



Declining pollination success reinforces negative climate and fire change impacts in a serotinous, fire-killed plant

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Abstract Climate change projections predict that Mediterranean-type ecosystems (MTEs) are becoming hotter and drier and that fires will become more frequent and severe. While most plant species in these important biodiversity hotspots are adapted to hot, dry summers and recurrent fire, the Interval Squeeze framework suggests that reduced seed production (demographic shift), reduced seedling establishment after fire (post fire recruitment shift), and reduction in

the time between successive fires (fire interval shift) will threaten fire killed species under climate change. One additional potential driver of accelerated species decline, however, has not been considered so far: the decrease in pollination success observed in many ecosystems worldwide has the potential to further reduce seed accumulation and thus population persistence also in these already threatened systems. Using the well-studied fire-killed and serotinous shrub species *Banksia hookeriana* as an example, we apply a new spatially implicit population simulation model to explore population dynamics under past (1988–2002) and current (2003–2017) climate conditions, deterministic and stochastic fire regimes, and alternative

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scenarios of pollination decline. Overall, model results suggest that while *B. hookeriana* populations were stable under past climate conditions, they will not continue to persist under current (and prospective future) climate. Negative effects of climatic changes and more frequent fires are reinforced by the measured decline in seed set leading to further reduction in the mean persistence time by 12–17%. These findings clearly indicate that declining pollination rates can be a critical factor that increases further the pressure on the persistence of fire-killed plants. Future research needs to investigate whether other fire-killed species are similarly threatened, and if local population extinction may be compensated by recolonization events, facilitating persistence in spatially structured meta-communities.

Keywords Climate change · Fire frequency · Interval squeeze · Pollination · Process-based simulation model · Mediterranean-type ecosystem

Introduction

Climate change projections for the end of the twenty-first century are alarming in many regions around the world (Diffenbaugh and Field 2013; IPCC 2021). Many terrestrial ecosystems are becoming hotter and drier, not only impacting plant demographic processes but also leading to more frequent, intense, and larger wildfires (Hantson et al. 2017; Silva et al. 2018; Nolan et al. 2020). Mediterranean-type ecosystems (MTEs) especially are showing extreme projections (e.g. more frequent and longer-lasting droughts or heatwaves) for the combination of fire and climate change (Mouillot et al. 2002; Flannigan et al. 2009; Lozano et al. 2017). Although most plant species of MTEs are adapted to hot, dry summers and recurrent fire, the combined effects of changes in climate and fire regimes foreshadowed in current projections may drive many plant species into decline, or even to extinction (Enright et al. 2015). This syndrome was designated ‘Interval Squeeze’ by Enright et al. (2015), which proposes three key drivers of species decline: demographic shift, post-fire recruitment shift, and fire interval shift. The first two shifts, demographic and post-fire recruitment, are direct climate impacts on biological processes. Demographic shift refers to the reduction of plant growth, survival and seed production rates as

climate warms (and dries), and consequently, a reduction in the availability of viable seeds for recruitment after a fire. Post-fire recruitment shift refers to a reduction in seedling establishment and survival after fire due to the increasing impact of dry years (drought) as climate continues to change. The combination of demographic and post-fire recruitment shifts defines the demographic window of time within which a population can persist in relation to a given disturbance regime (e.g. fire). The third shift, fire interval shift, refers to the projection of more frequent fires as climate changes, reducing the time between successive fires and thus increasing the immaturity risk window for many plants. The super-imposition of this fire-interval shift on the reduced demographic envelope squeezes the range of tolerable fire intervals for self-replacement of a plant population, and thus, its probability of persistence is reduced.

While both empirical data (Enright et al. 2014, 2015; Keith et al. 2014; Harvey et al. 2016; Barton and Poulos 2019) and conceptual modelling (Batllori et al. 2017; Henzler et al. 2018) in principle support the ‘Interval Squeeze Model’, many details of how exactly climate and fire regime changes interact in threatening fire-adapted species remain to be more fully investigated. In particular, it remains unclear which demographic pathways (e.g. flowering-pollination-fruit set) are contributing to observed and predicted changes at the population level.

Of all fire-adapted plant functional types, fire-killed (non-sprouter) serotinous species are hypothesized to be the most ‘at risk’ plant group to ‘Interval Squeeze’ effects due to their high dependency on successful recruitment immediately after a fire (Enright et al. 2015). One well-investigated example of such a non-sprouter species is *Banksia hookeriana*. This highly endemic shrub species is located in a very limited geographical range in the Mediterranean ecosystem type shrublands of South-western Australia. Demographic studies on *B. hookeriana* started in the 1980s with most research focusing on annual infructescence (here-after referred to as ‘cone’) production, growth, and mortality rates (Enright and Lamont 1989; Enright et al. 1998). Long-term data on *B. hookeriana* confirm post-fire recruitment and demographic shift predicted by the ‘Interval Squeeze Model’, with cone production decreasing by 50% over the past 30 years, correlating with an approximate 20% reduction in annual

rainfall over the same period (Keith et al. 2014; Enright et al. 2015).

Recent field observations for *B. hookeriana* suggest an additional demographic driver that has so far not been considered in evaluating possible future population dynamic shifts in serotinous (and other) plant species which may further impact them as climate changes; a decline in pollination success, leading to an increase in the proportion of sterile versus fertile cones. This would cause a further decline in the canopy seed bank of this species, exacerbating the seed production and storage impact already detailed for number of cones per plant produced per year. Declining pollination success is a phenomenon that is currently being observed in many systems worldwide (Allen-Wardell et al. 1998; Thomann et al. 2013; Bennett et al. 2020) and its relative contribution to negative climate effects on seed production remains largely unexplored.

To explore whether, and under which conditions, pollination success is an additional critical driver for the long-term persistence of *B. hookeriana* populations, we here develop a process-based non-spatial population model using empirical data spanning the last 33 years (1986–2018). The specific strengths of our process-based, mechanistic model are the disentanglement of the seed dynamics (i.e. seed storage and loss) into separated individual processes linked to empirical data, producing more quantitative and realistic predictions. Specifically, we address the following questions: (i) what is the additional effect of a decrease in pollination success on population dynamics as compared to the decrease in inflorescence (here after referred to as ‘flower’) production, increased mortality, and decrease in fruit set (i.e. number of follicles per cone) caused by changes in the climatic conditions alone, and (ii) under which fire-climate conditions is pollination success an additional critical factor for the long-term persistence of *B. hookeriana* populations. Thus, we investigate the synergistic effects of changes in the climate, fire regimes and pollination. From a more conceptual viewpoint our study provides additional insights into an important, yet so far neglected, additional pathway of how demographic processes can further augment the negative ‘Interval Squeeze’ effects.

Material and methods

Model description

We developed a non-spatial process-based plant population model. The overall *purpose* of our model is to explore the combined impacts of fire, pollination success and climate change on the population dynamics in serotinous, fire-killed plants to support their conservation. Simulations are based on the well-studied and highly serotinous shrub, *B. hookeriana*. All modelled demographic processes are directly linked to empirical field or laboratory data.

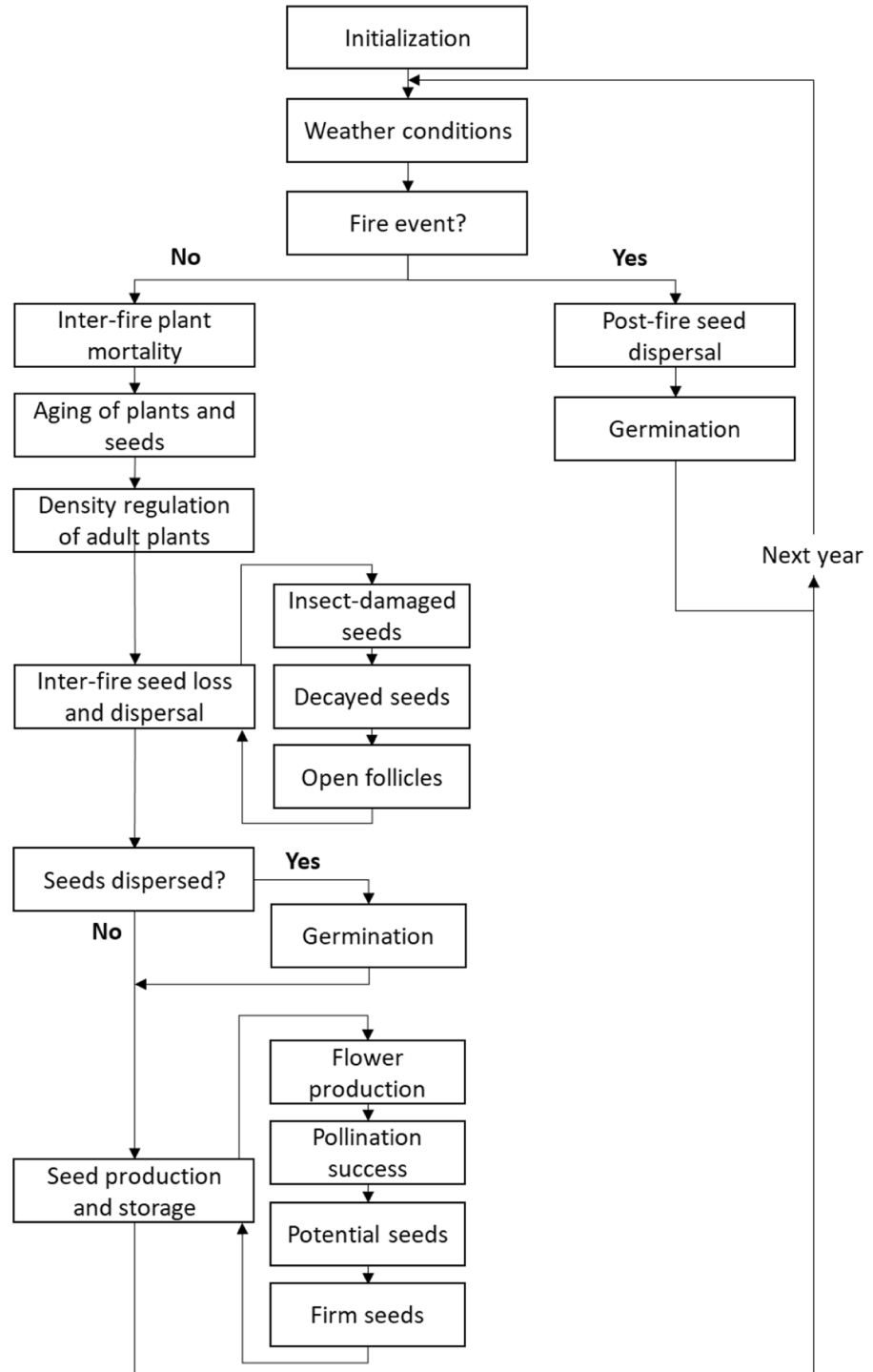
A complete, detailed model description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006, 2010, 2020) is provided in Supplementary Information S1. We implemented the model in C++11 and analysed the derived results with R v3.5.3 (R Core Team 2019). For data visualization we used the R packages ‘ggplot2’ v3.3.2 (Wickham 2016) and ‘plotly’ v4.9.2.1 (Sievert 2020). The link to the model code repository is available in Supplementary Information S1.

The model includes the following *entities*: populations and cohorts. The environment is described by annual weather conditions (rainfall) and fire events (boolean state, i.e. a fire occurs in a given year or does not). Cohorts are characterized by the age of the plants, the number of individuals, and the average size of the canopy seed bank per individual, where the seeds are classified according to their age. Furthermore, cohorts are classified as post-fire cohort or inter-fire cohort. Each population can consist of several cohorts. Populations are described by their carrying capacity (i.e. the maximum number of adult plants per unit area that it can hold), time since last fire, fire interval (i.e. time between fires), persistence time, and number of generations. In this study, we modelled one single isolated population, that is, there is no seed immigration from other populations. The population dynamics is modelled in annual time steps, and the simulation runtime was 500 years (maximum) or until population extinction. The spatially implicit model represents an area of 100 m by 100 m, in which one mature plant is assumed to require an area of 2 m by 2 m (Esther et al. 2008). This habitat size corresponds to the average size of the subpopulations found on the Eneabba Plain in southwest Australia (He et al. 2004).

The most important processes of the model, which are repeated every time step, are presented in Fig. 1. The model simulates the lifecycle of a *B. hookeriana* population, specifically the dynamics of the number

of individuals and their canopy seed bank in each cohort. Changes in the number of plants are caused by the probability of plant mortality between fires, which depends on plant age and weather conditions,

Fig. 1 The most important processes of the *B. hookeriana* population model are presented here. The model runs annually, starting after the fire season (~ April). At the beginning of each time step, (1) the annual weather conditions are picked randomly from real rainfall data, and (2) the fire event is evaluated. When fire occurs (i.e. the time since fire is equal to the fire interval), all plants die and two processes are executed: (1) post-fire seed dispersal, (2) post-fire germination of dispersed seeds. On the other hand, when a fire does not occur (i.e. the time since fire is lower than the fire interval), the following processes are executed: (1) inter-fire plant mortality, (2) aging of plants and seeds, (3) density regulation of adult plants, (4) inter-fire seed loss and dispersal, in which a proportion of seeds are lost from insect-damaged and decay, and from the remaining canopy seed bank, a proportion of seeds are dispersed due to sporadic rupture of follicles. If seeds are dispersed, (5) they germinate, forming a new cohort. Finally, (6) adult plants flower, set new seeds and store them in their canopy. The seed production process is composed of four subprocesses: flower production, pollination success, potential seeds, and firm seeds



or by a crown fire, in which case all plants die (Enright et al. 1998). Adult plants produce new seeds when the weather conditions are favourable, increasing the canopy seed bank. The seed production consists of four hierarchical sub-processes: first, the number of flowers is calculated as affected by plant age and antecedent weather conditions. Second, based on newly obtained field data, a percentage of flowers are converted into fertile cones (i.e. pollination success). Then, the potential seeds are calculated by multiplying the number of fertile cones by the number of follicles per cone and by the number of seeds per follicle. Finally, the proportion of those potential seeds that develop embryos (i.e. firm seeds) are stored in the canopy seed bank and have a maximum longevity of 12 years (Enright et al. 1996). When a plant dies during the period between fires, all the seeds are lost (Enright et al. 1998). The canopy seed bank is reduced by the age-dependent functions of inter-fire seed loss [insect-damaged and decayed seeds; Eqs. 5 and 6 from Enright et al. (1996)], and seed dispersal. Seeds are dispersed during the inter-fire period from age-dependent sporadic rupture of follicles (fitted logistic growth curve from unpublished data; Eq. 10 in Supplementary Information S1) leading to occasional recruitment of inter-fire individuals, or when a fire occurs, when all the follicles open due to the heat of the fire, releasing all stored seeds which then either germinate in the first winter after fire, or perish (Enright et al. 1998). A proportion of the dispersed firm seeds germinate to form a new cohort (i.e. viability of firm seeds).

Table 1 summarises the most important parameters of the model for the two climate scenarios investigated; (i) historical ‘baseline’ climate prior to recent warming and drying, and (ii) current climate. Most of the model parameters were based on older, published references to the baseline climate scenario for two main reasons: (i) new data were not available or were insufficient (e.g. sample sizes were too small for adequate statistical analysis, or rainfall data were unavailable due to weather station closure), and (ii) the inclusion of more differences between the climate scenarios would make it more complex to understand the results of the simulations for interpretation and to answer the research questions set out in our study. The parameters of the current climate scenario that differ from the reference scenario are the weather impacts on flower production, pollination success, and the number of follicles per cone (i.e. fruit set).

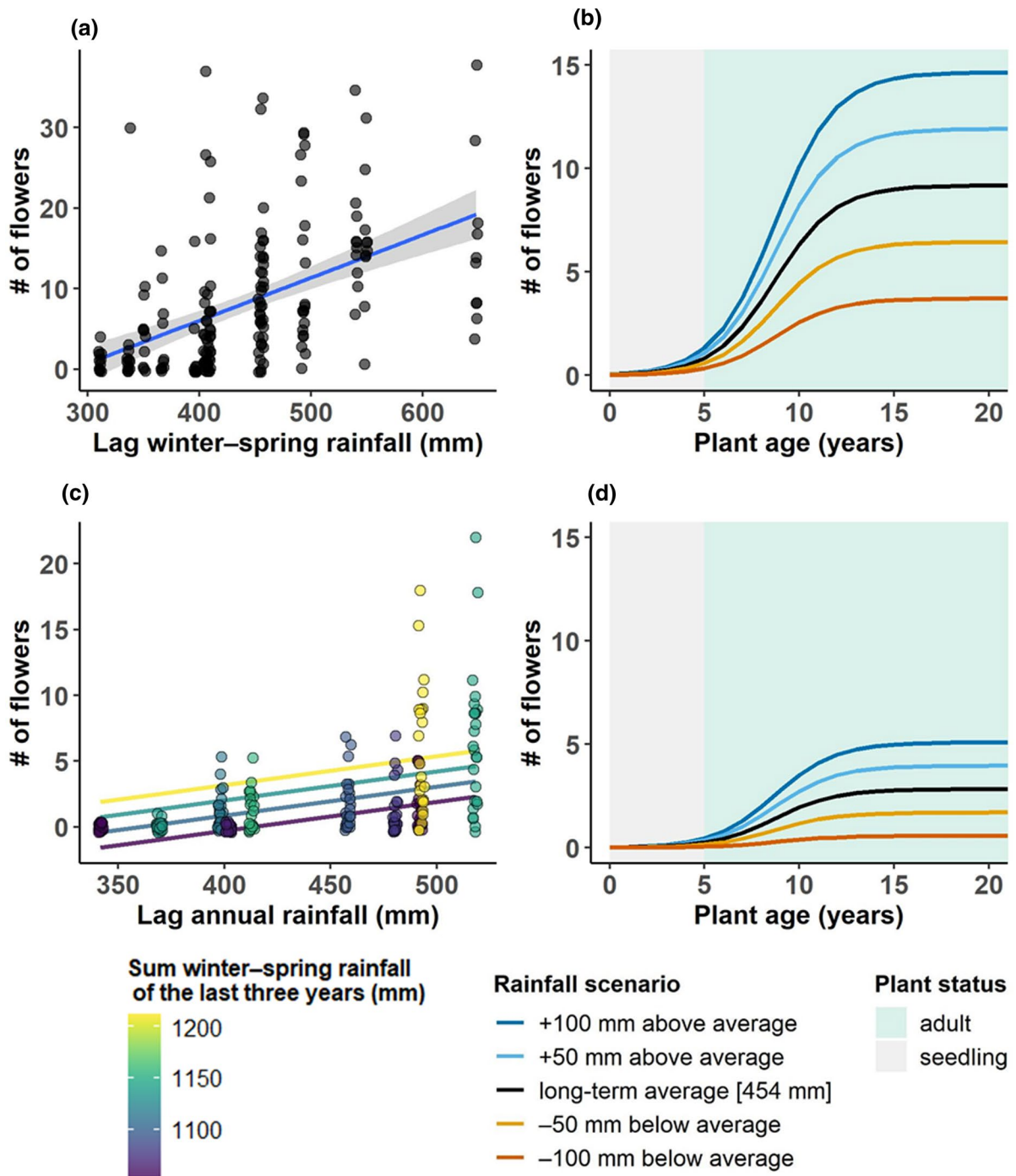
The primary outcome measure was ‘persistence time’, the simulation runtime at which the last plant dies, i.e. local extinction occurs. Therefore, the longer the persistence time of a single population, the greater the resilience of a larger metapopulation (the more likely it is that metapopulation dynamics will rescue a small population from extinction) (Hanski 1998).

All simulation experiments commence with a fire in a 17-year-old *B. hookeriana* population [based on the mid-point of estimated mean fire intervals of 13–21 years for shrublands at Eneabba calculated by Miller et al. (2007) and Enright et al. (2012) and theoretical optimum fire interval of 16–17 years reported by Enright et al. (1996)]. The number of individuals

Table 1 Summary of the most important parameters of the model

Parameter	Unit	Value	Range	References
Carrying capacity	Number	2500	1600–4444	Esther et al. (2008)
Seed longevity	Years	12	5–15	Enright et al. (1996)
Age of maturity	Years	5	3–8	Enright et al. (1998)
Age of increased mortality	Years	25	20–30	Enright et al. (1998)
Annual increase in mortality due to senescence	–	0.01	0.005–0.02	Enright et al. (1998)
Pollination success	%	Baseline: 90 Current: 65	62–95	Our data
Follicles per cone	Number	Baseline: 9.97 Current: 7.32	6.66–10.58	Our data
Seeds per follicle	Number	2	2	Enright et al. (1996)
Firm seeds	–	0.83	0.53–0.88	Enright et al. (1996)
Viable seeds	–	0.744	0.566–0.922	Enright et al. (1996)

The complete table of all parameters is in Table S4 (Supplementary Information S1)



and seed bank size of the 17-year-old starting population is 845 plants and 626 firm seeds per plant, representing the mean values calculated from 1000 simulation runs under baseline conditions. Model dynamics are driven by input data representing the real rainfall

conditions taken from the closest weather station to the study area (Eneabba Weather Station No 08225; Australian Bureau of Meteorology). Two climate scenarios were compared and tested systematically: baseline (1988–2002), and current (2003–2017).

Fig. 2 The two flower production scenarios used in the simulation experiments. Each row corresponds to a scenario: on the left side the selected model fit of the relationship between annual flower production per adult *B. hookeriana* plant and rainfall prediction variables is shown, and on the right side the impacts of the left best-fit model to the age-standardized flower production model, which corresponds to the black line in **b**. The first row shows the best linear mixed-effect model between the flower count baseline data set (1988–2002, plant age 17–31 years) and the total rainfall in winter–spring of the previous year (i.e. lag winter–spring). The second row shows the best linear mixed-effect model between current flower count data set (2008–2017, plant age 11–20 years) and the two covariates: total annual rainfall from previous year (i.e. lag annual rainfall, in the x-axis) and sum of winter–spring rainfall of the previous 3 years. The weather impacts of each best-fit model on plant age (right side) is shown with the same amount of rainfall to compare the flower production scenarios [the second predictor in the current data set (i.e. sum of winter–spring rainfall of the previous 3 years) was set to the average rainfall in the current climate scenario (1130 mm in 2003–2017)]. The shaded areas distinguish the status of the plant between seedling (grey), where all flowers failed to set seed, and adult (green), where a proportion of flowers are potentially pollinated

Antecedent rainfall conditions are strongly correlated with flower production and plant mortality (Keith et al. 2014). Each climate year is composed of a set of three predictor variables driving the annual flower production and plant survival: total winter–spring rainfall from the previous year, total annual rainfall from the previous year, and the sum of winter–spring rainfall of the previous 3 years. Fig. S5 (Supplementary Information S2) shows the distribution of rainfall for both climate scenarios for each prediction variable, with a 15% reduction in rainfall (climate drying) in the current scenario. Regarding fire events, we tested two scenarios: deterministic and stochastic fire events. While simulation results from the deterministic fires are easier to trace and interpret due to the lack of uncertainty, their comparison with stochastic fire events helps us to understand how fire fluctuations impact population demographics. To have a fair comparison between both fire scenarios, the time interval between fires in the stochastic fire scenario was drawn from a truncated symmetric normal distribution around a selected mean. The minimum fire interval of stochastic fires (i.e. truncated value) was selected so that population extinction due to overly short fire intervals cannot occur under baseline weather conditions. This calculated minimum fire interval was 7 years (Supplementary Information S1: Fig. S2) coinciding with the minimum age at

which experimental fires in this vegetation type successfully propagated (Fontaine et al. 2012) and was a fixed value throughout all simulation experiments. We assumed weather and fire as independent environmental factors because a more mechanistic modelling of complex climate–fire correlations would go beyond the scope of this study. This independence allowed us to explore a wider range of climate–fire scenarios.

The key processes in the model are flower production and inter-fire plant mortality. Both processes follow a two-step hierarchical approach: first, the value is calculated based on plant age, and then weather conditions modify this calculated value. For the implementation of flower production (Fig. 2), two flower counts per individual were used: baseline data set, i.e. 1988–2002 (plant ages 17 to 31 years) and the current data set, i.e. 2008–2017 (plant ages 11 to 20 years). For the baseline dataset, Enright (Keith et al. 2014) found a strong linear relationship between mean annual flower production and the total winter–spring rainfall of the previous year (Fig. 2a). In contrast, in our new current data we found two closely related but slightly more significant covariates: total annual rainfall of the previous year, and the sum of winter–spring rainfall of the last 3 years. We fit the current flower data set with linear mixed-effect models using the ‘lme4’ package v1.1.26 (Bates et al. 2015). For more detail on regression analyses, see Supplementary Information S2. Concerning flower production based on plant age, we adapted Eq. 1 of Enright et al. (1996) to a logistic growth curve, with the maximum value of the curve (approx. nine flowers per year) reached at age 15 years (Enright et al. 1996). The value of nine flowers was calculated from the best-fit linear relationship in the baseline flower count data set (Fig. 2a) with the predictor variable under long-term average winter–spring rainfall conditions (average total winter–spring rainfall in 1965–1990, i.e. 454 mm). The black curve in Fig. 2b corresponds to our age-standardized flower production equation. This logistic growth curve of flower production based on plant age is then modified by multiplying the weather coefficient. This coefficient is a linear division ratio between the flower production under specific rainfall conditions (Fig. 2a and c), and the flower production under long-term average weather conditions in the baseline data set (i.e. approx. nine flowers). The second column of Fig. 2 shows the impacts of the weather coefficient on the

logistic growth curve of flower production based on plant age in the baseline data set (Fig. 2b) and in the current data set with linear regression (Fig. 2d). We performed an additional scenario of the current flower data set using the generalised linear mixed-effects model for the negative binomial family due to the high number of zeros (Supplementary Information S2). In addition, we also tested the simulation experiments excluding the second explanatory variable (i.e. the sum of winter–spring rainfall of the last 3 years) for both linear and generalised linear mixed-effects models under current climate. The resulting flower production based on age and weather was limited to 16.5 (i.e. truncated value), as this is the highest average annual flower production on plants observed. In the model, the flower production process is initiated once plants are 5 years old or older, because few individuals are mature at younger age (Enright et al. 1996).

In the case of inter-fire plant mortality, the mortality probabilities based on plant age are constituted in three age segments: (i) for plant age 0–1 year (i.e. seedling recruitment stage) mortality is 0.923 (mean rate from Enright and Lamont 1989), (ii) for plant ages 1–25 years, the mortality probability curve was taken from the age-standardized equation of mean mortality rates used in Keith et al. (2014), and thereafter, (iii) the mortality probability increases by 0.01 each year due to plant senescence (Enright et al. 1998). Keith et al. (2014) found a strong linear relationship between the variation around the age-standardized equation of mean mortality rates mentioned above and the total winter–spring rainfall from the previous year. This linear equation has a positive slope of about 6% per 100 mm around the long-term average winter–spring rainfall, whose response variable corresponds to the percentage change that alters plant mortality by age. For plant age 0–1 (i.e. seedling recruitment), the range of the resultant post-fire mortality probability was restricted between 0.911 (the minimum mortality found by Enright and Lamont 1989) and 0.987 (Groeneveld et al. 2002). In contrast, seedling recruitment from seeds dispersed during the period between fires has a higher probability of mortality due to competition with already established vegetation. Thus, inter-fire recruitment is derived by taking 5% of the post-fire recruitment survival and transforming the calculated value to mortality (Enright et al. 1998). Figure 3 shows the inter-fire

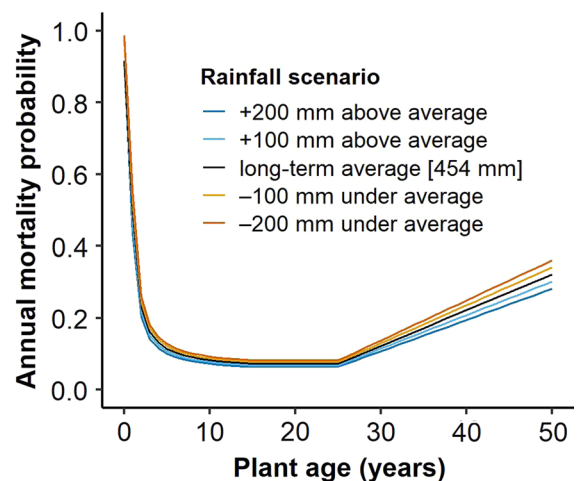


Fig. 3 Annual mortality probability curve between fires by age of the *B. hookeriana* shrub in Eneabba in different rainfall scenarios. Total winter–spring rainfall from previous year affects the age-standardized mortality probability curve by approx. 6% per 100 mm around the long-term average

plant mortality curves for five different levels of total winter–spring rainfall.

Sensitivity analysis

We performed a local sensitivity analysis varying one parameter at a time. Each parameter was altered by $\pm 5\%$ and $\pm 10\%$ for each combination of climate (baseline and current) and fire (deterministic and stochastic) scenarios. We calculated the mean persistence time as a result of the model from 1000 repetitions, with the maximum run time set to 500 years. We measured the sensitivity of each variation by calculating the percentage deviation between the mean persistence time of the reference values and the mean persistence time for each varied parameter. Parameter values that cannot exceed specific values, such as probabilities, were truncated when necessary. In addition, all parameters set as a natural number (i.e. a non-negative integer) were varied by taking the integer part of the altered value when the reference value was decreased and taking the next integer when it was increased. With this approach, all parameter variations were different from the reference value. For example, the reference value for seed longevity is 12 years, so the altered values are 10.8, 11.4, 12.6 and 13.2,

and since seed longevity is a non-negative integer, the altered values selected were 10, 11, 13 and 14, respectively.

Simulation experiments

Table 2 shows the four simulation experiments carried out in this modelling study. The simulation run time was 500 years or until population extinction. All simulations were replicated 1000 times. The results of simulation experiments 1 to 3 are shown as the mean $\pm$ SD of these 1000 replications in the Results section, and the median, upper and lower quartiles in Supplementary Information S3. Experiment 4 shows only the mean (in Results) and median (in Supplementary Information S3) because results are three-dimensional plots. Regarding the current climate scenario, four alternative regression equations of flower production based on rainfall conditions were used (see model description). We present the simulation outputs using the linear mixed-effect model with the two explanatory variables (i.e. total annual rainfall from the previous year, and total winter–spring rainfall of the previous 3 years) in Results (and summary results for the other three versions in Fig. S9 in Supplementary Information S3, since scenarios did not show significant difference).

Results

Canopy seedbank dynamics under baseline climate conditions

In the absence of fire (Fig. 4a), the maximum number of viable seeds stored by the *B. hookeriana* population occurred in year 19 (time since fire), with a mean canopy seed store of 380,437 viable seeds per ha (and 505 per plant). The simulated population went locally extinct with a mean persistence of 90.6 ± 12.7 years (mean $\pm$ SD). The mean maximum plant longevity (53 ± 2.9 years), and the frequency of inter-fire recruits from seeds dispersed in the absence of fire were not sufficient for population persistence (see Fig. S14 in Supplementary Information S3 for the comparison of the seed dynamics between the post-fire cohort and the inter-fire cohorts). In contrast, recurring fires with the mean fire interval estimated for Eneabba (i.e. 17 years) allowed the population to persist. This held for both deterministic and stochastic fire distributions: When fire events were deterministic (i.e. fixed, non-random fire intervals of 17 years) the population had a successful self-replacement with no significant signs of seed bank decline (Fig. 4b). However, when adding stochasticity to fire interval (Fig. 4c), the population also persisted but the propagule density declined over time. The mean number of viable seeds per hectare stabilized after 70 years in stochastic fires at approx. 109,000 seeds.

Table 2 Details of the four simulation experiments tested

Simulation experiment	Predicted variable	Driver			Interval squeeze shift
		Climate	Pollination success	Fire interval	
1. Canopy seedbank dynamics under baseline conditions	Viable seeds	Baseline	Baseline	No fire, deterministic, stochastic (mean = 17 years)	None
2. Canopy seedbank dynamics under different scenarios	Viable seeds	Baseline, current	Baseline, current	No fire	Demographic, post-fire recruitment
3. Impact of pollination success on population persistence	Persistence time	Baseline, current	0–100% in 5% steps	Deterministic, stochastic (mean = 17 years)	Demographic, post-fire recruitment
4. Combined effects of climate change, pollination decline, and changing fire intervals	Persistence time, # of generations	Baseline, current	0–100% in 5% steps	Deterministic, stochastic (mean 10–35 years)	Demographic, post-fire recruitment, fire interval

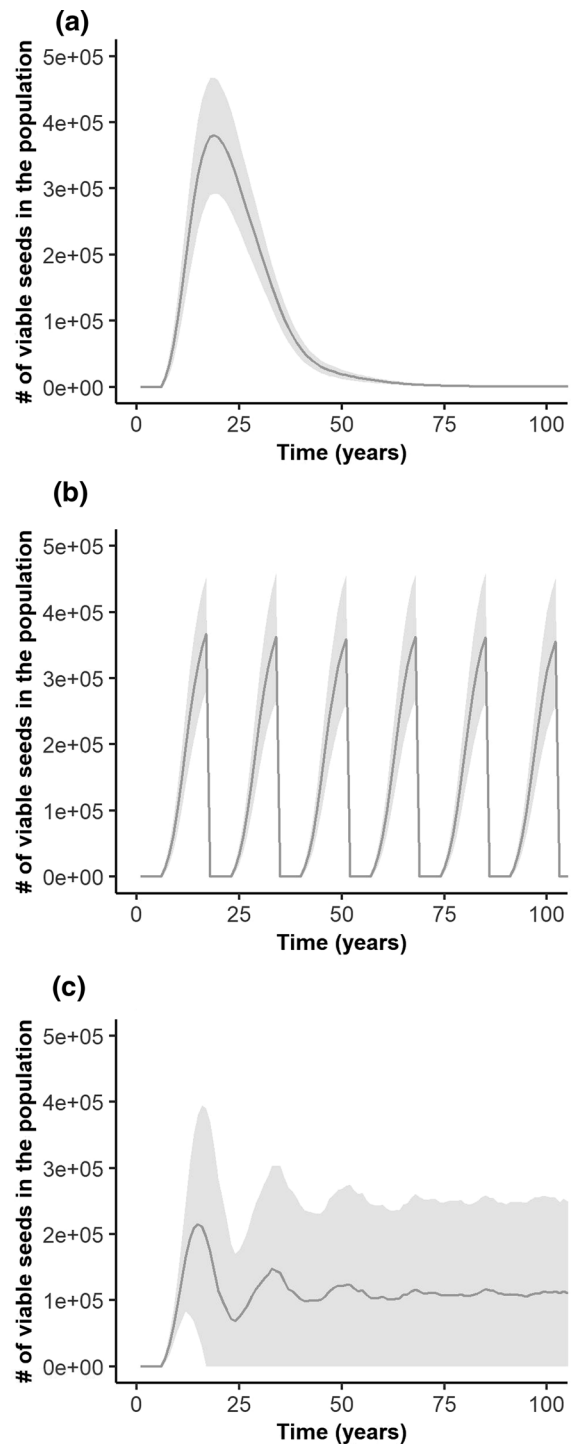
Fig. 4 Simulation experiment 1, control scenarios using the climate and *B. hookeriana* demographic data from 1988–2002. The simulations show the dynamics of the viable firm seeds of the *B. hookeriana* population (y-axes) over time (x-axes) in three different scenarios: **a** no fire events, **b** deterministic fire events of 17 years interval, and **c** stochastic fires events using symmetric truncated normal distribution (mean = 17, min = 7, and max = 27). The SD was calculated using the range rule, i.e. ($\text{max} - \text{min}/4$). Each scenario has 1000 replications in which the lines show the mean values and the shaded areas are $\pm$ SD

Canopy seedbank dynamics under different scenarios

Excluding fire, the comparison of the population dynamics under four alternative scenarios revealed the effect of climate change and pollination decline alone and in combination. Four scenarios are compared: (i) baseline climate with baseline pollination success (Fig. 5; grey), (ii) baseline climate with current pollination success (green), (iii) current climate with baseline pollination success (blue), and (iv) current climate with current pollination success (orange). In all scenarios, populations reached the maximum seed storage at 19 years since last fire (i.e. the start of the simulation). Climate change alone (i.e. grey vs blue) led to a reduction in the number of seeds stored in the population by 80% at 17 years after the fire. With a reduction in pollination success only, the seed-bank decreased by 27% at 17 years for both climate scenarios.

Impact of pollination success on population persistence

In the baseline climate scenario, both fire scenarios (i.e. deterministic and stochastic) led to a maximum persistence time with the baseline (past recorded) pollination success. A pollination decline to the current values caused no decline in time to extinction in the deterministic baseline scenario and only a 4% decline in the stochastic scenario (Fig. 6a). Under the current climate scenario (Fig. 6b), no simulation run reached the maximum persistence time (maximum persistence was 359 years at 100% pollination success for deterministic fires). The persistence time declined linearly as pollination success declined. The comparisons between past and recent pollination success rates in both deterministic and stochastic fire scenarios showed a decrease of the mean persistence time of approx. 16% (116.3



to 95.5 years) and 18% (97.8 to 82.1 years), respectively. As was the case in the baseline climate scenario, the stochastic fire scenario always led to a lower persistence time at all pollination success

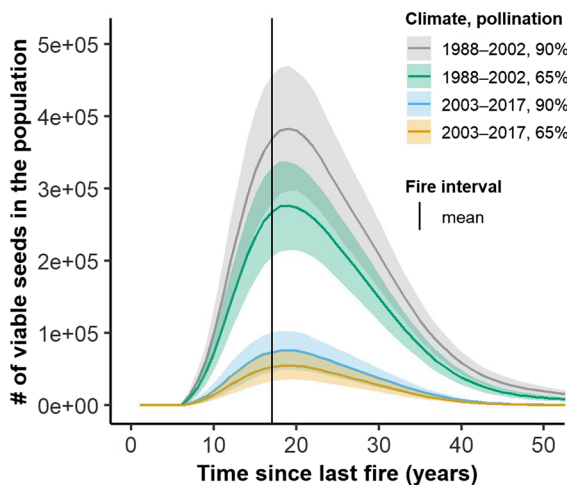


Fig. 5 Simulation experiment 2 shows the number of available viable seeds in simulated *B. hookeriana* populations over time in the absence of fire. Four scenarios are compared: (i) grey colour is the control scenario using baseline climate with the past recorded 90% pollination success, (ii) green is the control scenario with the current recorded 65% pollination success, (iii) blue is the current climate scenario using the past pollination success, and (iv) orange is the current scenario with the current recorded pollination success. Each scenario has 1000 replicates. The lines in the four scenarios show the mean values and the shaded areas are the $\pm$ SD. The black vertical line indicates the estimated mean fire interval at Eneabba (17 years)

scenarios as compared to the deterministic fire scenario.

Combined effects of climate change, pollination decline and changing fire intervals

With baseline climate conditions and deterministic fire events (Fig. 7a), the observed decline in pollination success caused a reduction of the optimal fire interval window from 12–32 to 14–28 years (with 90% and 65% pollination success, respectively) with no effect on population persistence. Similarly, for stochastic fires (Fig. 7c) the fire interval window was squeezed from 16–24 to 19–20 years, but the mean population persistence time decreased approx. 3% (from 500 to 485 years). Interestingly, using the maximum number of generations as a basic measure to compare past and present pollination success rates (instead of population persistence in years) showed a shift of the optimal mean fire interval from 12 to 13 years for deterministic fires and from 13 to 15 years for stochastic fires.

The current climate scenario with deterministic fires and baseline pollination success (Fig. 8a) showed a maximum mean persistence time of 144 years. As in experiment 3, no simulation run reached the maximum persistence time under current climate conditions (i.e. the maximum persistence was 394 years at 100% pollination success and a mean fire interval of 22 years for deterministic fires). The optimal fire interval window for deterministic fires from baseline to current pollination success under current climate conditions was shifted to 2 years later, i.e. from 20–27 years (with a persistence time of approx. 142 years) to 22–29 years (with a persistence time of 118 years), and to one year later for stochastic fires, i.e. from 21–26 (and 114 years persistence) to 22–27 years (and 100 years persistence). The persistence time change between baseline and current recorded pollination success in both deterministic and stochastic fires decreased by 16.9% and 12.3%, respectively.

As for number of generations, there was no unique mean fire interval that reached a significantly higher number of generations since the model results are rather homogeneous. Furthermore, the optimal fire interval window between the baseline and the current pollination success rates remained the same (18–20 and 17–20 for deterministic and stochastic fires, respectively), and only the number of generations was reduced: from 7.2 to 5.8 generations, and from 5.8 to 4.9 generations, respectively.

Table 3 shows the main results in the four climate-fire scenarios for the observed pollination decline.

Sensitivity

Most of the model parameters were robust to $\pm 5\%$ and $\pm 10\%$ shifts from their reference values, i.e. this variation of the parameters for each climate-fire scenario showed little effect on persistence time (Supplementary Information S4: Table S7). The most sensitive parameters were those related to post-fire recruit mortality: A 10% increase (8.3% actual change due to truncation) of the lower limit of post-fire recruit mortality reduced persistence time by approx. 65% in the baseline scenarios, and by approx. 37% in the current climate scenarios. The variation in the upper limit and mean post-fire recruit mortality only affected the current climate scenarios, where deterministic fires showed larger changes in persistence time compared

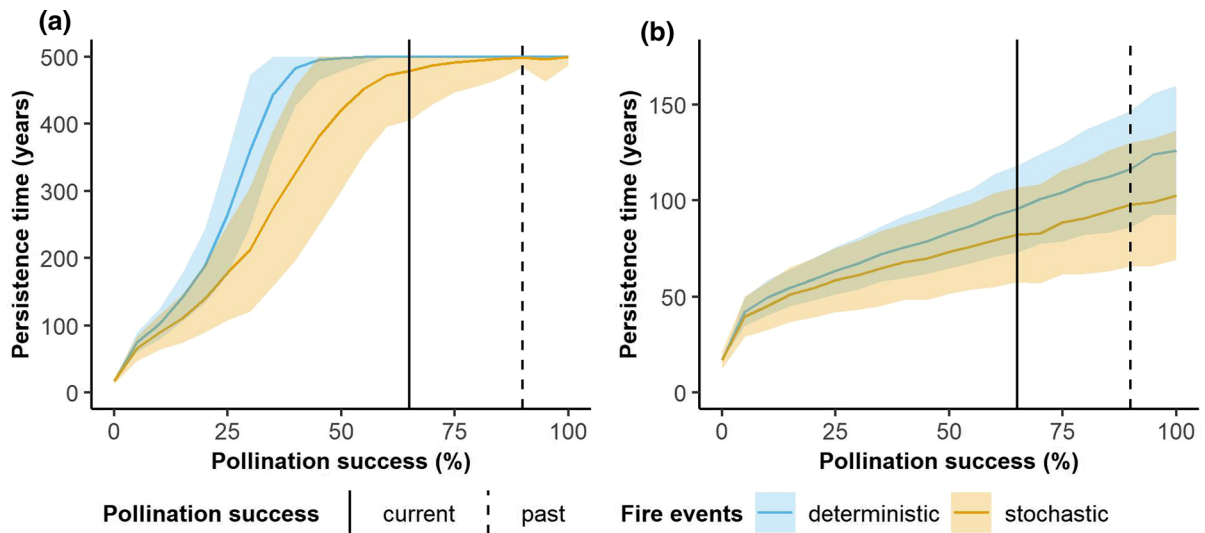


Fig. 6 Simulation experiment of persistence time of the *B. hookeriana* population (y-axis) for the entire gradient of pollination success (x-axis) under **a** baseline climate conditions, and **b** current climate conditions. Both fire scenarios (i.e. deterministic and stochastic) used the mean long-term fire interval of 17 years observed at Eneabba. Each pollination success rate (from 0 to 100% in increment steps of 5%) was

simulated up to 500 years and replicated 1000 times for both fire event scenarios. The blue (deterministic fires) and orange (stochastic fires) lines show the mean persistence time and the shaded areas the $\pm$ SD. The two vertical lines mark the pollination success rates recorded in the past (dotted) and at current times (black)

to stochastic fires (e.g. persistence time reduced by 112% and 78% at 10% decrease, respectively). Also important were the three estimated coefficients of the linear regression equation of flower production under current climate condition: The largest change was in the intercept coefficient for deterministic fires with 108% increase, and in all other cases, on average, the persistence time changed by approx. $\pm 30\%$ and $\pm 50\%$ (with $\pm 5\%$ and $\pm 10\%$ changes, respectively).

Discussion

Applying a newly developed process-based population model for the serotinous, fire-killed plant species, *B. hookeriana*, we explored the importance of pollination decline as an additional driver for the long-term persistence of populations. The non-spatial model was parameterized based on long-term demographic data spanning from 1986 to 2018. We tested the impact of declining pollination success under contrasting scenarios of past and current climate conditions, and different deterministic and stochastic fire occurrence intervals. Overall, model results indicate

that while under past climate conditions, population persistence was insensitive to observed variation in pollination success, in the current climate, pollination success decline has a linear negative effect on persistence time. This highlights an additional demographic pathway adding to the negative effects of climate and fire regimes changes previously conceptualized in the Interval Squeeze model (Enright et al. 2015).

Pollination success as a neglected stress factor

There is grave concern among ecologists over the extent to which pollination services have been disrupted in ecosystems globally over recent decades, from highly managed agriculture to natural ecosystems (Kevan and Viana 2003; González-Varo et al. 2013; Sánchez-Bayo and Wyckhuys 2019). Almost 90% of flowering plants depend on biotic pollinators such as insects, birds, and mammals to set seeds (Ollerton et al. 2011). Pollinator declines have been attributed to different global change pressures, including climate change, landscape alteration, species invasions, agricultural intensification, and spread of pathogens (González-Varo et al. 2013; Bennett et al.

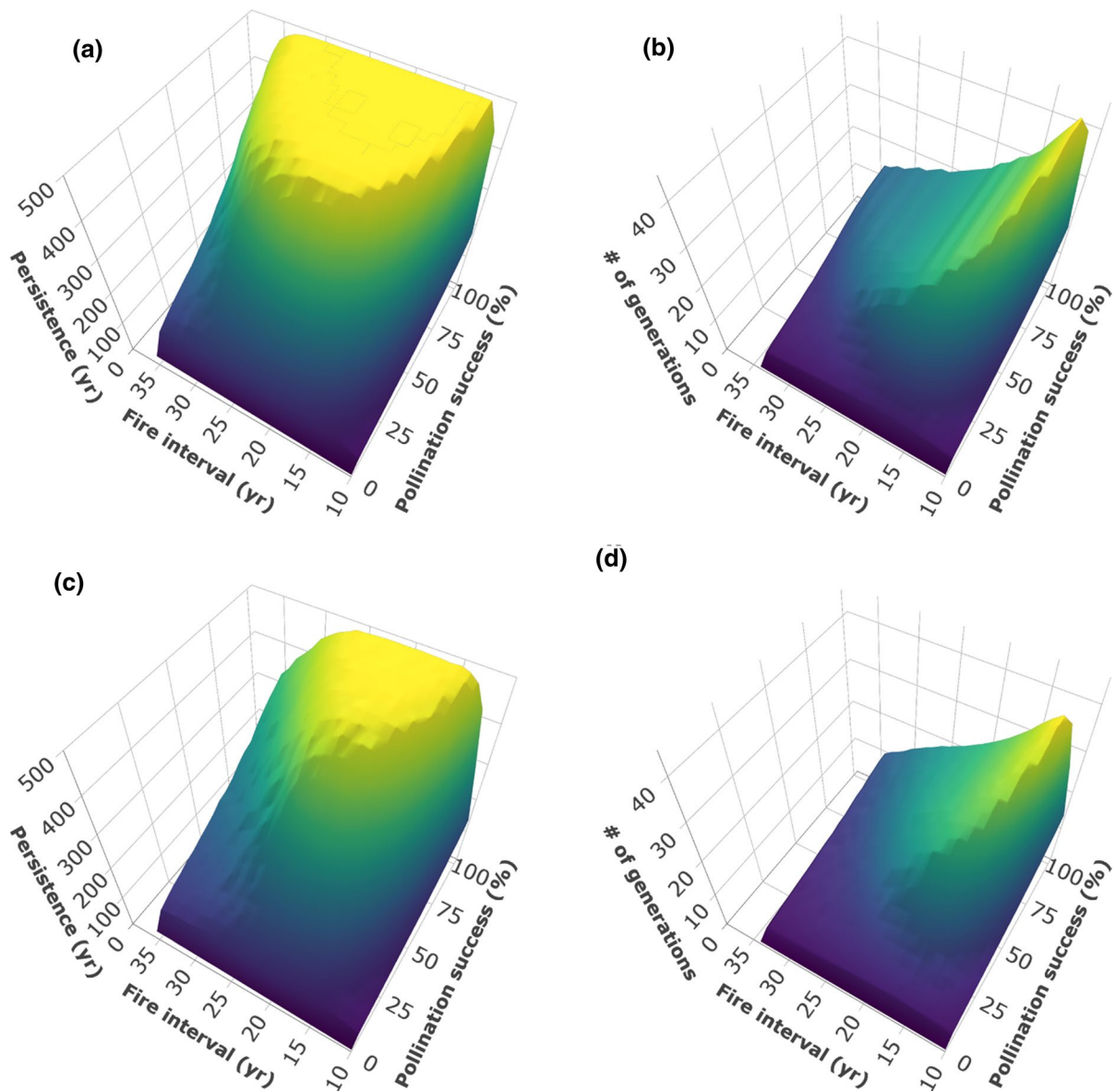


Fig. 7 Experiment 4 under baseline climate conditions (1988–2002). All scenarios from the combination of fire interval (from 10 to 35 in increment steps of 1) and pollination success rates (from 0 to 100% in increment steps of 5%) were analysed with two different measurements (z-axes): in the first column

(a, c) the mean persistence time, and in the second column (b, d) the number of generations. In the first row (a, b) fire interval events are deterministic, and in the second row (c, d), fires are stochastic

2020). The predicted decline of pollination success can be expected to further exacerbate the negative effects of climate change stress on plant populations.

Our simulation results reveal that pollination success indeed is a critical factor that increases the risk of population decline in *B. hookeriana*. In particular, under current and possible future climate conditions,

declining pollination success can be expected to further reduce the mean persistence time of populations by 12–17%. While the extent of impact clearly depends on the specific local conditions and species, our results suggest that the decline of pollinators should not be neglected in future studies on the effect of climate change and fire regime shifts on fire-prone

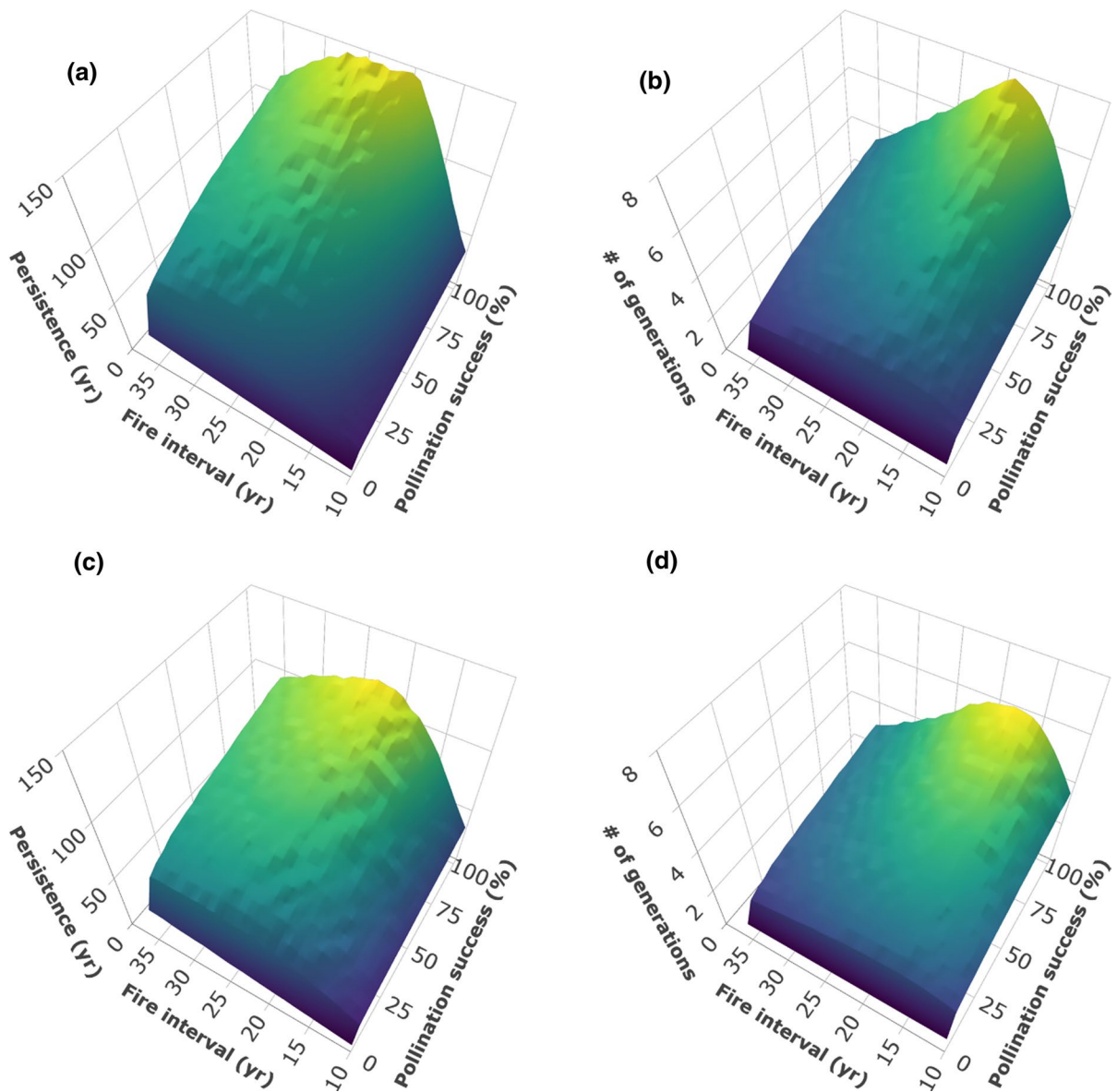


Fig. 8 Experiment 4 under current climate conditions (2003–2017). Same description as Fig. 7. Here the z-axes were modified to a maximum mean persistence of 150 years and mean number of generations of 8

vegetation. Declining pollination success may also be linked to declining population and flower densities in serotinous vegetation causing an Allee effect that further exacerbates the extinction vortex (Krauss et al. 2009; Nottebrock et al. 2013).

Banksia hookeriana flowers are predominantly pollinated by birds (honeyeaters), with small mammals, honeybees and other invertebrates also potential, but generally unimportant pollinators (He et al.

2004; Krauss et al. 2009; Thavornkanlapachai et al. 2019). Among *Banksia* spp. it can be expected that in particular those species that rely on birds for pollination are more in danger than those effectively pollinated by two or more different pollinator groups, such as *B. nivea* that is pollinated effectively by mammals and birds (Thavornkanlapachai et al. 2019). As indicated by Krauss et al. (2009), increased competition for declining vertebrate pollinators but also

Table 3 Main findings of experiment 4

Fire scenario	Pollination success (%)	Optimal fire interval ^a and model outcome ^b			
		Baseline climate		Current climate	
		Persistence time	# of generations	Persistence time	# of generations
Deterministic	90	12–32 (500)	12 (41.5)	20–27 (142)	18–20 (7.2)
	65	14–28 (500)	13 (37.7)	22–29 (118)	18–20 (5.8)
Stochastic	90	16–24 (500)	13 (34.7)	21–26 (114)	17–20 (5.8)
	65	17–23 (485)	15 (30.2)	22–27 (100)	17–20 (4.9)

^aReferring to the mean optimal fire interval in years, without parentheses

^bMean persistence time in years or mean # of generations, both in parenthesis

introduced, non-native pollinators such as European honeybees (*Apis mellifera*) affect pollen limitation and seed set in many species with already low conversion of flowers to fruits, increasing extinction risk. While we do not have data on the actual bird population trends, data show a clear decline in the proportion of fertile cones (i.e. pollination success) and in the number of follicles per cone (i.e. fruit set). While the main cause of pollination success decline is probably due to decline in pollinator visits (Krauss et al. 2009), decline in fruit set can be influenced also by soil nutrient availability (Copland and Whelan 1989; Witkowski and Lamont 1996). However, we have no evidence to suggest any change in nutrient availability due to changes in climate or fire regime, nor has any been presented by other workers.

Fire, climate, and pollination interactions

Our simulations support that *B. hookeriana* is ‘fire-dependent’ and will go extinct in the absence of fire, with inter-fire recruitment not sufficient for population persistence in the long-term absence of fire (Supplementary Information S3: Fig. S14). An earlier study (Enright et al. 1998) suggested that occasional inter-fire recruitment in the long-term absence of fire provided a bet-hedging strategy for *B. hookeriana*, allowing populations to persist at low density through occasional long inter-fire intervals that exceeded mean plant longevity, but able to recover to high densities again following fire. However, we now show that such bet-hedging is limited and that recurrent fire is essential for population persistence. We believe this is one of the few studies where evidence based on the modelling of empirical field data has identified

a plant species as truly fire-dependent, although we note studies of two endemic herbaceous species in fire-prone Florida scrub (*Hypericum cumulicola*, and *Eryngium cuneifolium*) that show high extinction risks at long fire intervals (Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio 2004).

Optimal fire frequency under past (i.e. baseline) climate conditions corresponds to the approx. 17 year-intervals observed for this system (Miller et al. 2007; Enright et al. 2012). Our study confirms this, identifying 19 years as the fire interval maximising the number of stored seeds, and so probability of self-replacement after fire. This holds for both deterministic and stochastic fire distributions. Strikingly, even without a decline in pollination success the current climatic conditions (which have warmed and dried markedly over the past 30 years; Enright et al. 2015) threaten local populations of this species substantially, e.g. with a reduction of seeds stored in the population by 80% assuming a constant fire interval of 17 years. On the other hand, under baseline climate conditions, we could identify a range of pollination success and fire interval rates where long-term population persistence was not affected.

For the fire scenarios, stochastic fires always let to lower persistence times than simulations with fixed fire intervals, even though we set a minimum fire interval to avoid local extinction from overly short fire intervals. This indicates that, in stochastic fire scenarios, very small or very long fire intervals are possible that do not allow for self-replacement.

The finding that climate change is threatening plant communities in this Mediterranean region supports other studies (Allen et al. 2010; Enright et al. 2015) and adds a quantitative perspective. We here

show that pollination decline adds another significant driver to the extinction dynamics.

Model sensitivities, shortcomings, and future directions

One important aspect of process-based modelling is its ability to reveal processes and parameters that have a disproportionate impact on the system's dynamics and that are particularly sensitive to changes. Our sensitivity analysis showed that changes in most model parameters ($\pm 5\%$ and $\pm 10\%$) had little effect on population persistence. However, a few parameters showed a disproportionately large effect, with the most sensitive being post-fire recruitment rate, one of the three key drivers of the Interval Squeeze model proposed by Enright et al. (2015). While our model is based on an exceptional empirical data set, field data on post-fire recruitment for this, and other, species are limited and future empirical studies should seek to reduce the uncertainty in this measure, especially as it is affected by post-fire weather conditions. Also, a continued thorough monitoring of cone production will be important to further improve model predictions.

In our model-based analyses we simulated weather conditions on an annual temporal scale based on long-term weather data. However, this did not include short-term sporadic extreme weather events explicitly. Such extreme events, including short periods of extreme drought or heat-waves may be becoming more frequent (Miralles et al. 2019). These extreme weather events can impact all stages of the plant life cycle, e.g. increased seedling mortality due to drought after fire, (Harvey et al. 2016), increased mortality of already established adult plants due to extreme droughts and heat-waves (Allen et al. 2010; Ruthrof et al. 2018), incomplete development of pollen (Mesihovic et al. 2016) and reduced seed bank persistence (Ooi 2012) due to heat stress, or reduced flower production caused by extreme summer heat-waves (Abeli et al. 2012). It can be expected that the explicit inclusion of such extreme weather event impacts in a future model version will further decrease population persistence under all scenarios.

In this study we focused on isolated populations of *B. hookeriana* to analyse the synergistic effects of changing climate, fire regimes, and pollination decline. Population isolation led to relatively short

periods of population persistence under current climate, fire and pollinations scenarios. One important process that we did not include in this analysis, in order to reduce complexity, is external seed input (i.e. immigration). Previous work has shown that seed immigration from other populations can be a critical process to prevent local population extinctions or recolonize locally extinct patches (Esther et al. 2008, 2010; Groeneveld et al. 2008; Krauss et al. 2009). One important future step will thus be to extend the model analyses to include meta-population dynamics and patchy fire occurrence.

Another aspect that could possibly improve the rather pessimistic model predictions is the adaptive evolution to climate change through heritable phenotypic plasticity. D'Agui et al. (2016) have shown phenotypic variation and differentiated gene expression in four fire killed species in an experimental study (including *B. hookeriana*) in response to declining rainfall. In particular, their study has shown that seedlings from plants that had established under water stress have a more effective water uptake, denser leaves and higher survival under stress (D'Agui et al. 2016). However, the extent to which such plasticity of response can buffer populations against decline is unknown and is likely to be limited.

Interval squeeze concept (from one species to general insights)

The results of our modelling analysis broadly support the conceptual foundations of the Interval Squeeze Model (Enright et al. 2015). The newly added effect of pollination decline shows an intensification of the negative effects of climate change through the pathway of reproduction. In agreement with the Interval Squeeze Model, the simulations support especially the importance of demographic (lower seed production) and post-fire recruitment shift (reduced seedling recruitment). The modelled response to climatic changes is so severe that demographic shift alone reduces the demographic window of time to levels where a population cannot reach long-term persistence from self-replacement. Thus, the effect of shifting fire regimes on the persistence of the population cannot be explored in full detail here. It has been suggested that drier (and warmer) climatic conditions will displace the age of maximum seed storage for the population to

later years (longer time-since-last fire). This change to longer fire intervals for optimal probability of self-replacement will put the population under an additional pressure since it is expected that fire will become more rather than less frequent.

Overall, the expected global environmental changes modelled here will put non-sprouters under severe pressure. Other plant functional types in the community may be better adapted to the expected changes. For example, plants that resprout after fire can cope with shortened fire intervals better, and many species are long-lived and may be better able to utilize rare good establishment years (i.e. the coincidence of fire with above average post-fire rainfall). In conclusion, changes in the environmental conditions, together with changes in the biotic conditions such as altered pollination success and competition will put non-sprouting populations at immense risk. Thus, a better understanding of possible management measures and adaptation potential of non-sprouting species together with buffering mechanisms is urgently needed to protect many of the iconic non-sprouting species of the fire-prone flora of South-western Australia and other MTEs globally.

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Data availability Supplementary material is provided in .docx and .csv file documents.

Code availability The model code is available at: <https://github.com/rsoutoveiga/population-interval-squeeze.git>

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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