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RESEARCH ARTICLE

The implications of seasonal climatic effects for managing disturbance dependent populations under a changing climate

Bethan J. Hindle[1,2] | **Pedro F. Quintana-Ascencio**[3] | **Eric S. Menges**[4] | **Dylan Z. Childs**[1]

[1]School of Biosciences, Alfred Denny Building, University of Sheffield, Sheffield, UK

[2]School of Applied Sciences, University of the West of England, Bristol, UK

[3]Department of Biology, University of Central Florida, Orlando, Florida, USA

[4]Archbold Biological Station, Venus, Florida, USA

Correspondence
Bethan J. Hindle
Email: bethan.hindle@uwe.ac.uk

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Abstract

1. The frequency of ecological disturbances, such as fires, is changing due to changing land use and climatic conditions. Disturbance-adapted species may thus require the manipulation of disturbance regimes to persist.
2. However, the effects of changes in other abiotic factors, such as climatic conditions, are frequently disregarded in studies of such systems. Where climatic effects are included, relatively simple approaches that disregard seasonal variation in the effects are typically used.
3. We compare predictions of population persistence using different fire return intervals (FRIs) under recent and predicted future climatic conditions for the rare fire-dependent herb *Eryngium cuneifolium*. We used functional linear models (FLMs) to estimate the cumulative effect of climatic variables across the annual cycle, allowing the strength and direction of the climatic impacts to differ over the year. We then estimated extinction probabilities and minimum population sizes under past and forecasted future climatic conditions and a range of FRIs.
4. Under forecasted climate change, *E. cuneifolium* is predicted to persist under a much broader range of FRIs, because increasing temperatures are associated with faster individual growth. Climatic impacts on fecundity do not result in a temporal trend in this vital rate due to antagonistic seasonal effects operating through winter and summer temperatures. These antagonistic seasonal climatic effects highlight the importance of capturing the seasonal dependence of climatic effects when forecasting their future fate.
5. *Synthesis*. Awareness of the potential effects of climate change on disturbance-adapted species is necessary for developing suitable management strategies for future environmental conditions. However, our results suggest that widely used simple methods for modelling climate impacts, that disregard seasonality in such effects, may produce misleading inferences.

KEYWORDS
climate change, *Eryngium cuneifolium*, extinction probability, fire, functional linear model, integral projection model, plant-climate interactions, seasonality

1 | INTRODUCTION

Disturbance events, such as fires or floods, drive the dynamics of local extinction and (re)colonisation, altering biodiversity and community structure (Thom & Seidl, 2016; Velle et al., 2014). Many species are adapted to live in frequently disturbed habitats; for example, fire-adapted plants may have persistent seed banks and require extreme heat or smoke for germination (e.g. Davies et al., 2013). Such disturbance adapted species may be outcompeted when disturbance regimes are suboptimal; for example, pine recruitment and growth decreased in a fire suppressed mixed-conifer forest, which became increasingly dominated by fir (Levine et al., 2016). The frequency of disturbances has been altered over recent time scales due to anthropogenic effects, including land use modifications and climate change (Knorr et al., 2014; Restrepo et al., 2009). Management strategies that restore natural disturbance regimes thus may be used to aid the persistence of such disturbance adapted species (Allen et al., 2002; Henry et al., 2020; Menges, 2007).

Population viability analyses (PVAs) have been widely adopted to determine the conservation status of threatened populations and identify appropriate management strategies (Jaffre & Le Galliard, 2016; Lindenmayer & Possingham, 1996; Todd et al., 2017). PVAs use population models to simulate future dynamics and calculate performance metrics such as population size, growth rate, and extinction risk (Menges, 2000). Determining how disturbance regimes can be optimised to maximise the probability of future persistence (e.g. Brys et al., 2004; Sanchez-Velasquez et al., 2002) or to eradicate invasive species (e.g. Emery & Gross, 2005) is a common goal, with one-quarter of environmentally explicit demographic models in plants considering the role of disturbance (Ehrlen et al., 2016). However, demographic responses to disturbance are often estimated as a function of discrete categories of disturbance events, such as whether or not a disturbance has recently occurred (e.g. Canales et al., 1994; Stevens & Latimer, 2015). This is despite the effect a disturbance has on a population or community potentially occurring over multiple years (Fieberg & Ellner, 2001; Menges & Hawkes, 1998) and such responses not necessarily occurring linearly over time (Doak & Morris, 2010). Furthermore, many of these studies have assumed that, with the exception of disturbance frequency, populations will continue to experience the same environmental conditions in the future as during the observation period (Bernardo et al., 2016; though see e.g. Bucharova et al., 2012).

In reality, anticipated directional changes in environmental variables—for example, due to climate change—will also affect population persistence (Flatley & Fule, 2016; Harris et al., 2006). As such changes may drastically alter demographic rates, ignoring their effects can produce inaccurate future population predictions (Coulson et al., 2001; Crone et al., 2013). Climate change has already been implicated in local population extinctions (Wiens, 2016) and is predicted to become a key driver of future extinction dynamics (van Vuuren et al., 2006). However, demographic studies predicting climatic impacts on plant population viability are relatively rare (Ehrlen et al., 2016; Selwood et al., 2015; though see e.g. Hadjou Belaid et al., 2018). Incorporating the effects of climate change may provide more accurate predictions of future dynamics (Crone et al., 2013; Fieberg & Ellner, 2001), allowing the development of management strategies that are appropriate for future environmental conditions (Bernardo et al., 2016; Bucharova et al., 2012; Souther & McGraw, 2014).

There is a pressing need to study the joint effects of climate and disturbance on population dynamics within fire-adapted systems, given the ongoing rapid environmental change in such systems (Nolan et al., 2021). Anthropogenic influences have been a critical driver of fire regimes over recent periods; however, the ability of humans to suppress fire activity is likely to decrease in the future, with temperature likely to be a key driving force in future fire regimes (Shindell, 2010). Despite this relatively few studies have focused on the demographic consequences of climate change on optimal disturbance regimes in fire-adapted systems (though see e.g. Stevens & Latimer, 2015).

Climatic effects can be complex, however. For example, the impact of a single driver may vary seasonally (Foster et al., 2014; Kruuk et al., 2015; Paniw et al., 2019), and those climatic variables that show the most prominent changes are not necessarily the strongest drivers of ecological responses (Czachura & Miller, 2020). The rate and direction of climatic change differs across the seasons, and whether an individual can survive or reproduce, for example, is often affected by the environmental conditions at particular times of the year rather than by changes to the annual mean of a specific climatic driver (Bassar et al., 2016; Cordes et al., 2020; Paniw et al., 2019). For example, in plants, the effects of climatic conditions may be likely to differ between the dormant and growing season. Considering the effects of environmental drivers at different times of year is thus vital for accurately predicting the impacts of future change at a population level (Evers et al., 2021).

Here, we address two key questions: (1) how does the impact of climatic drivers on population performance vary seasonally and (2) how does forecasted future climate change impact on optimal disturbance regimes? We tackle these using data from a multi-population study of a rare, fire-adapted plant species, *Eryngium cuneifolium* (Menges, 2007; Menges & Quintana-Ascencio, 2004). We used generalised additive models (Scanga, 2014; Wood, 2017) to capture nonlinear responses to time since fire. To allow the effect of the climatic drivers to differ seasonally, we used functional linear models (FLMs) to capture climatic responses, allowing the effect of the climatic covariates to be estimated as a smooth function of seasonal anomalies (Hindle et al., 2019; Roberts, 2008; Teller et al., 2016). This is likely to mainly capture the direct effects of climatic change, rather than indirect effects, for example mediated through changes to the growth of interspecific competitors, which may take place over longer timeframes. However, as little is known about the effect of climatic variation on the demography of the study species, this provides an important step to understanding the dynamics of this system and the potential future impacts of a changing climate. We compared the predictive performance of FLMs using a range of possible climatic drivers (minimum temperature, maximum temperature, precipitation, and drought). Finally, we used an integral projection model (IPM) to explore whether future forecasted climate change will affect population viability (extinction probabilities and minimum population sizes) in this species under a broad range of FRIs.

2 | MATERIALS AND METHODS

2.1 | Study system

Eryngium cuneifolium is a rare perennial herb endemic to Florida rosemary scrub (Menges & Kimmich, 1996; Menges & Quintana-Ascencio, 2004). Its vital rates are negatively affected by time since fire, as it is outcompeted by shrubs such as *Ceratoila ericoides* (Menges & Kimmich, 1996; Quintana-Ascencio & Menges, 2000), with fire return intervals (FRIs) of less than 15 years necessary for its persistence (Menges, 2007; Menges & Quintana-Ascencio, 2004).

We used demographic data from 12 populations, from 1990 to 2014, at the Archbold Biological Station, Florida (Menges & Quintana-Ascencio, 2004). A fieldwork permit was not required. The data included over 10,000 observations of more than 4000 individual plants. Time since fire in the Florida Rosemary scrub, the primary habitat of this species in the study area, varied from zero to 42 years. Individual measurements were recorded annually at the end of October/beginning of November. The square root of rosette diameter was used as a measure of plant size. The vital rates were assumed to be density-independent as interspecific interactions are typically considered more limiting than intraspecific competition in this species (Menges & Kimmich, 1996) and the collinearity between time since fire and abundance in this species makes it difficult to disentangle the impacts of interspecific density and time since fire.

Daily weather data were recorded onsite at the Archbold Biological Station. The site undergoes cold, dry winters and hot, wet summers, with the highest monthly temperatures in August and the majority of the precipitation falling between June and September. Four climatic covariates were considered; minimum temperature (°C), maximum temperature (°C), precipitation (mm) and the Keetch-Byram drought index (referred to as drought from here on in), which is a function of mean annual precipitation, daily maximum temperature and daily precipitation (Appendix A1; Keetch & Byram, 1968). The means of each of the daily climatic variables were calculated every fortnight from the beginning of November in year t until the end of October in year $t+1$, that is for the 12 months between each annual census.

Predicted climatic data were available from the Meteorological Research Institute atmospheric general circulation model, version 3.2 (MRI-AGCM3.2), with a 60 km grid size (Mizuta et al., 2012). Climatic data were simulated from 1979 to 2099 (Kusunoki & Mizuta, 2013), assuming the moderate emissions scenario, A1B (IPCC, 2007). Predicted climatic data from general circulation models (GCMs) often differ from that recorded at local weather stations due to model biases or differences in spatial scale between the predicted and observed data (Baker et al., 2017). Therefore, a cumulative distribution function transform (CDF-t) approach was used to downscale predictions from the GCM (Appendix A1; Lavaysse et al., 2012; Michelangeli et al., 2009).

2.2 | Parameterisation of the IPM

As *E. cuneifolium* has a persistent seed bank (Navarra et al., 2011), we constructed a two-stage stochastic IPM to simulate population dynamics (Appendix A2). Four vital rates were assumed to vary with time since fire and the climatic variables: survival, growth, fecundity and recruit size. A model with no climatic drivers was fitted first for each vital rate; these acted as baselines to evaluate the predictive performance of the climatic models. For example, the probability of survival ($s_{\bullet}(z)$) for individual i in year t and population p was estimated as a function of size (z) and time since fire (l) as follows:

$$\operatorname{logit}\left(s_{\bullet}(z_{it})\right) = \beta^0 + f_z\left(z_{it}\right) + f_l\left(l_{tp}\right) + \varepsilon_p + \varepsilon_{tp}. \tag{1}$$

β^0 is an intercept and f_z and f_l are smooth functions of size (z), where z_{it} is the size of individual i in year t, and time since fire (l), where l_{tp} is the number of years since a fire occurred in year t for population p. $\varepsilon_p \sim N\left(0, \sigma^p\right)$ and $\varepsilon_{tp} \sim N\left(0, \sigma^t\right)$ are random effects for population and year respectively. The random year effects (ε_{tp}) were estimated separately for each year-population combination (tp), but these were drawn from the same distribution, that is the standard deviation of the random year effects (σ^t) did not differ among populations. The smooth functions (f_z and f_l) were parameterised by spline basis expansion, for example $f_z(z) = \sum_{k=1}^{K} \beta_k^z b_k^z(z)$, where β_k^z are coefficients, $b_k^z(z)$ are basis functions, and K is the dimension of the spline basis (Wood, 2017; see Appendix A3 for comparison with a linear time since fire model). The growth and fecundity models are structurally analogous to the survival model, differing only in the assumed distribution and link function (Gaussian for the growth model and negative binomial with a log link for the fecundity model). A Gaussian distribution was assumed for the recruit size model, which also did not include the size spline.

Four climatic models were fitted for each vital rate, each containing a single climatic variable. The cumulative effect of the climatic variables over the 12-month period before the annual census was estimated using FLMs (for a more detailed explanation on using FLMs with demographic data see Teller et al., 2016). The FLMs incorporated the mean of the climatic variable every fortnight (w) from the beginning of November ($w=1$) to the end of October ($w=26$) as covariates. For example, the probability of survival was given by

$$\operatorname{logit}\left(s_{\bullet}(z_{it})\right) = \beta^0 + f_z\left(z_{it}\right) + f_l\left(l_{tp}\right) + \sum_{w=1}^{W} f_c(w) C_{tw} + \varepsilon_p + \varepsilon_{tp}, \tag{2}$$

where C_{tw} is climatic variable C in year t and fortnight w and $f_c(w)$ is a smooth function over time. The remaining parameters are defined above (Equation 2). The smooth function $f_c(w)$ is parameterised using spline basis expansion, as above.

Models were fitted in R (R Core Team, 2016) using the *gam* function from the MGCV package and a cubic regression spline basis (Wood, 2017). Six knots were used for the size and time since fire splines and eight for the climatic splines. Quadratic smoothing penalties, $\sum_j \lambda_j \beta^T \boldsymbol{S}_j \beta$, control the degree of smoothing in the splines, where $\boldsymbol{S}_j$ are known smoothing penalty matrices and λ_j are smoothing parameters (Wood, 2017). The smoothing parameters (λ) were estimated using restricted maximum likelihood (REML), as this is less prone to overfitting than generalised cross-validation (GCV; Reiss & Ogden, 2009; Wood, 2011). Cluster cross-validation was used to assess the predictive performance of each climatic model relative to the base model (Appendix A3).

As the data available to parameterise the remaining IPM functions were more limited (Menges & Quintana-Ascencio, 2004), these were assumed to not be driven by climatic variation. Early seedling survival (e) was estimated using a logistic mixed-effects model with a fixed effect of time since fire and a random year effect. The number of seeds per flowering stem (m) was set to the mean observed number (183; Menges & Quintana-Ascencio, 2004). Estimates of germination range from 0 to 0.1 in the first year $\left(c_f\right)$ and 0.005 to 0.04 from the seed bank $\left(c_b\right)$ (Menges & Quintana-Ascencio, 2004; Quintana-Ascencio & Menges, 2000), whilst seed mortality (d) was unknown. Populations were simulated using a range of germination estimates and a wide range of seed mortality estimates (0.1, 0.3, ..., 0.9) and compared to observed aboveground population dynamics (Appendix A5, Menges & Quintana-Ascencio, 2004). The selected fertility scenario had low germination $\left(c_f = 0, c_b = 0.005\right)$ and low seed bank mortality ($d = 0.3$; see Appendix A5 for effects of uncertainty in the seed bank parameters on the extinction probabilities).

2.3 | Population viability in a changing climate

We explored how climate change may affect population viability under a range of FRIs, by simulating populations under the observed climatic conditions during the study period (1990–2014; 'past climate') and forecasted future climate (2015–2099; 'future climate'). The downscaled GCM climatic data were used for the past and future climate simulations. Populations were simulated for 85 years, starting with a fire year (see Appendix A6 for a comparison between populations simulated over a shorter, 30-year, period). Temporal variation due to time since fire, climatic effects and random year effects were incorporated independently of one another. The forecasted climate projections from 2015 to 2099 were used (in sequence) for future climate simulations. For the past climate simulations, 1 year of climatic covariates was randomly selected from the 25 observed years at each iteration. FRIs were simulated using a Weibull cumulative distribution function (e.g. Evans et al., 2010) with a range of medians (3, 6, 9, ..., 30; Figure S1). The upper limit is less than that of the suggested FRI for the rosemary scrub habitat (Menges et al., 2017). However, there is relatively little demographic data available for *E. cuneifolium* beyond 30 years after a fire, as it is outcompeted. Thus, using less frequent FRIs would involve extrapolating these demographic relationships. The FRIs were stochastic, with the probability of fire increasing as time since the last fire increased. Fire was assumed to kill all rosettes (Menges & Kohfeldt, 1995).

The random year and population effects were incorporated using a kernel selection approach to preserve correlations among the vital rates (Metcalf et al., 2015; Rees & Ellner, 2009). A population was selected for each simulation from each of eleven populations, and all vital rates were estimated conditional on the population random effects throughout the simulation (one population with no recruits during the study period was excluded, as a random effect could not be estimated for recruit size). At each iteration, a year-population combination was selected at random and used for the random year effects across all of the vital rates.

Three sets of simulations were run to explore the effects of initial population size, variability in the FRI, and differences among the populations. Unless otherwise stated, 1000 simulations were run for each parameter combination. First, a range of initial population sizes were used (1000, 7000, 15,000, or 30,000 seeds). Here, the shape parameter (a) of the Weibull distribution, which gives the slope in the probability plot, for the FRIs was set to 64, resulting in little variation around the median FRI (Figure S1). Second, we explored how differences in the variability of fire occurrence affected extinction risk. Here, using an initial population size of 7000 seeds, four values of a (2, 8, 32 and 64; Figure S1) were used to simulate the FRIs. Third, to determine how extinction probabilities differed among populations, 500 simulations were run for each of the eleven populations, with a set to 64 and an initial population size of 7000. Quasi-extinction probabilities were given by the proportion of simulations falling below one individual (including seeds). Minimum population sizes were calculated as the mean of the minimum number of individuals in each simulation.

3 | RESULTS

3.1 | Climate model inputs

The climate inputs for the model are summarised in Figure 2. Temperature is generally predicted to increase under the forecasted future climate, with particularly strong effects over spring and summer (Figure 2b,c). Whilst precipitation does not appear to undergo a directional change over the forecast period (Figure 2d), drought appears to increase over summer, presumably due to the increase in maximum temperatures (Figure 2a). The climatic variables tended to be most variable over winter (Figure 2ii). There are no clear trends in the among year variability of the climatic predictors over this period (Figure 2ii).

3.2 | Response of vital rates to time since fire and climatic conditions

The vital rates respond nonlinearly to individual plant size (Figure S2) and time since fire (Figure 1). For all the vital rates, using a smooth

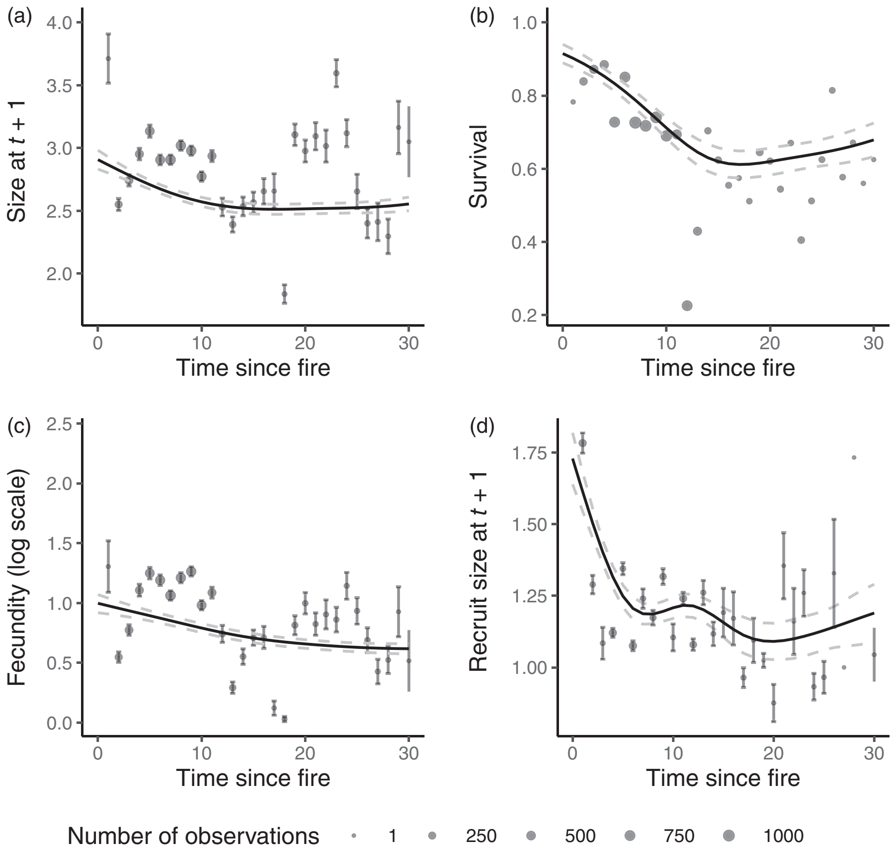


FIGURE 1 Time since fire models for (a) growth, (b) survival, (c) fecundity and (d) recruit size. Lines show predictions (±1 standard error) for a median sized individual on a square root scale (2.45) in an average population and year. Points and error bars show mean (± standard error of the mean) for each vital rate across all individuals.

function for the time since fire effect had a better predictive performance than assuming that the effect was linear (Appendix A3). The rates were negatively affected by increasing time since fire, with the fastest decreases in the first 10 years post fire. There was some indication of a slight increase in survival, growth and recruit size after 20 years since a fire, as well as a slight intermediate increase in recruit size around 12 years post fire. Such impacts could be a result of decreased competition, as population sizes are strongly related to time since fire. However, sample sizes did also decrease with time since fire (Figure S3), dropping to an average of 13 individuals per population 25 years post fire and the effect sizes of these features is small; thus they may simply be a result of sampling variation and are unlikely to affect the population level predictions. There was also some evidence of senescence in survival, which appears to decrease in very large (i.e. older) individuals (Figure S2).

Higher temperatures across the year increased growth, with particularly strong effects over winter and spring (Figure 3a; Table 1). Maximum temperatures were a better predictor of growth than minimum temperatures (Table 1). Higher temperatures during summer, when temperatures were at their peak, had a small positive effect on growth compared to the rest of the year (Figure 3a). Including drought as a covariate improved the predictive performance of the survival model (Table 1).

Increased drought over winter and spring and decreased drought over summer and autumn were associated with increased survival (Figure 3c; Table 1). Seasonal effects were also evident in the fecundity model, where higher minimum temperatures over winter and spring increased fecundity, whilst higher temperatures during summer decreased fecundity (Figure 3e, Table 1). Recruits emerge between January and March (Menges & Quintana-Ascencio, 2004); higher maximum temperatures shortly after this period increased recruit size (Figure 3g; Table 1).

Despite climatic effects being identified in all four of the vital rates (Table 1; Figure 3) the predicted future climatic change (Figure 1) only appears likely to lead to a strong directional change in growth and recruit size (Figure 3a,h, respectively). There are no strong temporal trends in survival and fecundity (Figure 3d,f, respectively). For survival, this is due to a lack of sizeable directional change in drought, which is the critical climatic driver for this vital rate, and only shows an indication of increasing during summer (Figure 2; Appendix A4). For fecundity, however, this is due to antagonistic seasonal effects, with increasing minimum temperatures during winter and early spring predicted to increase fecundity over the forecasted study period, but temperature increases during late spring and summer predicted to decrease fecundity (Figure 3e and Appendix A4). Conversely, the forecasted temperature increases over the next 85 years (Figure 1) appear likely to increase growth (Figure 3b) and recruit size (Figure 3h).

3.3 | Optimal FRIs under a changing climate

In all scenarios, the predicted extinction probabilities were lower and minimum population sizes higher under future climatic conditions than

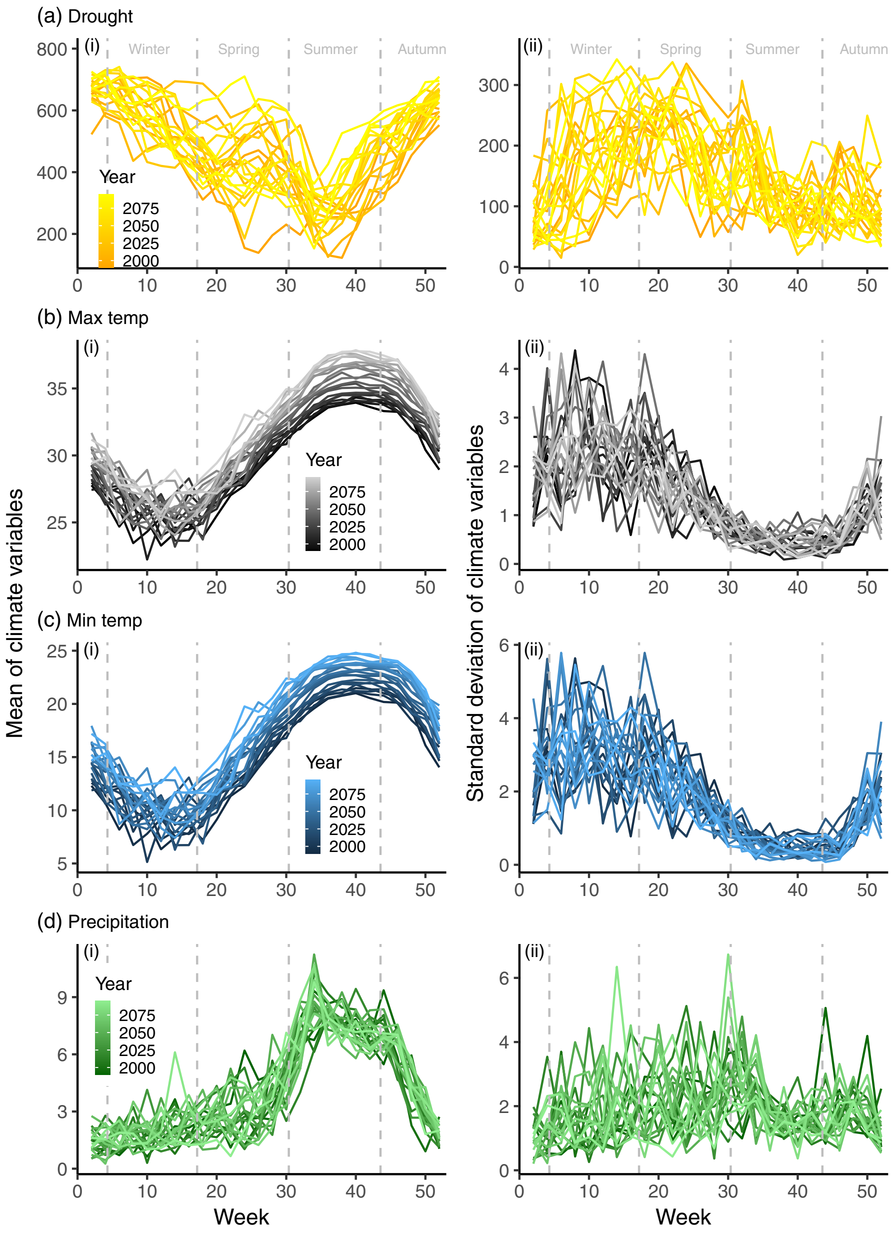


FIGURE 2 Intra-annual change in the mean (i) and standard deviation (ii) for (a) drought, (b) maximum temperature, (c) minimum temperature and (d) precipitation. Data shown over the 25-year study period (1990–2014) and 85 year forecast period (2015–2099). Each line is the mean (left column) or standard deviation (right column) over a 5 year period. The annual census takes place at the end of October or beginning of November. Drought is on a scale from zero (soil fully saturated) to 800 (maximum possible drought).

past. Under past climatic conditions, optimal median FRIs were between 9 and 15 years, with extinction probabilities less than 5% for all initial population conditions over 1000 individuals and below 20% with an initial population size of 1000 seeds (Figure 4ai). Outside of this optimal range, mean minimum population sizes were less than 600 individuals, even with an initial population size of 30,000 individuals (Figure 4aii). In the future climate simulations, extinction probabilities were below 5% for all median FRIs above 3 years (Figure 4aii). The optimal median FRIs were not affected by the climate, with the largest minimum population sizes still seen with FRIs between nine and 15 years under the future climate simulations. Mean minimum population sizes under these FRIs were between five and eight times as large as those predicted for the same FRIs under past climate (Figure 4aii).

Changes to the median FRI had relatively little effect on the population performance metrics when the shape parameter for the Weibull distribution was set to 2; the minimum population size increased while the median FRI was below 10 and then plateaued (Figure 4b). There was little difference in extinction probability or minimum population size at the higher values of the shape parameter (Figure 4b; $a = 8$, 32 and 64); that is, where the fire return intervals were more concentrated around the median (Figure S1).

Extinction risk among populations was very variable. Under past climates, the probability of extinction with a median FRI of 30 years varied from 25% in one population to nearly 100% in another (Figure 4ci). With a median FRI of 15 years, the mean minimum population size ranged from 10 to over 850 and from 1500 to over 3000 among populations under past and future climates, respectively (Figure 4cii).

The results are robust within the range of uncertainty evaluated for the seedbank parameters; altering the fertility scenario estimates (g_f, g_b and d) affected the absolute predictions of extinction risk and minimum population size, but not the pattern with respect to FRI or climate (Appendix A5). The probability of extinction remained less

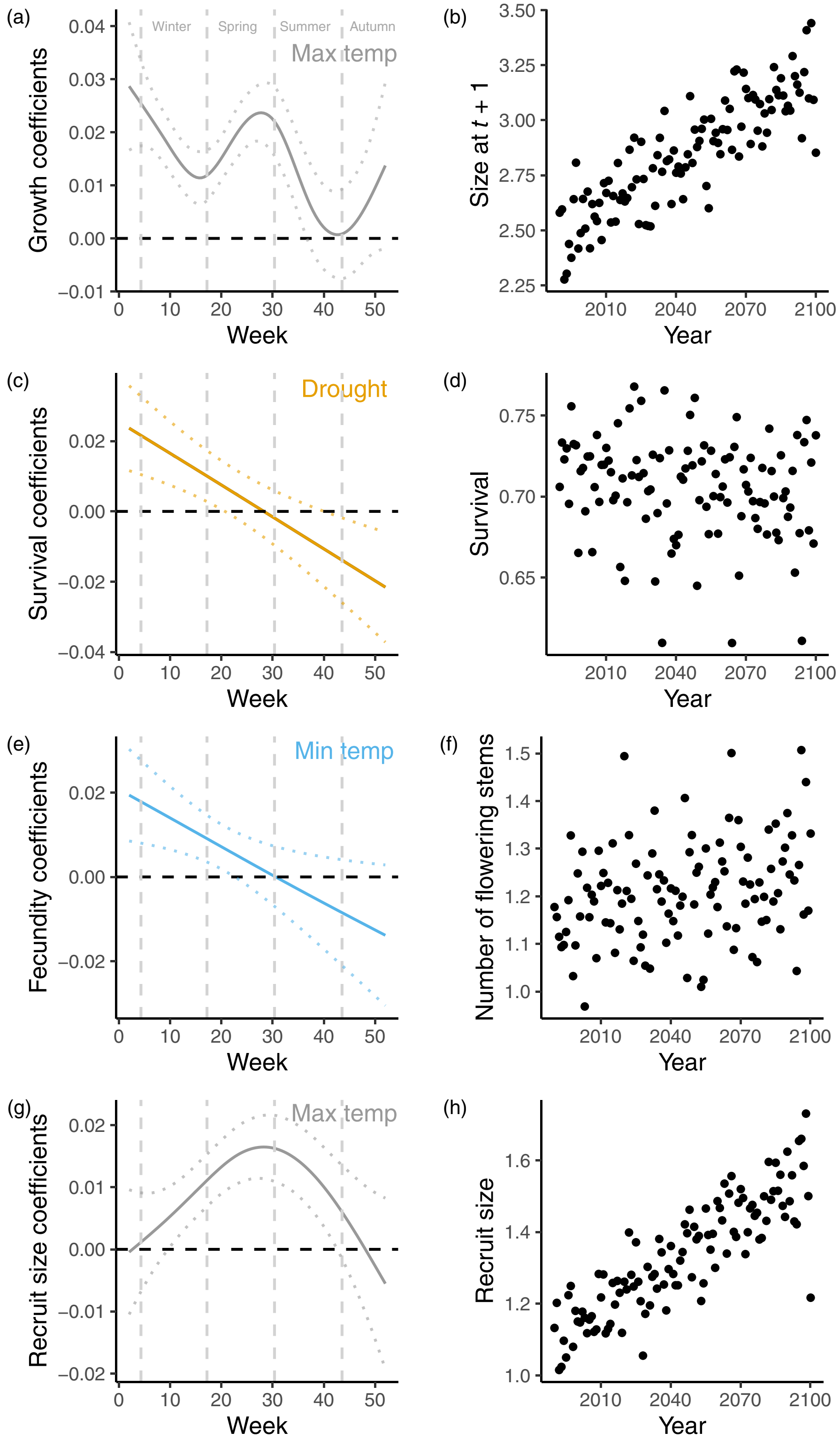
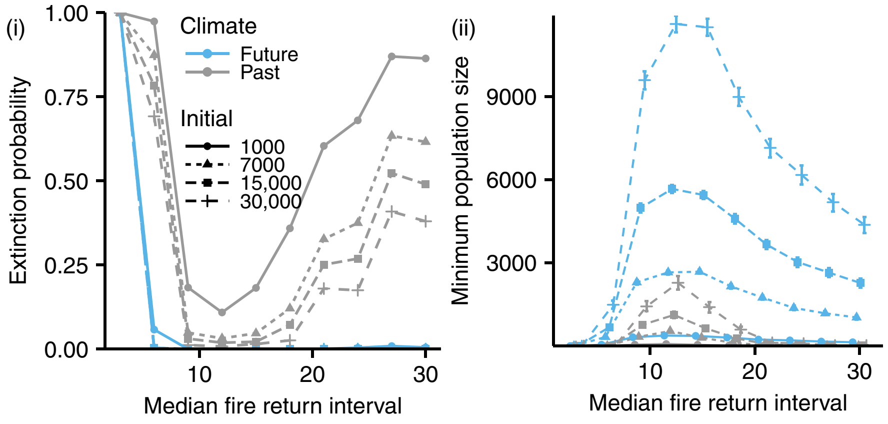


FIGURE 3 Climatic coefficients over the year preceding the census (left column) and the average annual vital rates estimated using the downscaled climate predictions from 1990 to 2099 (right column), for growth (a & b), survival (c & d), fecundity (e & f) and recruit size (g & h). Only the climatic variables with the highest predictive performance are plotted and included in the IPM (Table 1). The coefficients are scaled by the standard deviation of the respective climatic covariate for plotting. Dotted lines indicate the model ±1 standard error. In the right column, each point is the prediction for a median sized individual on a square root scale (2.45) 10 years post fire and in an average population and year. Increasing the number of knots did not change the pattern in any of the FLMs.

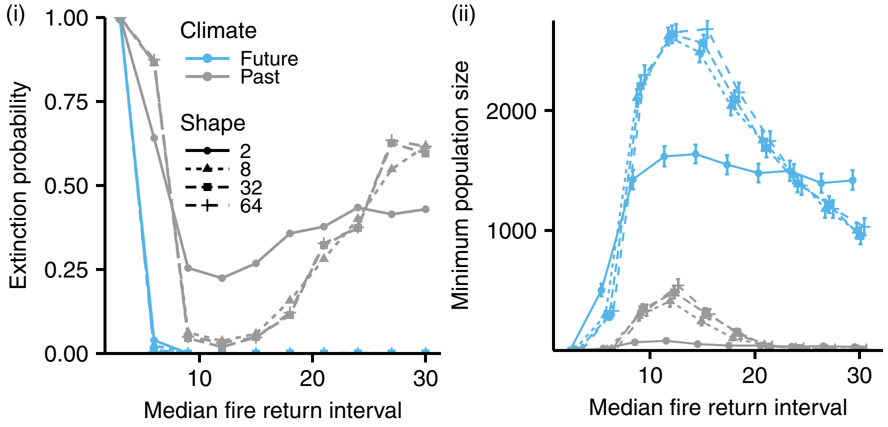
TABLE 1 Cross validation results comparing the predictive performance of the climatic models. Lower values indicate better predictive performance. Climatic models with a better predictive performance than the base model (with no climatic effects) are highlighted in bold. * denotes the model with the best predictive performance for each vital rate; these are used to parameterise the IPM.

Climate model	Growth	Survival	Fecundity	Recruit size
Base	3950.1	5039.4	30044.6	990.8
Min temperature	**3909.5**	5054.9	**29823.2***	1007.0
Max temperature	**3857.8***	5080.8	30082.2	**967.3***
Drought	3954.4	**5029.9***	30250.9	1003.9
Precipitation	3969.9	5060.5	30389.4	1001.5

(a) Initial population size



(b) Shape of fire return interval distribution



(c) Between population variability

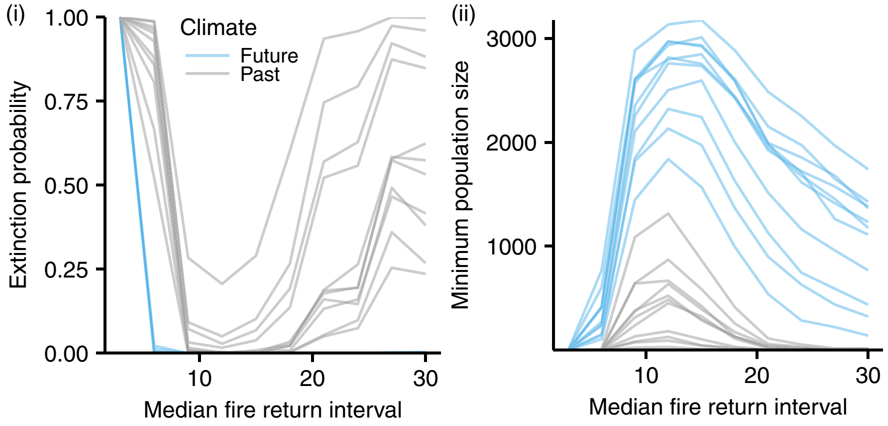


FIGURE 4 Quasi-extinction probabilities (left column) and minimum population sizes (right column) across a range of FRIs and under past and future climatic conditions. (a) shows different initial population sizes (number of seeds in seed bank). (b) shows the effect of changing the level of variability in the FRI, where increasing the shape parameter (*a*) decreases the variability. In (c), each line represents a different population. Points show mean of 1000 simulations (500 in c). Error bars in the right column show bootstrapped 95% confidence intervals for the mean. Points were jittered to minimise overplotting.

than 5% under future climate when the FRI median was over 6 years (Appendix A5).

4 | DISCUSSION

Our model predicts that the range of FRIs under which *E. cuneifolium* is able to persist is likely to increase under forecasted climate change. Climate change is expected to substantially alter population viability across a broad range of taxonomic groups and geographical locations (Bellard et al., 2012; Maclean & Wilson, 2011), with implications for the design of appropriate conservation strategies (Bucharova et al., 2012). Optimal disturbance regimes will differ among species within a community, necessitating compromises when determining optimal regimes for the community as a whole (Menges, 2007; Menges et al., 2017). Under recent climatic conditions, the probability of persistence for *E. cuneifolium* was low at the upper end of the recommended FRI for Florida rosemary scrub

(15–30 years; Menges, 2007; Menges & Quintana-Ascencio, 2004). Our model predicts that temperature increases towards the end of the 21st century are likely to allow *E. cuneifolium* to persist even with FRIs of 30 years, largely due to increasing individual growth. The ability of populations to persist at lower FRIs is also increased, thus resulting in a much wider range of potential FRIs for this species.

Our results highlighted seasonal differences in the impacts of environmental drivers on *E. cuneifolium*. Seasonality in climatic effects have previously been recorded across a diverse range of species, including mammals (Hindle et al., 2019), plants (Tenhumberg et al., 2018) and birds (Kruuk et al., 2015). There are a range of possible mechanisms by which such effects may occur. Direct physiological responses may differ according to season. For example, in the case of *E. cuneifolium* increased minimum temperatures during the coldest part of the year had a positive effect, whilst increased temperatures during the hot summers had a negative impact. Seasonal effects may also however be the result of indirect effects mediated through interacting species, such as competitors, pollinators or soil micro-organisms (Evers et al., 2021) or potentially trade-offs between demographic rates such as survival and fecundity (Tenhumberg et al., 2018).

While including the effects of environmental drivers may increase the accuracy of future population projections (Bakker et al., 2009), accurately quantifying future extinction risk is only possible where sufficient data are available to reliably estimate the vital rates and their responses to environmental drivers (Coulson et al., 2001; Fieberg & Ellner, 2001). Demographic studies typically make a priori assumptions about the temporal windows over which climatic covariates influence the vital rates, usually selecting a single window (Ehrlen et al., 2016; Evers et al., 2021; Van der Pol et al., 2016). This choice may impact on inferences, if failure to capture seasonal differences in the climatic effects leads to inaccurate predictions of future population performance. Our model suggests that in the case of *E. cuneifolium*, fecundity would be predicted to increase under future temperatures if a winter period was selected but decrease if a summer period was selected. By capturing the effect of temperature over the whole year, we found that these effects cancel one another out, resulting in very little net change in predicted future fecundity. Given the antagonistic seasonal effects in fecundity here, it seems probable that in some cases choosing a seasonal period a priori has the potential to lead to misleading inferences. A useful direction for further study would thus be a systematic comparison of the predictive performance, at the population level, of models with and without seasonal effects.

As with all approaches forecasting the future an awareness of uncertainties is important if the output is used to guide management (Schindler & Hilborn, 2015). For example, here, despite relatively small distances among populations, we found large differences in their predicted population dynamics; highlighting the importance of studying multiple populations and considering such uncertainty when making management decisions (Ellner & Fieberg, 2003). Furthermore, though this study system is data-rich relative to many others (Crone et al., 2011; Menges, 2000) data describing the seed bank dynamics and early seedling survival are relatively limited. Almost half of matrix population models exclude the seed bank completely (Doak et al., 2002; Nguyen et al., 2019), despite it having important implications for estimating population persistence (Arroyo-Cosultchi et al., 2022; Nguyen et al., 2019; Quintana-Ascencio et al., 2019). We found that extinction probabilities under forecasted climate change remained low under two possible scenarios of seed bank dynamics. However, due to data constraints, we did not consider how the seed bank dynamics or early seedling survival may be affected by environmental change. Germination, seed mortality and early seedling survival are likely to respond to environmental conditions (e.g. Hawkes, 2004; King & Menges, 2018; Mackenzie et al., 2016), with consequences for future seed bank and population persistence (Ooi et al., 2012). This study represents a step in understanding the future dynamics of this system; further studies quantifying the effect of drivers of such dynamics under a broad range of environmental conditions are necessary to fully understand population responses to future change (Menges, 2000).

Our study has focused on the main effects of two key abiotic drivers, climate and disturbance. Whilst we were unable to quantify them here, interactions between these drivers are likely to also be important, which could result in the optimum FRI differing between past and future climatic conditions (Ehrlen et al., 2016). Such interactions are likely in this study system, as the impacts of both climate change and disturbance may both, at least partly, be mediated indirectly through biotic interactions (Adler et al., 2012; Araujo & Luoto, 2007; García-Cervigón et al., 2021). Under past environmental conditions, the performance of *E. cuneifolium* has been limited by shrubs such as *C. ericoides* (Menges & Kimmich, 1996; Menges & Quintana-Ascencio, 2004). The increase in the demographic performance of *E. cuneifolium* following a recent fire is directly related to the creation of gaps within the shrub matrix, which will close over time. Future optimal FRIs for *E. cuneifolium* will thus likely depend on how *C. ericoides and other species* respond to the changing environments. Caution should also be taken in the interpretation of the result of population persistence with FRIs of over 30 years, as such gaps are likely to remain ephemeral in the future, and the data used to parameterise the model may not allow adequate extrapolation of this effect. Further studies on the influence of climatic conditions on *C. ericoides* and other species, and their competitive effects on *E. cuneifolium* are needed to determine the direct and indirect climatic effects operating and to fully understand how these will affect optimal FRIs (e.g. Adler et al., 2012).

We have shown how forecasted climate change may broaden the range of disturbance regimes under which a rare endemic can persist, potentially decreasing the intensity of management needed. Climate change is expected to drive widespread population change (Maclean & Wilson, 2011; Parmesan & Yohe, 2003). Failure to account for these effects may lead to suboptimal conservation planning (Hannah et al., 2002; Hulme, 2005; Ibanez et al., 2013), yet many population-level studies continue to determine optimal management assuming stationary environments (though see Bernardo et al., 2016; Bucharova et al., 2012; Sletvold et al., 2013). Furthermore, simple estimators of climatic drivers using windows of influence, chosen a priori, may lead to inaccurate predictions of future population responses (Evers et al., 2021). The impacts of even a single environmental driver can be complex and seasonally dependent. Thus the widespread use of statistical tools, such as FLMs, which negate the need to select a single time period (Teller et al., 2016), are necessary to fully understand the impacts of climate change on optimal management strategies.

AUTHOR CONTRIBUTIONS

Pedro F. Quintana-Ascencio and Eric S. Menges collected the demographic data; analysis was carried out by Bethan J. Hindle with guidance from Dylan Z. Childs. Bethan J. Hindle and Dylan Z. Childs led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and R code used in this study are available at https://github.com/bhindle/eryngium-flm and archived on zenodo: https://doi.org/10.5281/zenodo.7925890 (Hindle et al., 2023). The *E. cuneifolium* data (Menges & Quintana-Ascencio, 2004) and observed climatic data were originally provided by the Archbold Biological Station (https://archbold-station.org/html/datapub/data/dataovr.html). The forecasted climatic data were originally provided by the Program for Risk Information on Climate Change (SOUSEI) of the Ministry of Education, Culture, Sports, Science and Technology (MEXT) of Japan carried out by the Meteorological Research Institute (MRI) of the Japan Meteorological Agency (Kusunoki & Mizuta, 2013; Mizuta et al., 2012).

ORCID

Bethan J. Hindle https://orcid.org/0000-0003-3710-6776
Pedro F. Quintana-Ascencio https://orcid.org/0000-0001-7587-8166
Eric S. Menges https://orcid.org/0000-0002-9486-4189
Dylan Z. Childs https://orcid.org/0000-0002-0675-4933

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Cumulative probability of a fire occurring under the Weibull distribution with different medians (3, 6, 15, or 30) and shape parameters (2, 8, 32, or 64).

Figure S2. Effect of size on (a) survival, (b) growth, and (c) fecundity. Red lines show the fitted splines, points show raw data, which are split into size bins for the survival data. Predictions were made assuming a time since fire of 15 years and with the random year and population effects set to zero. The square root of rosette diameter was used as the measure of plant size. Raw data are from all 12 populations. Survival decreases at large sizes, presumably due to senescence. Plants either do not flower or produce very few flowering stems until they are sufficiently large.

Figure S3. Total number of individuals with survival data, across all 12 populations, against the number of years since fire.**Appendix A1.** Downscaling of the predicted climate covariates.

Appendix A2. Structure of the IPM.

Appendix A3. Cluster cross validation.

Appendix A4. Exploring seasonality in the climatic effects.

Appendix A5. Selecting seed bank parameters.

Appendix A6. Effect of simulation length.

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