Optimal resource allocation in a serotinous non-resprouting plant species under different fire regimes

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Summary

1. Serotiny, the retention of mature seeds in closed fruits within the canopy for over a year, is a common trait in fire-prone environments. When competition with adult plants prevents seedling establishment between fire events and in the absence of post-release soil seed dormancy, strong serotiny, i.e. the retention of all seeds until the next fire, appears as the best strategy. Despite the low levels of inter-fire seed recruitment for several species in both Australian and South African fire-prone environments, considerable variation in the duration of fruit retention is nevertheless observed among species.

2. Our aim is to predict optimal age-specific reproductive schedules in a perennial, serotinous species, when cone maintenance is costly. We focus on species where adults are killed by fire, without a soil seed-bank. We explicitly consider a trade-off between growth (which determines plant survival), seed production and seed maintenance. In our model recruitment relies upon fire events. We use dynamic programming to determine, for given fire regimes, the optimal pattern of resource allocation. We further study the effect of changes in fire regime on the viability of populations adapted to some historical fire regime.

3. We find that, whenever maximal plant survival probability is low, the optimal strategy consists in reducing resource allocation to seed maintenance while increasing resource allocation to annual seed production. This illustrates a trade-off between current and future reproduction.

4. A low rather than a strong level of serotiny should evolve whenever the variance of fire intervals is large and the mean fire interval is low. Low levels of serotiny could constitute a bet-hedging strategy with decreasing predictability of the arrival of fire.

5. Once adapted to some historical fire regime, serotinous populations are highly sensitive to a change in mean fire frequency and to an increase in the variance of fire intervals. Populations adapted to a historically high level of variance in fire return are more robust to changes in fire regime.

6. *Synthesis:* Life-history trade-offs and low predictability of fire intervals may favour low rather than strong levels of serotiny even when recruitment essentially occurs just after fire events.

Key-words: dynamic programming, fire regime, fynbos, optimal life-history strategy, plant development and life-history traits, population growth rate, serotiny

Introduction

In fire-prone environments, the evolution of life histories is strongly influenced by the fire regime (Keddy 1992; Pausas *et al.* 2004; Keeley *et al.* 2011; see Bradshaw *et al.* 2011 for a controversial point of view). Perennial plant species established in Mediterranean-type ecosystems, have developed a range of specific adaptations to fire, which differ in the source of new recruits following fire events (Enright, Lamont & Marsula 1996; Knox & Morrison 2005; Keeley *et al.* 2011).

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Resprouting species are characterized by the persistence of adult plants, which regenerate vegetatively from protected buds (Gill 1981; Pausas *et al.* 2004; Knox & Morrison 2005). Thus, populations of resprouting plants can persist after a fire event, even if no individual produced any seeds. In contrast, other species that do not exhibit this capacity, called 'obligate seeders' are killed by fire. Populations of these 'obligate seeders' will only persist through seeds stored either in the soil or in the canopy (serotiny). More specifically, serotiny refers to the retention of seeds in closed fruits or cones within the crown for more than 1 year (Lamont 1991; Enright *et al.* 1998a).

Although all serotinous species bear cones, the process of cone opening and seed release is variable (Lamont 1991; Lamont *et al.* 1991; Clarke, Knox & Butler 2010). Pyriscent cones are sclerified and their opening is only triggered by the heat of fire which melts resins (Lamont 1991). Pyriscence is common in some genera of Australian *Proteaceae* such as *Banksia* and in some conifers (Lamont 1991). Conversely, necriscent cones are living structures for which opening is triggered by plant or branch death, which is caused by either plant senescence or destruction of the aerial part by fire (Lamont 1991). Seeds of necriscent cones are short-lived, after being released, and germinate with the first occurrence of rain (Weiss 1984; Wellington & Noble 1985; Cowling & Lamont 1987; Yates *et al.* 1995; Enright *et al.* 1998a). If the adult plant dies before the occurrence of fire or if the necriscent cones open because the plant stops allocating resources to cone maintenance, seeds are released and if they escape predation and desiccation, they may germinate. However, in many situations, these germinating seeds are unlikely to establish because of strong intra- or interspecific competition with adult plants. Even when they can establish, they rarely reach maturity before the next fire event, at least in the South African fynbos and in Australia (Cowling & Lamont 1987; Enright *et al.* 1998a). Thus, populations establish synchronously after fire and are even-aged (Keeley, Fotheringham & Baer-Keeley 2006). Necriscence is the most common form of serotiny in Proteaceae of South Africa and some genera of Australian *Proteaceae* such as *Hakea* (Lamont 1991). Throughout this paper we will restrict our study to serotinous plants bearing necriscent cones. For the sake of simplicity, we will refer to these as serotinous plants.

Serotinous plants must stay alive and allocate resources to cone maintenance to keep them closed until the occurrence of fire, otherwise the seeds released would germinate during the non favourable inter-fire period. Given that such seeds would likely be lost, retention of all seeds produced until the next fire would then appear as the best strategy (Midgley 2000). However, the degree of serotiny (quantified as the expected cone longevity) seems highly variable among species and even within species among populations in Australia and South Africa (Cowling & Lamont 1987; Enright & Lamont 1989; Lamont *et al.* 1991; Midgley 2000; Cramer & Midgley 2009). Low levels of serotiny are usually defined as inter-fire cone loss after <3 years following cone production (Cramer & Midgley 2009). To explain the variation in the degree of serotiny, Enright *et al.* (1998a) used a population dynamic model investigating how the long-term population growth rate varies with the degree of serotiny and the mean fire return interval. They found that populations with low levels of serotiny could persist (i.e. have a replacement rate above one) even in the absence of inter-fire recruitment, provided that the seed establishment probability was high within the months after a fire. However, in their model, the level of serotiny maximizing the population growth rate was always very large, except in the case of high inter-fire recruitment for which they predicted low optimal levels of serotiny. They concluded that low serotiny could be a bet-hedging strategy enabling some level of inter-fire recruitment. However, germination success in the inter-fire period is very low in many natural populations of serotinous species in both Australia and South Africa (Kruger 1983; Enright & Lamont 1989; Enright & Goldblum 1999; Midgley 2000). Indeed, while monitoring 15 populations of *Banksia hookeriana* Meissn (*Proteaceae*) over 13 years in Australia, Enright *et al.* (1998a) found that during the inter-fire intervals no such recruits survived until reproduction. The apparent contradiction between the model output and field observations might be explained by the fact that Enright *et al.*'s model did not consider the possibility that serotiny might be costly. We presently lack empirical evidence for how costly cone maintenance can be. However, Cramer & Midgley (2009) found that cones of a range of Australian and South-Western Cape *Proteaceae* species were continuously losing small amounts of water and carbon. Additionally, using a comparative analysis, Harris & Pannell (2010) found a strong positive correlation between the degree of serotiny (measured as maximal cone age) and sexual dimorphism in the genus *Leucadendron*, with males producing many more ramifications than females. They interpreted this correlation as evidence that the cost of cone maintenance is large enough to select for such dimorphism.

In the present paper, our aim is to study the optimal age-specific reproductive schedules in a serotinous species, assuming trade-offs among plant traits. In our model, we assume a perennial, serotinous, obligate seeder (fire-killed) species, with necriscent cones, no soil seed bank and no inter-fire recruitment. We assume that seed released between fires do not become dormant in the soil. Our model is inspired by the biology of South African fynbos *Proteaceae,* yet our main hypotheses are also relevant for a number of Australian genera, such as those from necriscent Proteaceae. To model a possible cost of serotiny, we explicitly consider a trade-off between the following three functions coupled by resource acquisition and allocation: growth (which is hereafter assumed to determine the probability of plant survival), seed production and seed maintenance. Thus, our aim is to explain the differences in life-history traits among species which incur a continuous maintenance cost of cones (i.e. necriscent) rather than to study the evolution of necriscence versus pyriscence. We hypothesize that the probability distribution of fire intervals might affect the optimal pattern of annual resource allocation between these functions, as recruitment in such serotinous species relies upon fire events. Furthermore, more

predictable fire return regimes should promote serotiny. The model presented here tests the effect of underlying trade-offs and environmental factors, on the optimal life-history schedules of a serotinous plant species. We use dynamic programming (Clark & Mangel 2000) to determine the optimal pattern of resource allocation for given fire regimes. We show that both changes in the fire regime and trade-offs influence the optimal level of serotiny. We further study the effect of changes in fire regime (mean and variance of fire intervals) on the viability of populations adapted to a given historical fire regime. The aim of the study is to predict, in a qualitative rather than a quantitative way, how patterns of life-history trait variation depend on statistics of the fire regime.

Materials and methods

A RESOURCE ALLOCATION MODEL

Modelling the probability distribution of fire intervals

If a fire event occurs in year t, then the next fire event will occur with some probability in year $t + i$, where i ($i = 1, 2,\ldots, k$) represents the time elapsed since the last fire and k is the maximum number of years between two fire events. The fire interval probability, p_i, describes the probability that a fire occurs for the first time after i. We assume a zero probability of having a fire in the first year after a fire event and also assume that fires occur after the reproductive season. We used a two-parameter (γ, scale parameter and c, shape parameter) Weibull distribution (Weibull 1951) to model the probabilities p_i, because such distributions fit the empirical data on fire intervals well (Johnson 1978; Polakow & Dunne 1999). In particular, Van Wilgen *et al.* (2010) provide estimations for the two parameters of the Weibull distribution for ten National Reserves of the Cape Region. We shifted these Weibull distributions by 1 year in all cases, so that fires cannot occur before the second year. We varied parameter γ over a range of values corresponding to the variation observed in fynbos Reserves (Van Wilgen *et al.* 2010), to generate testable predictions for serotinous fynbos species. In the Weibull distribution, the mean is not independent from the variance, making it difficult to investigate the effects of independent changes in the mean and the variance of fire intervals. We therefore also used a Uniform and a Gaussian distribution to investigate the effects of the mean and variance of fire intervals on the optimal life histories. We also shifted these distributions by 1 year. Our results indicate that the family of probability distribution chosen to model fire return does not affect the global patterns of optimal resource allocation.

Modelling the optimal resource allocation pattern

In serotinous species of Mediterranean-type ecosystems, burnt plants release their seeds immediately after a fire. These seeds then germinate with the first following rains. We assume in our model that there is no successful recruitment between two fire events. Thus, all plants in a population have the same age, corresponding to the number of years since the last fire. We use age classes indexed from 1 to k to define age-structured demographic models. Parameter k is the maximal age plants can reach, given the fire regime. All variables and parameters of our model are described in Table 1.

The chronology of the different events within a year is described in Fig. 1. When plants enter age class i, they have R_i units of resources available. A proportion β_i of these resources are first allocated to the maintenance of seeds formerly produced. Here, we assume no difference between cone and seed maintenance. Then, $(1-\beta_i)R_i$ resources remain for growth, survival and reproduction. The parameter A expresses the fixed amount of resources produced during the growing season per unit of resources available at the beginning of the growing season. The amount of resources at the end of the growing period and prior to the reproductive season is $A(1-\beta_i)R_i$ and plant survival depends on this amount of resources. Finally, a proportion λ_i of these remaining resources are allocated to the production of new seeds. The recurrence equation (eqn. 1) describes the amount of resources stored in the plant at the end of the reproductive season i, given that the plant is still alive. We assume that this amount cannot exceed R_{max}, that is, we assume a limited plant size. When entering age class $i + 1$, the plants have $R_{i + 1}$ units of resources.
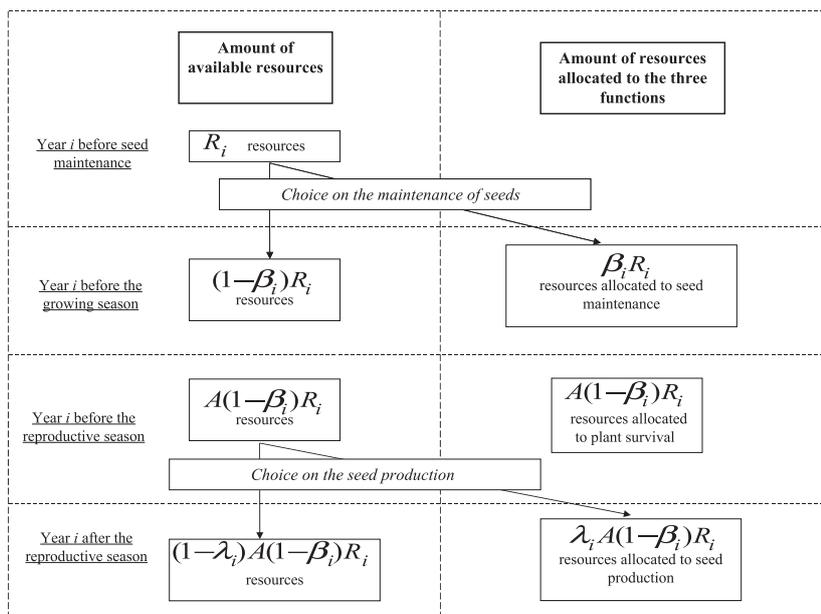

Fig. 1. Summary flow diagram of the resource allocation model in year *i*.

Table 1. List of variables and parameters used in the resource allocation model

Variables	Parameters Description	Mean value used	Range used for sensitivity analysis
R_i: Amount of resources available at the start of age i	A: Resource rate of increase across the growth period	2	2–5
T_i: Number of seeds produced by individuals of age i	b: Efficiency parameter linking the number of seeds produced T_i at age i to the amount of resources allocated to seed production	0.01	0.006–0.04
Z_i: Number of seeds alive at the beginning of age i	T_{max}: Maximal number of seeds produced during a reproductive season	400	
v_i: Seed survival rate from age $i-1$ to i	κ: Efficiency parameter linking the seed survival rate v_i to the amount of resources allocated to seed survival rate	1	0.2–1
ϕ_i: Plant survival rate from age $i-1$ to i	ω: Efficiency parameter linking the plant survival rate ϕ_i to the amount of resources not allocated to the maintenance of seeds	0.002	0.0006–0.002
	R_{max}: Maximum amount of resources produced during the growth period	1200	

$$R_{i+1} = \min((1 - \lambda_i)A(1 - \beta_i)R_i; R_{max}) \qquad \text{eqn 1}$$

For each age class i, the amounts of resources allocated to seed maintenance $\beta_i R_i$, to plant survival $A(1-\beta_i)R_i$, and to seed production, $\lambda_i A(1-\beta_i)R_i$ are converted, respectively, in seed survival probability v_i, plant survival probability ϕ_i and number T_i of new seeds produced:

$$v_i = 1 - e^{\frac{-\kappa \beta_i R_i}{Z_i}} \qquad \text{eqn 2}$$

$$\phi_i = 1 - e^{-\omega A(1-\beta_i)R_i} \qquad \text{eqn 3}$$

$$T_i = T_{max}(1 - e^{-b\lambda_i A(1-\beta_i)R_i}) \qquad \text{eqn 4}$$

Parameters κ, ω and b rescale the amounts of allocated resources per demographic effect and determine the shapes of the curves corresponding to the investment return of allocated resources (Fig. 2, eqns 2, 3 and 4). These parameters can be interpreted as conversion efficiencies, or as 1-costs of affecting survival and fecundity. We can reasonably assume that the cost of adult survival is larger than the cost of individual seed production, which is itself larger than the cost of individual seed survival (that is, $(1-\kappa) < (1-b) < (1-\omega)$). We also consider that the maximal number of seeds which a plant produces each year is T_{max} (eqn 4), in accordance with our assumption of a maximal plant size. The parameters corresponding to the costs in the three functions cannot presently be parameterized with real data, and as a consequence amounts of resource units in our model are arbitrary. We choose to model the underlying allocation of resources rather than life-history traits, to take into account likely functional constraints more explicitly (see Van Noordwijk & de Jong 1986).

Finally, we assume that the time window for reproduction is short, so that no plants die during the reproductive season. Thus, the number of canopy-stored seeds when age class $i + 1$ is reached, is equal to the number of seeds formerly produced and present when age class i was entered, times seed survival probability from plant age $i-1$ to age i (v_i), plus the number of seeds produced during the reproductive season in year i, T_i:

$$Z_{i+1} = v_i Z_i + T_i \qquad \text{eqn 5}$$

We aim to optimize the following pair of age-specific variables: β_i, the proportion of resources allocated to the maintenance of seeds in age class i and λ_i, the proportion of resources allocated to
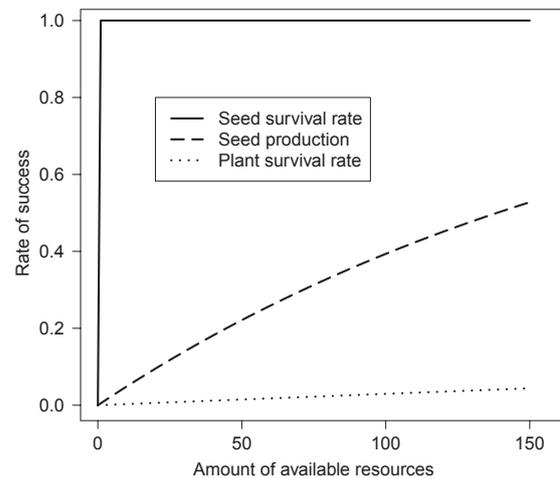

Fig. 2. Assumed functions modelling seed survival rate v_i, plant survival rate ϕ_i and seed production (the number of seeds produced/maximum possible number T_i/T_{max}). All are a function of the amount of allocated resources ($A = 2$, $T_{max} = 400$, $R_{max} = 1200$, $\omega = 0.0006$, $b = 0.01$, $\kappa = 1$).

the production of new seeds during the reproductive period in age class i.

Maximization of the population geometric growth rate

The purpose of this modelling study is to determine for each age class i, the optimal values of the pair (λ_i, β_i) which together maximize the long-term geometric growth rate of the population, which we call fitness, under a particular probability distribution of fire intervals. We assess population growth rate over an infinite number of generations, to avoid sampling effects of fire events (see Appendix S1). We define $Y_i = \{\lambda_i; \beta_i\}$ as the allocation decision taken in age class i and $X_i = \{R_i; Z_i\}$ as the individual state when entering age class i (i.e. at age $i-1$). The state when entering age class $i + 1(X_{i+1})$ depends on the previous state (X_i) and the decisions taken during year i (Y_i).

To simplify the notations, we define l_i as the probability of surviving up to age i (up to the start of age class $i + 1$) in the absence of fire (eqn 6).

$$l_i = \prod_{j=1}^{i-1} \phi_j \qquad \text{eqn 6}$$

We use the logarithm of the long-term average geometric growth rate (eqn 7), as a proxy for fitness. p_i describes the probability of having a first fire after i years without fire and k is the maximum number of years between two fire events.

$$\rho(Y_1, Y_2, \ldots, Y_k) = \log\left(\prod_{i=1}^{k} (l_i Z_i v_i)^{p_i}\right) \qquad \text{eqn 7}$$

Fitness, $\rho(Y_1, \ldots, Y_k)$ depends on the successive decisions taken at each age and on the initial amount of resources at germination (which we fix at value 1 without loss of generality). During a fire, all adult plants die and the number of germinating seeds determines the contribution to the next generation. It is assumed that newly produced seeds cannot germinate yet when a fire arrives the year they were produced and are lost. Only the seeds stored on the plant from previous years are ripe at the arrival of fire and able to germinate. To calculate the long-term population growth rate, we therefore need to calculate the expected geometric growth rate of the number of germinating seeds over successive fire events (eqn 7).

We use dynamic programming to solve this multi-parameter optimization problem defined by the allocation strategy and fitness, given a certain fire regime (see Appendix S1 and Clark & Mangel 2000 for an overview of this method).

Numerical analyses

For all numerical analyses, the results are summarized in terms of age-dependent life-history strategies, that is, annual patterns of resource allocation (between growth, seed production and seed maintenance), plant survival probability, seed survival probability and number of seeds produced at each age.

As mentioned before, we cannot realistically parameterize our model for a particular species or genus. Instead, we chose values of parameters such that resources would be limiting at every time step. We assessed the extent to which a change of parameter values would affect the results of the model. Specifically, we considered changes in parameters such as the efficiencies parameters respectively of plant survival, seed production and seed survival (κ, b, ω) and the growth rate of resources A. We also investigated the impacts of a change in the mean and variance of fire intervals on the optimal resource allocation pattern.

Lamont *et al.* (1991) and Enright *et al.* (1998a) defined the degree of serotiny as the expected cone longevity. We extended this definition to include the possibility that seed retention might depend on the age of a plant, and calculated this degree of serotiny as a function of plant age i, for each optimal resource allocation pattern. For a plant of age i, let r_i be the slope of the linear regression of a log transformation of the proportion of surviving seeds on seed age where seed survival is the probability for a seed to reach age x, with $x \leq i$. The degree of serotiny of a plant aged i is measured as $-1/r_i$ (see Appendix S2 and Fig. S4 for further details). This measure has been applied to South African fynbos plants (Midgley 2000), and it allows us to make predictions easily testable in natural populations.

To determine the impact of changes in the probability distribution of fire intervals, we calculated the optimal life history for a given fire regime. We then calculated the fitness of plants with the same life history but with different probability distributions of fire intervals (i.e. with changes in the mean or variance of the distribution).

Results

GENERAL PATTERNS OF RESOURCE ALLOCATION

The general pattern of optimal resource allocation between growth, production of new seeds and maintenance of old seeds was found to be very robust to a change in the type of probability distribution chosen to model fire return: either Weibull (Figs 3 and 4, Figs S1, S2 and S3), uniform (Figs 5 and 6) or Gaussian (results not shown). During the first years of life, the optimal pattern consists in allocating all available resources to growth, thus increasing both the amount of resources stored in the plant and plant survival (Fig. 3a,d). When the amount of resources accumulated by an individual reaches its maximum level R_{max}, the plant enters a second phase in the life cycle combining allocation to growth, production of new seeds and maintenance of old seeds. The optimal strategy then consists in stabilizing the proportion of resources allocated to growth to uphold the amount of stored resources at its highest level. Plant survival probability reaches a stable value determined by the parameters R_{max} and
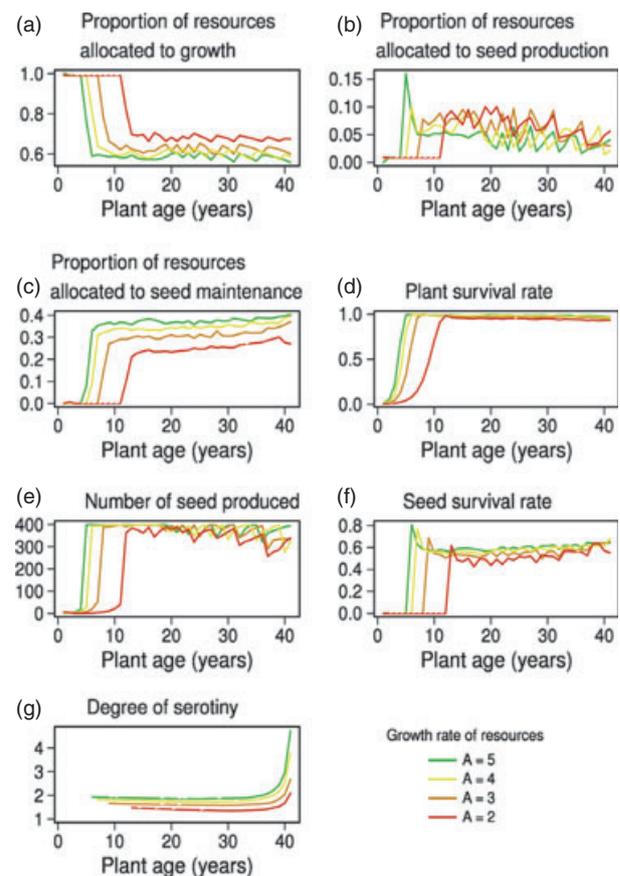

Fig. 3. Effect of the resource growth rate (A) on the optimal life history. We assumed a zero probability of having a fire in the first year after a fire event. ($c = 1.29$, $\gamma = 27.39$, $\omega = 0.002$, $b = 0.01$, $\kappa = 1$, $R_{max} = 1200$, $T_{max} = 400$, $k = 42$).
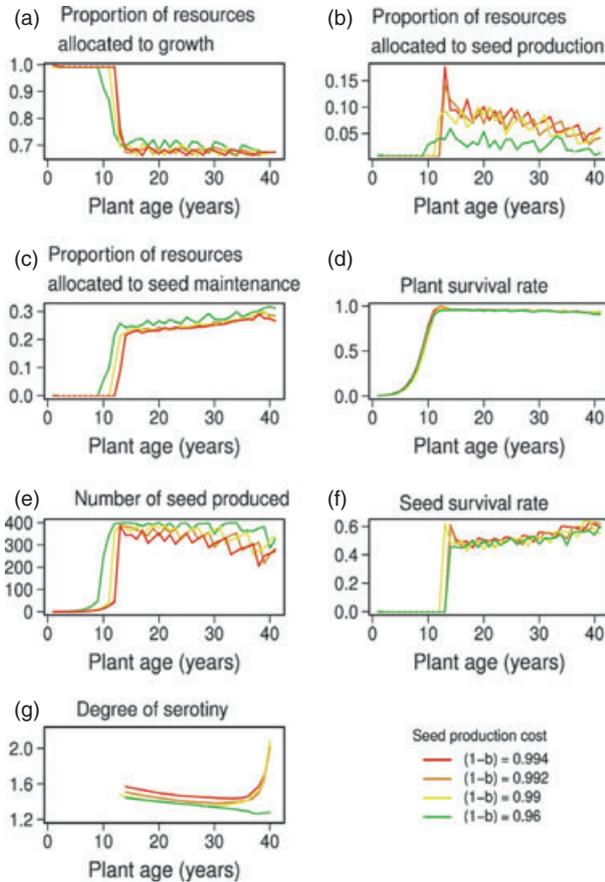
Fig. 4. Effect of the seed production cost $(1-b)$ on the optimal life history. We assumed a zero probability of having a fire in the first year after a fire event. ($c = 1.29$, $\gamma = 27.39$, $\omega = 0.002$, $\kappa = 1$, $A = 2$, $R_{max} = 1200$, $T_{max} = 400$, $k = 42$).

Fig. 5. Effect of the variance of the fire interval σ^2 on the resource allocation pattern and the resulting optimal life history. We used a uniform distribution to model fire intervals. We assumed a zero probability of having a fire in the first year after a fire event. Each reaction norms continues until the age in years where the cumulative probability of fire arrival has become one, which constrains maximal plant age. ($\mu = 16$, $\omega = 0.002$, $b = 0.01$, $\kappa = 1$, $A = 2$, $R_{max} = 1200$, $T_{max} = 400$, $k = 25$–32)

ω (Fig. 3d). At this particular point, the proportion of resources allocated to seed production and seed maintenance increases; in the following, we will refer to this point as 'age at maturity' (Fig. 3b,c). Thereafter, the maximal possible number of seeds T_{max} is rapidly reached (Fig. 3e). From then on, the proportions of resources allocated to the three functions remain constant, ensuring a maximal plant survival probability and a maximal seed production (Fig. 3d,e). With increasing plant age, the proportions of resources allocated to growth and seed production slightly decrease while the allocation to seed maintenance increases (Fig. 3a,b,c). The degree of serotiny slightly decreases with plant age and sharply increases in the last years of the life history (Fig. 3g). Thus, the optimal life-history strategy consists in (i) maximizing plant survival probability, (ii) starting to reproduce only when the maximal plant survival probability is reached, (iii) combining seed production and seed maintenance to get an increasing number of viable seeds with plant age (Fig. 3e,f).

IMPACT OF LIFE-HISTORY PARAMETERS ON RESOURCE ALLOCATION

The general pattern of optimal resource allocation between growth, seed production and seed maintenance was found
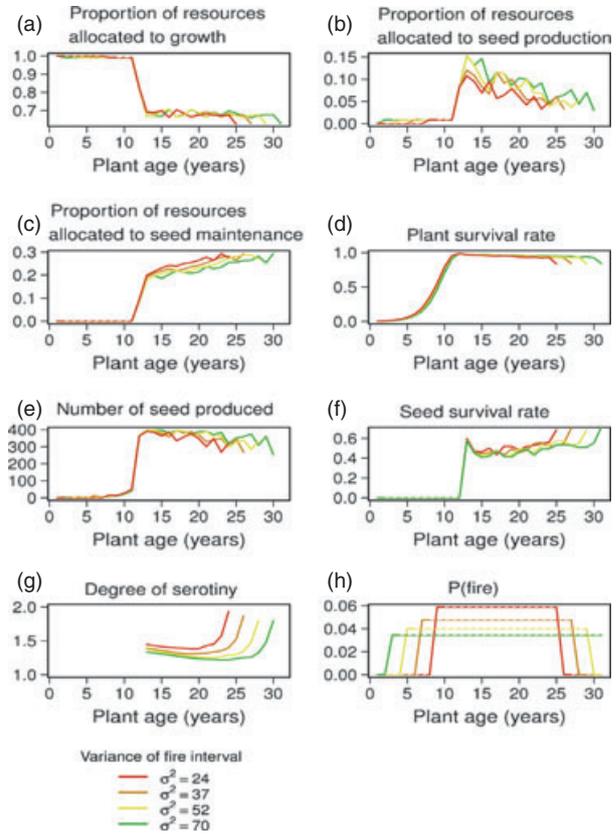
to be very robust to a change in the resource allocation parameters.

The growth rate of resources A determines the number of years needed to reach the maximal amount of available resources R_{max}. Decreasing the values of A, (i.e. the amount of resources available to the plant increases more slowly so that plant survival is more difficult to maximize) leads to (i) a slower increase in the plant survival probability (Fig. 3d) and (ii) a later age at maturity (Fig. 3b,e). As a consequence, decreasing the growth rate of resources A, increases the optimal level of resource investment to growth (Fig. 3a). The allocation to seed production also increases (Fig. 3b), while the allocation into seed maintenance decreases with decreasing values of A (Fig. 3c). When values of A are relatively small, the optimal life-history strategy is thus to keep both the plant survival probability and current reproduction at a maximal level, at the expense of seed maintenance. The degree of serotiny decreases with decreasing values of A (Fig. 3g).

Variation in the plant survival cost $(1-\omega)$ does not affect the age at maturity. For all other traits, exactly the same tendency is found when the survival cost increases as when A is decreasing (Fig. S1).
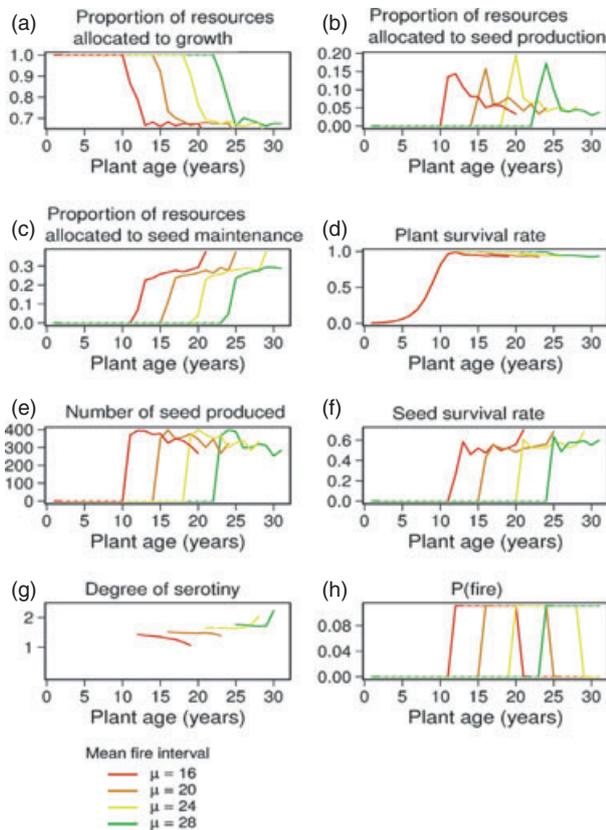
Fig. 6. Effect of the mean fire interval μ on the resource allocation pattern and the resulting optimal life history. We used a uniform distribution to model fire intervals. We assumed a zero probability of having a fire in the first year after a fire event. Each reaction norm halts at the maximum attainable age given the fire regime. ($\sigma^2 = 24$, $\omega = 0.002$, $b = 0.01$, $\kappa = 1$, $A = 2$, $R_{max} = 1200$, $T_{max} = 400$, $k = 20–32$)

Decreasing seed production cost $(1-b)$ leads to an earlier age at maturity (Fig. 4b,e), and affects the trade-off between seed production and seed maintenance in the second phase, but does not affect the optimal proportion of resources allocated to growth. The optimal proportion of resources allocated to seed production decreases with lower seed production cost, while the number of seed produced still increases (Fig. 4b,e). Decreasing seed production cost also leads to increasing resource allocation to seed maintenance (Fig. 4c). However, this increase leads to a decreasing degree of serotiny because the number of seeds to be maintained is higher (Fig. 4g).

In contrast, a decrease in seed maintenance cost $(1-\kappa)$ affects neither the optimal resource allocation pattern between the three functions nor the optimal age at maturity (Fig. S2). As a consequence, the observed increase in seed survival probability and degree of serotiny are solely the direct effect of the change in the seed maintenance cost $(1-\kappa)$ (Fig. S2).

LIFE-HISTORY TRAITS AND FIRE INTERVALS

Changes in the mean and variance of the probability distribution of fire intervals strongly affect the optimal pattern of resource allocation and the resulting life-history traits such as age at maturity and the degree of serotiny (Figs 5 and 6). Here, we show the results for a Uniform distribution. We obtained similar results using a more realistic Weibull distribution, where the mean and the variance of fire intervals vary simultaneously (Fig. S3).

Changes in the variance of fire intervals do not affect the first phase of the resource allocation pattern and the age at maturity remains identical (Fig. 5). In the second phase, an increase in the variance leads to an optimal strategy requiring more resource investment in seed production and less in seed maintenance (Fig. 5b,c). As a consequence, with increasing variances of fire intervals, seed production increases while seed survival decreases (Fig. 5e,f). The degree of serotiny decreases with increasing variance of fire intervals (Fig. 5g). Thus, for a high variance of fire interval, the optimal strategy is to maximize the yearly production of seeds at the expense of seed maintenance, that is, a low degree of serotiny is optimal.

Decreasing the mean fire interval for a constant variance, we found no serotiny for very short fire intervals. Increasing the mean fire interval leads to a later age at maturity and slightly increases the optimal degree of serotiny (Fig. S4). With very large mean fire intervals, populations are no longer viable because all plants die before the arrival of a fire (results not shown).

DISTURBANCE OF HISTORICAL FIRE REGIME

Our dynamic programming optimization algorithm allows predicting optimal life histories for populations that have evolved under given historical fire regimes. In Fig. 7, we use populations that evolved in fire regimes characterized by the same mean fire interval (16 years) but different variances in fire return. The growth rates of these populations decline rapidly when the mean fire interval is increased or decreased with respect to the historical fire regime. Populations with life histories optimized in a regime with a smaller variance of fire intervals are more sensitive to a change in the mean fire interval (Fig. 7).

The geometric growth rate of the population decreases with increasing values of the variance of fire intervals whatever the former fire regime under which the population has evolved (Fig. 8). Populations historically adapted to a low variance of fire intervals are however more sensitive to an increase in this parameter than populations adapted to a high variance (Fig. 8).

Discussion

GLOBAL PATTERNS OF RESOURCE ALLOCATION AND LIFE HISTORY

We found that the optimal resource allocation patterns of a serotinous, necriscent, non-resprouting plant and its corresponding life history consisted in first maximizing the plant survival probability. Plant survival indeed plays a major role in the life history of a serotinous plant as its lifetime reproduction is ensured only if the plant is still alive when fire
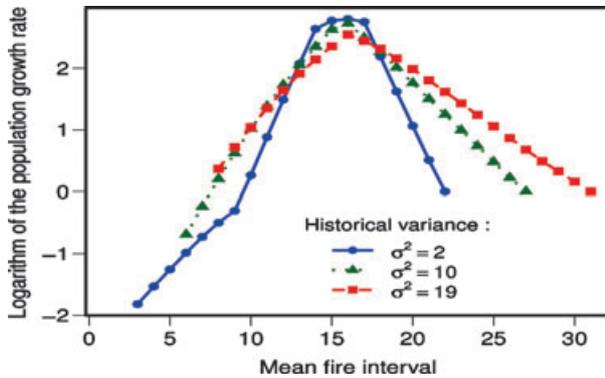
Fig. 7. Effect of changes in the mean (μ) of the probability distribution of fire intervals (uniform distribution) on the log geometric growth rate of three serotinous populations adapted to different historical fire regime. For each population, the life history was optimized with a historical mean fire interval of 16 years. Each population had evolved under different variance of fire intervals (optimal life history obtained for the following set of shared parameters: $\mu = 16$, $\omega = 0.002$, $b = 0.01$, $\kappa = 1$, $A = 2$, $R_{max} = 1200$, $T_{max} = 400$, $k = 42$). We assumed a zero probability of having a fire in the first year after a fire event.
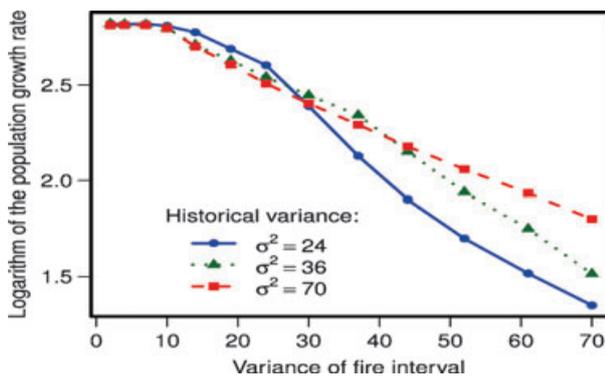

Fig. 8. Effect of changes in the variance (σ^2) of the probability distribution of fire intervals (uniform distribution) on the log geometric growth rate of three serotinous populations adapted to a different historical fire regime. For each population, the life history was optimized with a historical mean fire interval of 16 years. Each population had evolved under different variance of fire intervals (optimal life history obtained for the following set of shared parameters: $\mu = 16$, $\omega = 0.002$, $b = 0.01$, $\kappa = 1$, $A = 2$, $R_{max} = 1200$, $T_{max} = 400$, $k = 40$). We assumed a zero probability of having a fire in the first year after a fire event.

arrives. These predictions are similar to the life-history patterns observed by Enright, Lamont & Marsula (1996) while monitoring 13 populations of the strongly serotinous *Banksia hookeriana Meissn* (*Proteaceae*) over 6–8 years. Plant survivorship was lowest in the first year and quickly increased so that mortality rates were very low afterwards (< 1% per year). In our model, age at maturity is determined by both the seed production cost and the ability of resource accumulation. In a similar way, Stearns & Koella (1986) predicted that organisms should evolve to mature at an earlier age and a larger size when growth conditions are good and at later age and a smaller size when growth conditions are poor. Our optimization model thus predicts a rather long juvenile phase, consistent with the age at

maturity observed for serotinous plants in the South African fynbos (Rebelo 2001). When the maximal plant survival is reached, the optimal life history is to start producing seeds and to quickly invest in their maintenance. When the plant approaches its maximal possible age given the fire regime, we predict a decrease in allocation to growth and seed production to the benefit of seed maintenance leading to an increase in the degree of serotiny with plant age. This final investment in seed maintenance leads to an increase in the number of viable seeds with plant age and is consistent with classical predictions of terminal investment into reproduction (Williams 1966). *B. hookeriana* in Australia begins to flower at 3–4 years old and seed production increases with plant age until 15 years and then fluctuates widely around a plateau (Enright, Lamont & Marsula 1996). In agreement with our predictions, an increase in the proportion of closed cones with plant age has been reported for the lodgepole pine (Crossley 1956; Critchfield 1985), the mallee pine (Bradstock & Cohn 2002), *Hakea decurrens* (Enright & Goldblum 1999), *Banksia Hookeriana* (Enright, Lamont & Marsula 1996), *Banksia speciosa* and *Banksia baxteri* (Witkowski, Lamont & Connel 1991). Our model does not explicitly account for the separate maintenance of cones and seeds contained in those cones. We assume that resource investment in cone maintenance leads to a direct increase in seed survival. However, in natural systems, plants allocate resources such as water to maintain cones closed, which does not affect directly seed survival within the closed cones. Viability of seeds within cones is known to decrease with cone age (Crawford *et al.* 2011), but the relationship between the duration of cone maintenance and the longevity of seed within cones has never been explored.

FIRE REGIME, OPTIMAL LIFE-HISTORY STRATEGY AND DEGREE OF SEROTINY

Enright *et al.* (1998a) predicted that lower levels of serotiny were optimal only when the probability of seed recruitment between two fire events was very high. We predict that, in the absence of inter-fire recruitment, no or a very low level of serotiny would be optimal in the two following cases: (i) when the mean fire interval is very short, because plants do not have time to accumulate enough resources to both produce and maintain seeds before the fire comes or (ii) when the variance of fire intervals is high, as the uncertainty of fire arrival is too important for a serotinous strategy to be favoured given both costs of plant survival and seed maintenance. When the variance of fire intervals increases, the optimal strategy is to invest more in seed production and less in seed maintenance. Assuming inter-fire recruitment of seeds, Enright *et al.* (1998a) similarly found a slight decrease in the degree of serotiny when stochasticity around the mean fire interval was added in their model. In places where inter-fire recruitment is possible, weak serotiny can be explained as a bet-hedging strategy enabling some level of inter-fire recruitment, as suggested by Enright *et al.*'s (1998a). It has been shown for different species (respectively, *Pinus banksiana* in Canada, *Hakea decurrens* and *Banksia serrata* in Australia)

that stands became progressively less serotinous as a result of increasing inter-fire establishment opportunity (Gauthier, Bergeron & Simon 1996; Whelan, de Jong & von der Berg 1998; Enright & Goldblum 1999).

Our model highlights the optimal position on the trade-off between seed production and seed maintenance. We predict that increasing optimal allocation to growth (through decreasing adult survival efficiency, decreasing ability of the plant to accumulate resources, or increasing variance in fire intervals) will lead to both greater investment into annual seed production and smaller investment in seed maintenance. A given level of serotiny can thus be seen as a particular way of solving the well-known trade-off between current and future reproduction (Schaffer 1974; Stearns 1992). With increasing variance of fire intervals, the decrease in seed maintenance and the increase in seed production ensuring a minimal reproduction in case of an early arrival of fire can be considered as a bet-hedging strategy (Slatkin 1974). More general models considering environmental stochasticity predict that environmental variability should favour reproductive bet-hedging (Murphy 1968; Roff 1992; Haccou & Iwasa 1995). Our findings suggest that the variance of fire intervals plays a major role in determining the optimal level of serotiny in the absence of inter-fire recruitment. Serotiny can also be compared with parental care strategies in animals, which are expected to diminish with increasing environmental variability (Stearns 1976; Bonsall & Klug 2011). With increasing mean fire intervals, our model predicts a slight increase in the optimal degree of serotiny along with a delayed age at maturity because plants have more time to accumulate resources before they start to reproduce.

The model presented in this paper allows us to make a series of predictions about the influence of different factors such as fire interval distribution, soil fertility or water availability on the optimal degree of serotiny. The resources in our model are dimensionless; however, a decrease in the degree of serotiny could be expected (i) with decreasing water availability, leading to increasing difficulties in maintaining cones closed or decreasing plant survival, and (ii) with decreasing soil fertility leading to slower plant growth. Such qualitative predictions can be tested by investigating the relationship between these environmental factors and the degree of serotiny for different populations of several species in areas where the history of fire regime has been recorded. As mentioned before, the degree of serotiny is also expected to vary with plant age. Thus, this variable should be measured and studied as a covariate in the statistical models. The definition of the degree of serotiny used in this paper (following Lamont *et al.* 1991) assumes an exponential decay of the number of surviving cones in a cohort with increasing cone age. It only estimates the mean duration of cone maintenance exactly when cone survival is independent of both cone age and plant age (for further discussion see Appendix S2). When plant allocation to cone maintenance varies with plant age, as modelled here, this measure is only an approximate estimation of the mean duration of cone maintenance. To get a better insight in plant investment into cone maintenance and more general life-history allocation strategies, one could additionally examine other indicators such as the age structure of cones on a plant (e.g. maximal cone age, mean age of cones and its variance). Plant age can be measured by the stem node ageing method described by Lamont (1985) or can be inferred as time since last fire when such data are available.

FIRE REGIME AND OTHER FIRE ADAPTATIONS

In this paper, we considered serotinous species bearing necriscent cones (i.e. where release of seeds is triggered by stem/plant death). In pyriscent cones, there is no release of seeds before the arrival of fire because the cone structure prevents its opening in the absence of fire. Thus, pyriscent species pay the cost of serotiny at the time of cone production, and cones are then kept systematically on the plant whatever the plant's age. In some cases such as in conifers, pyriscent cones consist in producing chemical bonds that result in high melting point resins. Such production implies very high costs of cone production and almost no cone maintenance cost. Pyriscence may be favoured over necriscence in more arid areas because pyriscent species probably require less water for cone maintenance compared with necriscent species. Nathan *et al.* (1999) also suggested that seed release associated with environmental conditions such as droughts (i.e. xeriscence) could be adaptive by promoting increasing distance of dispersal by wind when wind is positively correlated with the occurrence of droughts.

Perennial serotinous plants of Mediterranean-type ecosystems can also have the ability to regrow from protected buds (Gill 1981). The ability of individuals to resprout after a fire reduces the dependence on seeds for population persistence and likely reduces the selective advantage of seed production and serotiny. Indeed, most non-resprouting species for which data are available show lower levels of seed production or storage (either on the plant or in the soil) than nonresprouting species (Enright *et al.* 1998b). In contrast to obligate seeder species, resprouting individuals may experience several recruitment occasions (i.e. the numbers of fire cycles they survive in) which is likely to lead to large differences in the optimal levels of life-history traits such as the degree of serotiny, requiring further theoretical exploration. For instance, resprouting plants might be less sensitive to changes in fire regime than obligate seeders.

FIRE REGIME AND POPULATION GROWTH RATE

We found that a change in the probability distribution of fire intervals had dramatic consequences for the population growth rate of a serotinous population. In particular, we found that the population growth rate was very sensitive to a change in the mean fire interval and to an increase in variance. We also predicted that populations adapted to small variances should be more sensitive to changes in fire regime. A decrease in the population growth rate is predicted to occur when fire occurs before the plants have reached maturity or when they have not had enough time to accumulate enough seeds in the canopy to ensure successful recruitment follow-

ing fire. These results are also in agreement with previous studies focusing on fire management in Mediterranean-type ecosystems. For example, Van Wilgen (1981, 1982) showed that very short fire intervals could diminish the specific richness of fynbos communities. Moreover, Bradstock *et al.* (1998) showed that the risk of extinction of Australian shrubs was high with a strategy of prescribed burning with low fire intervals. Conversely, when the mean fire interval is too long, the geometric population growth rate decreases because the number of plants still alive by the time the fire occurs decreases. Bond (1980) reported a decline of serotinous *Proteaceae* populations that had remained unburnt for 30–65 years in the South African fynbos. Lloret, Pausas & Vilà (2003) and Pausas (2006) showed elimination of some *Pinus* species under long fire intervals. For the Florida fire-prone environment, population viability analyses based on demographic parameters measured *in situ* allowed the determination of an optimal fire interval for species with soil-stored seed banks (Menges & Quintana Ascencio 2004; Menges *et al.* 2006). Using an age-structured stochastic population dynamic model we found an increasing probability of extinction with changes in the mean fire interval and increasing variance of fire intervals (results not shown), in agreement with our analysis of population growth rate. In the fire ecology literature, these two predictions are often called the 'immaturity risk' and the 'senescence risk', respectively (Gill 1981; Lamont *et al.* 1991) and are also predicted by Enright *et al.* (1998a).

Our model is the first to consider the effect of the variance of the distribution of fire intervals on the optimal level of serotiny and population growth rate. Our findings confirm the idea that species or populations are not adapted to fire *per se* but rather to a particular historical fire regime and that the viability of populations is threatened when the fire regime changes (Keeley *et al.* 2011). Management strategies relying on fire regimes with a given mean and minimum variance, such as with prescribed burning, are likely to select for species that are strictly adapted to a given fire interval and less able to handle changes in fire regimes. Our results highlight the importance of preserving the historical heterogeneity in fire regimes in the Mediterranean-type ecosystems to preserve its important biodiversity.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Dynamic programming approach in the context of resource allocation patterns in a serotinous plant

Appendix S2. Illustration of the calculation of the degree of serotiny

Figure S1. Effect of the plant survival cost $(1-x)$ on the optimal life history (Weibull distribution of fire intervals)

Figure S2. Effect of the seed maintenance cost $(1-j)$ on the optimal life history (Weibull distribution of fire intervals)

Figure S3. Effect of the γ parameter of the Weibull distribution on the optimal life history

Figure S4. Degree of serotiny for plants of 25 and 40 years old with optimal life history

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