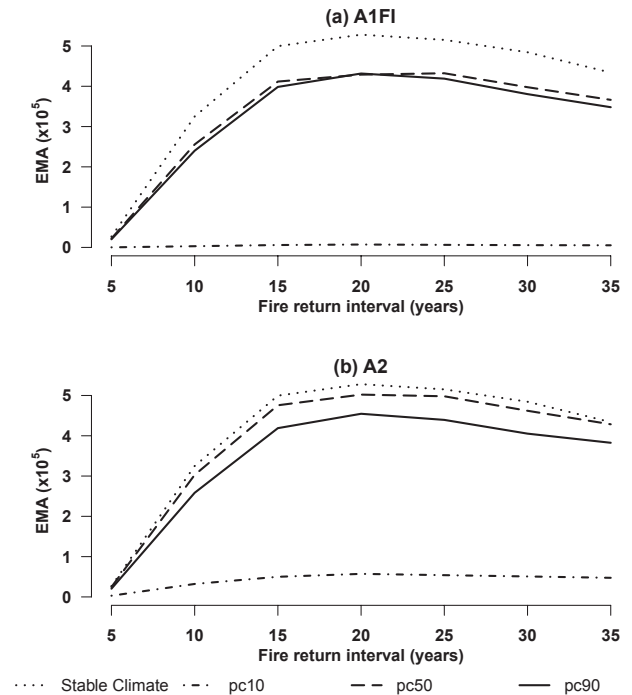
**Figure 3** (a) Extinction risk and (b) expected minimum abundance (EMA) versus fire return interval (in years) for the Australian shrub *Leucopogon setiger* in one patch for a stable climate. Fires occur at exact intervals or at irregular intervals as for wildfires.

especially for shorter fire intervals – probably due to the fact that smaller patches are more susceptible to bad years. For the maximally fragmented landscape with correlated wildfires, EMA increased as fire return interval increased.

When comparing EMAs from regular and irregular uncorrelated fire return intervals, increases or decreases in the EMAs were apparent depending on the number of patches and the average fire return intervals tested. EMAs were lower for irregular fire scenarios than they were for exact fire intervals when the average fire return interval was greater than 10–15 years for one, two, four and eight patches. They were higher for irregular than regular fire intervals for all but the optimal range when there were 16 and 32 patches (Fig. 2). Decoupling fires across the landscape by increasing the number of patches while maintaining the same initial abundance reduced the risk of decline of *L. setiger* for all average fire return intervals except 5 years (Fig. 2). Thus, spatial decoupling of fire events and longer fire return intervals increased population persistence for *L. 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 1 incorporating wildfires. Extreme shortened fire return intervals (5 years) gave the lowest EMAs

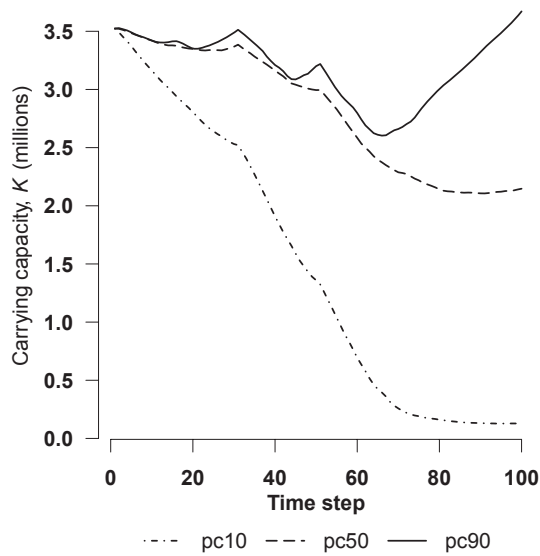


**Figure 4** Expected minimum abundance (EMA) versus fire return interval (in years), with uncorrelated wildfires, for the Australian shrub *Leucopogon setiger* with A1FI and A2 climate scenarios as follows: current climate remaining stable, 10th, median and 90th percentiles (Stable, pc10, pc50, pc90, respectively) for a composite of climate models.

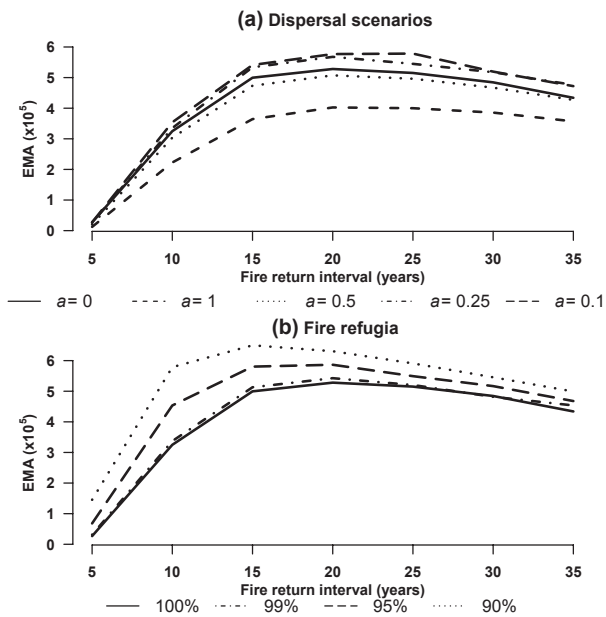
for the species in every model scenario, in some cases resulting in extinction. *Leucopogon setiger* was not sensitive to shifting habitat under the pc50 or pc90 scenarios for both A1FI and A2 climate scenarios (Fig. 4). However, the pc10 scenario dramatically reduced EMA. These responses to climate are consistent with expectations given the level of changes in habitat suitability, shown as change in carrying capacity (Fig. 5).

### Dispersal, threshold and fire refugia

Dispersal of a small portion of seeds produced optimal EMA, but only slightly higher than no dispersal (Fig. 6a). Dispersal of all seeds from a patch had a negative effect on EMA. This was true whether climate remained stable or changed (not shown). Including fire refugia within patches by decreasing the percentage of standing plants killed in fire increased EMAs, but maintained sensitivity to shortened fire intervals (Fig. 6b). Lowering the habitat suitability threshold allowed more habitat to be designated as suitable for the species, increasing EMA (Fig. 7 cf. Fig. 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 had an impact on the EMA, and the impacts were less severe than scenarios with the higher threshold.



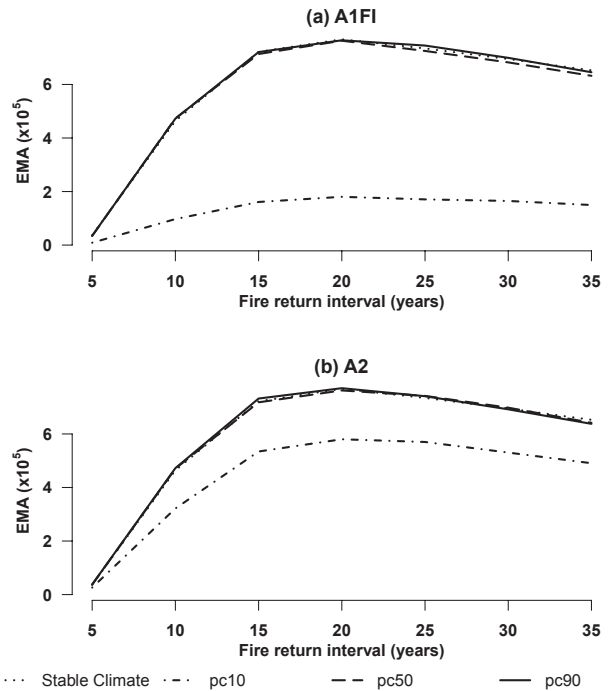
**Figure 5** Carrying capacity,  $K$ , for the Australian shrub *Leucopogon setiger* by time step.  $K$  was calculated using the A2 climate scenario 10th, median and 90th percentile (pc10, pc50, pc90, respectively) projections for a composite of climate models.



**Figure 6** Expected minimum abundance (EMA) versus fire return interval (in years), with uncorrelated wildfires, for the Australian shrub *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 percentage of death with fire, allowing for unburned refugia in patches.

**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



**Figure 7** Expected minimum abundance (EMA) versus fire return interval (in years), with uncorrelated wildfires, for the Australian shrub *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 climate models. For these simulations, patch structure was created using minimum training presence value, 0.007, as a threshold for suitable habitat.

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 the percentage of standing plant death during fire, but not sensitive to most changes in fecundity (see Appendix S1 in Supporting Information). 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, seed bank turnover and survival rates under the 5-year return interval than any other.

**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 *L. 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, although 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 extremely 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.*, 2012). 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 or not climate had an impact on 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 (Fig. 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 the competitive strategy of obligate seeders, 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, probably because range contractions rather than shifts were predicted. Keith *et al.* (2008) also found dispersal to be inconsequential for 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 *L. 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 (Figs 4 & 5). Thus, results from the niche model in conjunction 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 (Figs 2 & 3). Although models predict slight declines in EMA with longer fire intervals,

extirpation risk is only increased for shortened intervals (Fig. 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 *L. 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 differently aged patches across a landscape might have a beneficial effect on the persistence of *L. setiger*, although 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 were plentiful, information on the species at later ages (10–15 years) was sparse, and beyond 15 years information was primarily derived through extrapolation. Thus, the predictions incorporating long (over 15 years) 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 that the influence of climate change will affect 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<sub>2</sub> could alter the growth rate and thus affect maturity, survival and fecundity (LaDeau & Clark, 2001). 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 5-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 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<sub>2</sub> 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 modelled, and this study predicts that frequent fire remains the most serious threat even under future climate change scenarios.

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## SUPPORTING INFORMATION

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### Appendix S1 Results of sensitivity analyses.

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## BIOSKETCH

**Rebecca M. Swab** is a PhD student in the Evolution, Ecology and Organismal Biology Graduate Program at the University of California, Riverside. Her research includes incorporating multiple threats into niche model assessments and evaluating the impact of life-history traits on species responses to climate change.

Author contributions: H.M.R., D.A.K. and R.M.S. conceived the ideas, M.K.J.O. and D.A.K. provided data and species information, T.J.R. assisted with research direction and edits, R.M.S. and H.M.R. led the writing, R.M.S. created the model and ran simulations.

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