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Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants

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Summary

- Several Cape species of the genus *Erica* are known to present seeder and resprouter phenotypes, and this variation seems to have a genetic basis. Therefore, this genus provides ideal model systems for using to elucidate the evolution of non-sprouting or seeder and resprouter life-histories in woody, fire-recruiting plants.
- A simple simulation model was developed to identify, under life-history optimality, the ecological conditions (*viz.* rainfall conditions and fire frequency) that conferred a selective advantage to the seeder phenotype over the resprouter in a given Cape *Erica* species.
- The model illustrated that the seeder life-history was able to invade and replace a resprouter population only under a mild mediterranean climate, with short, moderate summer droughts.
- This simulation approach will contribute to a better understanding of the biogeographical pattern of seeder and resprouter lineages of one of the paradigmatic fynbos woody taxa throughout the Cape floristic region.

Key words: Cape fynbos, extinction, iteroparity, optimality theory, nonsprouting, phenotypic evolution, postfire recruitment, semelparity.

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Introduction

One of the major issues in evolutionary ecology is to understand how semelparity (i.e. one reproductive event per lifetime) can evolve in long-lived organisms, such as perennial plants (Young & Augspurger, 1991; Takada, 1995). The sprouter and nonsprouter life-histories in fire-recruiting woody plants constitute an effectively analogous system to iteroparity and semelparity in long-lived organisms (Bond & van Wilgen, 1996). Although flowering and fruiting occur annually after reaching sexual maturity in both life-histories, seeds remain dormant in a canopy- or a soil-stored seedbank, and seed germination, and hence recruitment, is triggered by fire (Keeley & Bond, 1997). As adult plants of the fire-recruiting sprouter (hereafter resprouter) life-history survive and regenerate after fire, they can replenish their depleted seedbanks and thus experience further postfire recruitment events (i.e. iteroparous). In the fire-recruiting nonsprouter (hereafter seeder) life-history, by contrast, offspring recruitment occurs in a single event in their lifetime (i.e. semelparous), because of postfire seedling recruitment being preceded by the parent's death.

As germination of the seedbank is simultaneous (triggered by fire), seeder plants behave as non-bet-hedging semelparous (cf. Simons & Johnston, 2003), and a single recruitment failure will jeopardize the viability of any large population. Seeder populations will hence be highly sensitive to variance in per-generation recruitment (Higgins *et al.*, 2000). By contrast, the fitness of a resprouter (iteroparous) population is less likely to be severely affected by variance in recruitment failure, because of the ability of resprouter adults to survive fire (Higgins *et al.*, 2000; Zammit & Westoby, 1987). In addition, resprouter plants do not necessarily relinquish occupied space to competitors after fire, while seeders do. Nevertheless, woody taxa from fire-prone floras, in which both life-histories occur, usually include a higher number of seeder species (Wells, 1969; Lamont & Markey, 1995; Schutte *et al.*, 1995; Ojeda, 1998), despite the apparent fitness advantage of the resprouter life-history.

Therefore, what are the ecological conditions under which the seeder life-history overcomes its inherent long-term fitness limitation so as to become selectively advantageous over the resprouter? Bond & van Wilgen (1996) highlighted the importance of differences in juvenile survival (i.e. recruitment success) to answer this crucial question. They appealed to classic life-history theory and, by applying Charnov & Schaffer's (1973) model, concluded that the seeder life-history (i.e. semelparity) will have an evolutionary advantage over the resprouter (i.e. iteroparity) if seeder postfire recruits outnumber resprouter postfire recruits plus postfire survivors. In this context, several species-pair studies have shown that seeder species produce more seeds (Groom & Lamont, 1996; Lamont *et al.*, 1998, but see Hansen *et al.*, 1991; Pannell & Myerscough, 1993) and/or have higher seedling survival under seasonal water stress (Keeley & Zedler, 1978; Zammit & Westoby, 1987; Thomas & Davis, 1989; Richards & Lamont, 1996; Enright & Goldblum, 1999) than their resprouter counterparts. However, Bond & van Wilgen (1996) did not further investigate how ecological factors (e.g. fire frequency, water stress) influenced juvenile survival (i.e. recruitment), and hence fitness, of seeders and resprouters.

Here we present a simple simulation model that shows, by using life-history optimality criteria (Parker & Maynard-Smith, 1990; Mäkelä *et al.*, 2002), how changes in seasonal (summer) water stress and fire affect the long-term survival of seeder and resprouter life-histories in a given species of the Cape genus *Erica*. This Cape genus offers an ideal model system for using to elucidate the evolution of seeder and resprouter life forms in the context of life-history optimality because: (1) most species, either seeder or resprouter, are fire-recruiting (Oliver, 1991; Brown *et al.*, 1993), and fitness components are thus quite easily measured (Bond & van Wilgen, 1996); (2) approx. 4% of the Cape *Erica* species are known to include intraspecific seeder and resprouter variants ('mixed' species *sensu* Ojeda, 1998) with remarkable morphological, anatomical and functional differences (Bell & Ojeda, 1999); and (3) this substantial within-species phenotypic variation has a genetic basis and can be detected from early ontogenetic stages, which accounts for the existence of a root:shoot allocation trade-off (Verdaguer & Ojeda, 2002) and may determine differences in seedling survival between both life-histories under seasonal (summer) water-stress.

A recent, detailed, anatomical analysis has evidenced that both life-histories are, in fact, two character states within two *Erica* species, the seeder state being derived (Verdaguer & Ojeda, 2005). Therefore, the model explores under which ecological conditions – *viz.* fire frequency and seasonal (summer) soil-water stress – a 'mutant' seeder phenotype is able to invade and replace a 'resident' resprouter population.

This model will help to identify the ecological conditions that confer a selective advantage to the seeder or nonsprouter (i.e. semelparous) phenotype over the resprouter (i.e. iteroparous) in a given fire-recruiting woody species in which such phenotypic variabilty may occur. Furthermore, it will also contribute greatly to understanding the biogeographical pattern of seeder and resprouter lineages of one of the most paradigmatic woody taxa in the South African Cape region.

Methods

1. Model system: the South African Cape fynbos

The South African Cape region is a major hotspot for plant biodiversity (Goldblatt & Manning, 2002). Most plant diversity is concentrated in fynbos, the most characteristic biome in the Cape region (Goldblatt & Manning, 2002). Poor soils, mediterranean to all-year-round rainfall regimes, and, particularly, the recurrence of wildfires, constitute the main selective regime of fynbos (Bond, 1980; van Wilgen, 1987; Manders, 1990; Deacon *et al.*, 1992).

Regarding rainfall, three main areas can be recognized within the Cape fynbos: south-west (SW), north-west (NW) and south-east (SE) (Campbell, 1983; Ojeda, 1998). Mountain areas in the SW Cape are characterized by a mild mediterranean climate with a generally short and moderate summer drought (Linder, 1991; Ojeda, 1998). The NW Cape – also mediterranean – has, in general, longer and more severe summer droughts (Taylor, 1996; Ojeda, 1998). Finally, coastal mountains of the southern and SE Cape present a nonmediterranean, all-year-round rainfall regime (Campbell, 1983; Ojeda, 1998).

Historically, most fynbos fires occur in summer to autumn (Kruger & Bigalke, 1984; van Wilgen, 1987), and there are virtually no differences in fire frequency throughout the Cape region (Kruger & Bigalke, 1984; van Wilgen, 1987). The mean fire-return interval in fynbos was in the order of 20 yr (with a range of 6–40 yr at random) until approx. 2000 yr BP, when it became 15 yr (with a range of 6–30 yr at random), probably as a result of increasing human sources of ignition (van Wilgen, 1987). Fynbos stands older than 30 yr after the last fire become senescent (Bond, 1980), and very few fynbos patches last for longer than 40 yr without fire (van Wilgen, 1987).

2. Model system: the Cape genus *Erica*

With approx. 650 species and a high level of endemism, the genus *Erica* represents the epitome of plant biodiversity in the South African Cape region (Goldblatt & Manning, 2002). Most *Erica* species occur in high-rainfall coastal or mountain areas within the fynbos biome (Baker & Oliver, 1967; Oliver, 1991). Virtually no *Erica* species are found in arid or semiarid (mean annual rainfall < 300 mm) conditions (Oliver *et al.*, 1983).

The vast majority of *Erica* species are fire-recruiting and, with the exception of *E. sessiliflora* (Van Staden *et al.* 2000), they keep a soil-stored seedbank (Oliver, 1991). Up to 90% of the species are seeder, approx. 6% are resprouter, and the

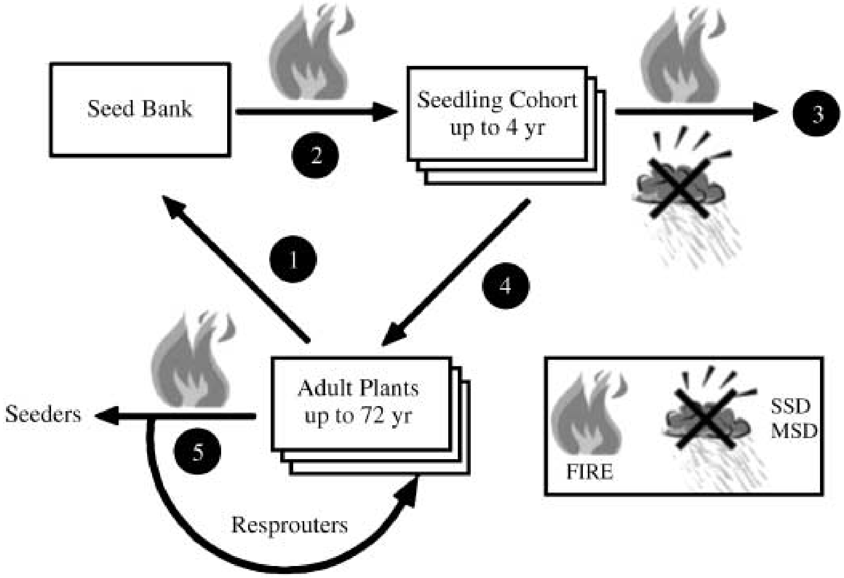

Fig. 1 Simplified scheme of the model. Multiple boxes (arrays) indicate the existence of age cohorts, while the single box (seedbank) is indicated as one unique age. 1, Adult plants produce seeds that are incorporated into the seedbank; 2, seed germination occurs only after fire; 3, seedling survival to fire, severe summer drought (SSD) and moderate summer drought (MSD) is both life-history-specific and age-specific; 4, surviving seedlings move into the adult plant population when they reach sexual maturity (i.e. 5 yr old); and, 5, adult seeders die after fire, whereas a large fraction of adult resprouters survive.

remaining 4% are known to include both seeder and resprouter life-histories ('mixed' species *sensu* Ojeda, 1998). Verdaguer & Ojeda (2002, 2005) presented evidence that the seeder and resprouter phenotypes are character states within two *Erica* species. As seeder seedlings presented 'atrophied lignotubers' in both species, the seeder state was suggested to be derived (i.e. loss of the resprouting ability; Verdaguer & Ojeda, 2005).

3. Description of the model

The model assumes the invasion of a 'mutant' seeder individual in an isolated resprouter population of a given Cape *Erica* species and assesses the long-term survival of both seeder and resprouter phenotypes across two rainfall gradients in two different fire-return interval scenarios. The first gradient is related to drought intensity within a mediterranean-type regime, and represents a NW to SW geographical gradient within the Cape fynbos (see 'Model system: the South African Cape fynbos'), while the second gradient is related to the likelihood of a (moderate) mediterranean-type summer drought occurring and represents a SW to SE gradient. Both concatenated gradients aim to accomplish a main climatic-geographical gradient within the Cape fynbos biome that is related to rainfall seasonality (Campbell, 1983; Ojeda, 1998).

As competition is low for seedlings in the postfire environment (Keeley & Fotheringham, 2000), and the model assumes life-history optimality (i.e. asexual reproduction of both phenotypes; Parker & Maynard-Smith, 1990, see also Bull *et al.*, 2004), both the density logistic-model (cf. Mueller *et al.*, 1991; Mylius & Diekmann, 1995, see Takada, 1995) and the 'Allee effect' (Fowler & Ruxton, 2002) were neglected. Nevertheless, considering that population density necessarily affects each phenotype's growth rate, even under optimality (Meszéna *et al.*, 2001), density has been taken into account simply by setting in the model default values of population-carrying capacity for adult plants, seedlings and seeds (see Table 1). Once carrying capacity values are reached, further additions are simply dismissed and lost.

The model is made up of three linked age-transition matrices for seed (one age class: 0 yr), seedling (four age classes: 1–4 yr), and adult plant (up to 68 age classes: 5–72 yr) life-stages, within each phenotype. The state vectors represent the number of individuals in each age class within each life-stage (seeds, seedlings and adult plants) at a given time. The transitions between age classes are regulated by control variables, namely rainfall and fire (Fig. 1, Table 1).

Rainfall Two distinct summer drought events were considered to simulate both rainfall gradients and their effects on survival rates within the seedling life-stage (see below in 'Seedlings'): (1) a short and moderate summer drought (MSD); and (2) a severe (longer and/or more intense) summer drought (SSD). A decreasing drought intensity gradient (NW to SW) was obtained by considering eight P(SSD) values (i.e. probability of an SSD occurring), from 0.7 to 0.01, keeping the P(MSD) fixed at 0.95 so as to remain under a mediterranean-type regime (see above). To construct a decreasing gradient of (moderate) mediterranean-type summer (SW to SE), six P(MSD) values, from 0.9 to 0.01, were considered, keeping the P(SSD) fixed at 0.01. As stated under 'Description of the model', these two linked gradients aim to represent a main climatic-geographical gradient of seasonality within the Cape region, excluding arid or semiarid biomes, where *Erica* species do not occur (Baker & Oliver, 1967; Oliver, 1991). The model assumes that autumn-winter rainfall is reliable (Cowling *et al.*, 2005).

Table 1 Model parameters and initial or default values for both life-histories (when values are the same for seeder and resprouter life-histories, they are placed in the column between these headings)

	Value		
Parameter	Seeder		Resprouter
Number of seeds per adult plant and yr[a]		100	
Longevity (yr)[b]		Up to 72	
Carrying capacity (individuals per ha)[a]			
Adults		10^4 (S+R = 1.8×10^4)	
Seedlings		5×10^4	
Seeds		10^6	
Age at maturity (yr)[c]	5		5 3 after resprouting[d]
Adults			
Probability of fire survival[e]	0.01		0.9
Seedlings			
Probability of survival under nonlimiting conditions[a]		0.5 at 1 yr 0.7 at 2 yr 0.8 at 3 yr 0.9 at 4 yr	
Probability of fire survival	0		0 at 0–2 yr 0.1 at 3 yr 0.5 at 4 yr
Probability of SSD survival[a]		0.01 at 1 yr 0.05 at 2 yr 0.5 at 3 yr 0.7 at 4 yr	
Probability of MSD survival[e]	0.2 at 1 yr 0.6 at 2 yr 0.8 at 3 yr 0.9 at 4 yr		0.1 at 1 yr 0.3 at 2 yr 0.4 at 3 yr 0.7 at 4 yr

[a] Arbitrarily set to those values for the sake of simplicity.

[b] Lloret *et al*. (2003) consider a lifespan of 40 yr for the resprouter *Erica multiflora*, and Pausas *et al*. (2004) estimate an average longevity of 49.1 ± 39.6 yr (mean ± standard deviation) for resprouter shrubs from Australian heathlands.

[c] Verdú (2002).

[d] Personal observation.

[e] See text.

MSD, moderate summer drought; SSD, severe summer drought; S+R, seedling+resprouter.

Fire In order to ascertain whether a change in the average fire frequency, from 20 to 15 yr (see above), might have had a strong effect in the evolution of seeder and resprouter life-histories in *Erica*, the two average fire-return interval scenarios were simulated. To do this, the model generated random numbers (each being the number of years between two consecutive fires) from a Poisson distribution with mean 20 and 15 in each fire-return interval scenario, discarding numbers lower than 5 (i.e. fire cycles shorter than 5 yr are extremely rare in fynbos; van Wilgen, 1987; Vlok & Yeaton, 2000). In this way, the time between two consecutive fires ranged from 5 to 40 yr, and from 5 to 31 yr in the 20- and 15-yr fire-return interval scenarios, respectively, basically agreeing with the historical (2000 yr BP) and present fynbos fire regimes posed by van Wilgen (1987). The model assumes that fires occur during the summer (Kruger & Bigalke, 1984).

Seeds For the sake of simulation, the number of seeds produced by seeder and resprouter adult plants was set at 100 seeds per plant per year, although a further exploration of fecundity effects was also carried out (see the Discussion). Sexual maturity (i.e. the start of seed production) was established at the age of 5 yr (Verdú, 2002) for both seeder and resprouter life-histories, and at 3 yr after resprouting in adult resprouter plants (see Table 1). When population-carrying capacity values are achieved, new seeds produced are simply discharged from the seedbank (the model considers only one age class, i.e. no differences between old and new seeds), maintaining a maximum value equal to the carrying capacity. Seed germination occurs only after a fire event in both life-histories. Nonetheless, the model assumes that 1‰ of the seeds do not germinate – remaining available for the next fire – in a way to reflect what might happen in nature (e.g. seeds deep enough in the soil that escape from a fire-induced dormancy-break). Post-fire

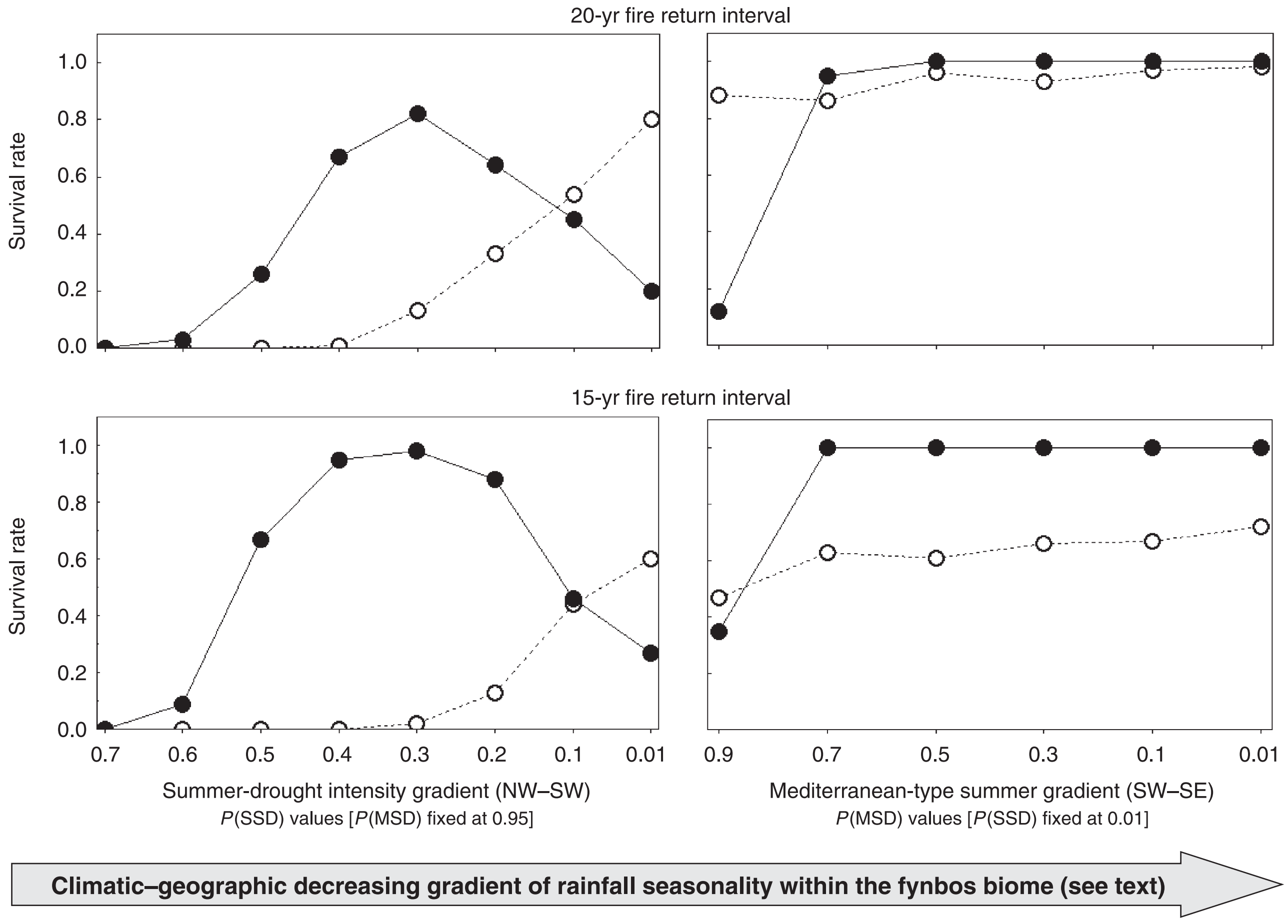

Fig. 2 Survival rate of the 'mutant' seeder (white circles) and the 'resident' resprouter (black circles) life-histories across the summer drought intensity and the mediterranean-type summer gradients at the end of the 2000-yr simulated period in the two fire-return interval scenarios. Probability values were obtained after 100 replicate simulations per each of the 14 rainfall conditions. MSD, moderate summer drought; NW, north-west; SE, south-east; SSD, severe summer drought; SW, south-west.

germinated seeds are incorporated in the seedling state vector in the first age class, until reaching carrying capacity (Table 1).

Seedlings Seedling dynamics of both seeder and resprouter phenotypes in the population are represented in the model by two age-transition matrices with four age classes (1, 2, 3 and 4 yr). Seedling survival rate was divided into three different components for each life-history: natural, summer-drought, and fire survival. Natural survival is the probability of surviving into the next age class; it depends on seedling age, and was set to the same values in both life-histories (Table 1). Summer-drought survival also depends on seedling age, and survival to an SSD was set to the same values for both seeder and resprouter seedlings (Table 1). By contrast, resprouter seedlings were assumed to be twice as sensitive as seeder seedlings to an MSD (see Table 1). This latter assumption is the keystone of the model and, although it remains to be tested in *Erica*, it can be inferred without much trouble from the significantly different root:shoot allocation patterns of seeder and resprouter *Erica* seedlings (Verdaguer & Ojeda, 2002). It has been already demonstrated in other woody taxa from other mediterranean-type, fire-prone ecosystems (e.g. Zammit & Westoby, 1987; Thomas & Davis, 1989; Richards & Lamont, 1996). Finally, fire survival was both life-history- and age-dependent; while fire survival was set to zero in seeder seedlings, the probability of surviving fire increased with seedling age in resprouter seedlings (see Table 1). Once individuals reach sexual maturity (5 yr), they are removed from the seedling stage and added to the adult state vector in the first age class until reaching carrying capacity.

Adult plants The dynamics of adult seeder and resprouter phenotypes were also described by means of age-transition matrices with different age classes (from 1 up to 72 yr) and a natural survival rate affecting each age-class step, which was equal for both life-histories. The model assumes that both seeder and resprouter adult plants are no longer vulnerable to summer drought (either MSD or SSD). While the fire-survival rate of resprouter adult plants was set to 0.9 (a slightly higher survival than reported for resprouter *Erica* species; le Maitre *et al.*, 1992; López-Soria & Castell, 1992; but see Canadell *et al.*, 1991), postfire survival in seeder plants is virtually nil (i.e. seeder plants are killed by fire), although the value was set to 0.01 in the model to account for events that may occur in nature, such as plants escaping fire because of protection by broken and rocky terrain, or by a particularly moist microenvironment. After fire, resprouting adult plants remain in their age class (i.e. they do not revert to the 1 age class), and every resprouter individual dies as soon as it exceeds its maximum life-span.

As the frequency of the MSD, SSD and fire is stochastic, 100 replicated simulations were performed within each of the 14 combinations of the two summer drought events considered to construct both concatenated gradients (see above), in each fire-return interval scenario. By doing so, the final outcome of both seeder and resprouter life-histories in the population can be described statistically. The model was constructed with the aid of the STELLA RESEARCH® 7.0.1 software, where differential equations were transformed to difference equations by means of numerical integration (Euler's method; Jeffries, 1988). Every simulation started with a resprouter population of 10^4 adult plants, which were uniformly distributed in the age classes, 10^6 seeds in the seedbank, and one seeder adult plant in a 1-ha area. Each simulation ran for a period of 2000 yr (i.e. an average of 100 and 133 generations in the 20- and 15-yr fire-return intervals, respectively), with a Δt of 1 yr. A run-time version of the model is available online (http://www2.uca.es/grup-invest/ecosist-acuaticos/informacion.html) and upon request. Model parameters and default values are summarized in Table 1. After each simulation run, it was registered whether the seeder life-history established (if so: adults+seedlings+seeds > 0) and whether the resprouter life-history became extinct (if so: adults+seedlings+seeds = 0), in order to obtain the rate of survival of seeder and resprouter forms after 100 replicated simulations. The final numbers of seeder and resprouter adult individuals after each single run were also computed.

Results

The model showed that only under a mild-mediterranean regime [*P*(MSD) from 0.95 to 0.9; *P*(SSD) = 0.01] was the survival rate of the seeder component of the population higher than that of the resprouter at the end of a 2000-yr period (Fig. 2). Under these mild-mediterranean conditions, virtually every replicate simulation that ended with the survival of the seeder phenotype was also accompanied by the demise of the resprouter component of the population (i.e. the 'mutant' seeder replaced the 'resident' resprouter). The resprouter phenotype only survived in those simulations under which the seeder phenotype was soon wiped out by the occurrence of close consecutive fires, or by an SSD before postfire seedlings reached the adult life-stage. This explains that the survival rate of the seeder phenotype across both gradients was higher in the 20-yr than in the 15-yr fire-return interval scenario (Fig. 2).

In both fire-return interval scenarios, survival of the seeder phenotype decreased rapidly with increasing drought intensity, because of the subsequent higher probability of (postfire) recruitment failure. This decrease favoured an increase in the survival rate of the resprouter phenotype, until a threshold level of drought intensity [*P*(SSD) = 0.3)] was reached, from where it also decreased (Fig. 2). Differences in the survival of the resprouter life-history between both fire-return interval scenarios seemed negligible (Fig. 2).

Although the survival rate of the 'mutant' seeder phenotype did not differ from that of the 'resident' resprouter in the 20-yr fire-return interval scenario under very mild mediterranean conditions [*P*(MSD) = 0.7; *P*(SSD) = 0.01], or it was even lower in the 15-yr scenario (see Fig. 2), the average final density of resprouter individuals was more than three times lower than that of resprouters in both fire-return interval scenarios (Fig. 3). On the other hand, although the same pattern regarding survival rate of both life-histories was found under nonmediterranean, all-year-round conditions [*P*(MSD) = 0.01; *P*(SSD) = 0.01; see Fig. 2], the average final density of resprouter individuals was higher, particularly in the 15-yr fire-return interval scenario (Fig. 3). Hence, the capacity, if any, of a 'mutant' seeder phenotype to invade and replace a 'resident' resprouter population is expected to be very low under a nonmediterranean rainfall regime.

Finally, the model rendered similar results regarding the probability of survival of the 'resident' resprouter population under partially strong [*P*(MSD) = 0.95; *P*(SSD) = 0.3], very mild [*P*(MSD) = 0.7; *P*(SSD) = 0.01] and nonmediterranean conditions [*P*(MSD) = 0.01; *P*(SSD) = 0.01], in both fire-interval scenarios (see Fig. 2). However, the average density of resprouter adult individuals (i.e. the number of adult plants per ha) at the end of the 2000-yr simulations was remarkably different in these three contrasting situations (Table 2). It was highest under nonmediterranean conditions and lowest in the strong-mediterranean conditions.

Discussion

Life-history optimality models are often criticized because they neglect the role of underlying genetic mechanisms (e.g. pleiotropic effects, recombination, gene flow), which may constrain adaptive divergence (e.g. Baatz & Wagner, 1997). However, the effect of these genetic mechanisms becomes less important when differences in fitness between phenotypes are remarkable (Weissing, 1996, see also Hendry *et al.*, 2001), as is the case of seeder and resprouter life-histories in fire-prone environments (e.g. Zammit & Westoby, 1987; Higgins *et al.*, 2000). In such instances, life-history optimality models still provide a useful tool for inferring to what extent environmental factors have driven the selection of life-history traits (Orzack & Sober, 1994; Weissing, 1996; Mäkelä *et al.*, 2002).

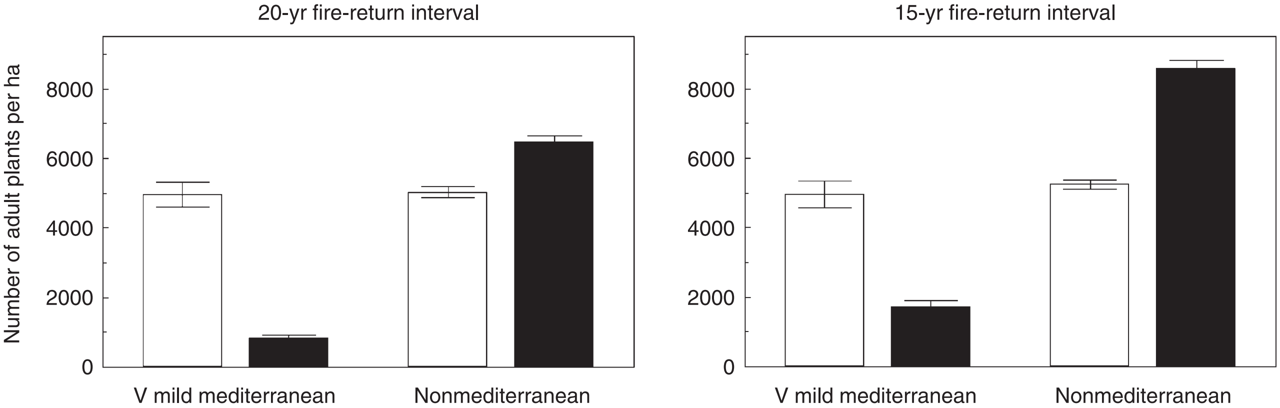

Fig. 3 Average density (± standard error) of seeder (white bar) and resprouter (black bar) adult individuals after replicate simulations under very (v) mild mediterranean [*P*(MSD) = 0.7; *P*(SSD) = 0.01] and non-mediterranean [*P*(MSD) = 0.01; *P*(SSD) = 0.01] (MSD, moderate summer drought; SSD, severe summer drought) rainfall conditions in the two fire-return interval scenarios. Simulations in which the seeder life-history failed to establish were discarded so as to compare average density values when both life-histories coexisted. Simulations that ended with a fire (i.e. number of seeder plants = 0) were also discarded to make sure that possible differences were not produced by those zero values.

Table 2 Average density (no. of individuals per ha; mean ± standard deviation) of resprouter adult individuals at the end of the 100 replicate 2000-yr simulations under partially strong [*P*(MSD) = 0.95; *P*(SSD) = 0.3], very mild [*P*(MSD) = 0.7; *P*(SSD) = 0.01] and nonmediterranean [*P*(MSD) = 0.01; *P*(SSD) = 0.01] conditions in the two fire-return interval scenarios (MSD, moderate summer drought; SSD, severe summer drought)

	20-yr scenario	15-yr scenario
Partially strong mediterranean	491.4 ± 621.7	699.1 ± 721.7
Very mild mediterranean	816.3 ± 877.3	1738.4 ± 1653.2
Nonmediterranean	6471.4 ± 1861.9	8586.2 ± 2366.0

The results of the model presented in this article indicate that a 'mutant' seeder or nonsprouter (i.e. semelparous-like) phenotype would invade and replace a 'resident' fire-recruiting, resprouter (i.e. iteroparous-like) population of a given Cape *Erica* species only under a mild-mediterranean climate with short, moderate summer droughts. In other words, a mild-mediterranean rainfall regime will act as a selective filter against the resprouter phenotype in those *Erica* species that include seeder and resprouter life-histories. This filter effect is more effective in the 20-yr fire-return interval scenario than in the 15-yr interval scenario, owing to the less likely occurrence of two close consecutive fires, which jeopardizes the success of any seeder population ('immaturity risk' *sensu* Keeley & Fotheringham, 2000). It should be stressed, though, that the model ignores the negative effect of two close consecutive fires on the survival of resprouter *Erica* plants (Canadell & López-Soria, 1998). Should this effect have been included, the performance of the resprouter life-history in the 15-yr fire-return interval scenario would have been lower than what the model predicts.

In mediterranean regimes with longer or more intense summer droughts, the probability of failure in postfire recruitment failure increases dramatically and differences between life-histories disappear (as stated in 'Description of the model'; see also Enright & Lamont, 1992). A high probability of recruitment failure is fatal for populations with no ability to store reproductive potential over generations (Warner & Chesson, 1985), as is the case with seeder populations (Higgins *et al.*, 2000). By contrast, although resprouter populations would also be affected by recruitment failure, they would maintain their storage potential over generations (i.e. adults can survive fire) and would thus be able to persist for longer through occasional postfire recruitment in (unusual) favourable years (Higgins *et al.*, 2000). This would explain the inability of the seeder phenotype to invade under highly seasonal conditions and, particularly, the apparently contradictory higher resistance of resprouter populations (see Fig. 2), despite the comparatively lower capacity of resprouter seedlings to endure (moderate) summer drought.

Finally, the model indicates that seeder plants will not outnumber resprouters under a nonmediterranean, all-year-round rainfall regime. Besides, seeder cohorts will be always be more prone to local extinction as a result of the occurrence of two too close consecutive fires, more likely in the 15-yr fire-return interval scenario. Hence, it would not be expected that the seeder life-history would take over the resprouter life-history under all-year-round rainfall conditions.

Qualitative test of the model

In general, the validity of a model may be tested by comparing its predictions against actual observations and measurements in the real system. How an optimality model should be tested (i.e. quantitative vs qualitative testing, cf. Orzack & Sober,

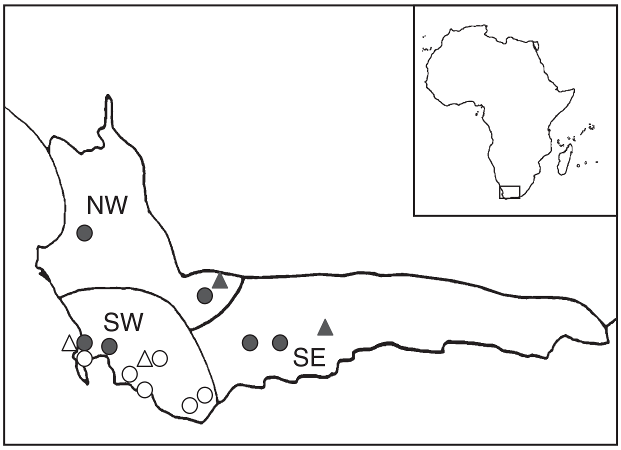

Fig. 4 Geographical location of seeder (white symbols) and resprouter (black symbols) populations of two 'mixed' *Erica* species, *E. coccinea* (circles) and *E. calycina* (triangles) in the three main climatic areas within the Cape fynbos. NW, north-west; SE, south-east; SW, south-west.

1994) depends on the question one wishes to answer. If the question is whether natural selection accounts for shifts in dominance of contrasting life-history traits along environmental gradients, then a qualitative test would be sufficient (Orzack & Sober, 1994; Mäkelä *et al.*, 2002). In this regard, the pattern of geographical distribution of seeder and resprouter life-histories of *Erica calycina* and *E. coccinea*, two species that include both seeder and resprouter forms (Verdaguer & Ojeda, 2002, 2005), in the Cape region seems to be satisfactorily explained by this model. Populations of these two species from mountain areas of the SW Cape, characterized by a mild mediterranean-type rainfall regime (Ojeda, 1998), are mostly seeder, whereas most populations of the two species from both the NW (highly seasonal) and the SE (nonseasonal) are resprouter (Fig. 4; F. Ojeda, personal observation). The two resprouter populations of *E. coccinea* in the SW Cape, shown in Fig. 4, are actually found in two particular locations – Swartboskloof and Table Mountain – whose climatic conditions are more similar to those of the southern and SE Cape (i.e. virtually nonexistent summer droughts) (Versfeld *et al.*, 1992; Ojeda, 1998).

Moreover, while resprouter populations of *E. coccinea* in locations of the NW Cape, under relatively high probability of SSD (e.g. Piketberg; Ojeda, 1998), are formed by a few scattered individuals (less than 200 plants per ha in Piketberg; F. Ojeda, unpublished data), resprouter populations of this species from southern Cape locations with a high, all-year-round rainfall (e.g. Langeberg; Ojeda, 1998) are formed by thousands of individuals (approx. 20 000 plants per ha in the southern middle slopes in the Langeberg; F. Ojeda, unpublished data). This contrast in values of density between resprouter populations from highly mediterranean and nonmediterranean conditions are also predicted by the model (Table 2).

Our model is conservative in the sense that it assumes the same number of seed production in both seeder and resprouter life-histories, while several species-pair studies have shown that seeder species produce more seeds than resprouters (e.g. Groom & Lamont, 1996; Lamont *et al.*, 1998). If such differences in seed production had been incorporated in the model, the outcome would have been more conspicuous regarding the invasion success of the seeder 'mutant' when the risk recruitment failure is low (e.g. SW Cape). However, would our results have also been similar if the model included a higher seed production of seeder plants, but equal seedling survival between life-histories? The model was run assuming twice, five, and 10 times higher seed crop in seeder plants than in resprouters, but identical seedling survival in all instances. With such assumptions, the model was able to explain the inability of the seeder life-history to establish under high probability of SSD (i.e. NW Cape), but it failed to show an advantage of the seeder form under mild-mediterranean conditions (i.e. SW Cape; data not shown). In other words, under the assumption of equal seedling survival to MSD between seeder and resprouter life-histories, a 'mutant' seeder plant would never invade a resident 'resprouter' population.

The entire modelling approach in this study builds upon the premise of a 'mutant' seeder life-history invading a 'resident' resprouter population ('seeder invasion'). Although this premise is supported by detailed anatomical analyses in two *Erica* species that include both life-histories (see Verdaguer & Ojeda, 2005), some authors have argued against ancestrality of the resprouting life-history in other mediterranean woody taxa (e.g. Bond & Midgley, 2003; Vesk & Westoby, 2004). Therefore, to explore this possibility, the whole simulation was repeated, keeping all the assumptions and parameters, but assuming now the invasion of a 'mutant' resprouter individual in a 'resident' seeder population ('resprouter invasion'). In this diametrically opposite situation, the model predicted a slightly wider resilience window of the 'resident' seeder phenotype and, particularly, a conspicuous inability of the 'mutant' resprouter life-history to invade and replace the seeder one in highly seasonal conditions (Fig. 5). In other words, when assuming 'resprouting invasion', the model fails to explain the occurrence of resprouter populations of both *E. coccinea* and *E. calycina* in the NW Cape (Fig. 4), under higher levels of summer drought intensity (Campbell, 1983; Ojeda, 1998). It would also fail to explain the relatively higher abundance of resprouter lineages in the NW Cape at the genus level (Ojeda, 1998).

Biogeographical implications

The optimality model presented in this work predicts that only a mild-mediterranean rainfall regime (i.e. reliable winter rains, MSD and virtually no SSD), together with the historical presence of fire (Linder *et al.*, 1992; Cowling & Pressey, 2001), would favour the replacement of a resprouter *Erica* population by seeder individuals if a seeder 'mutant' enters the population.

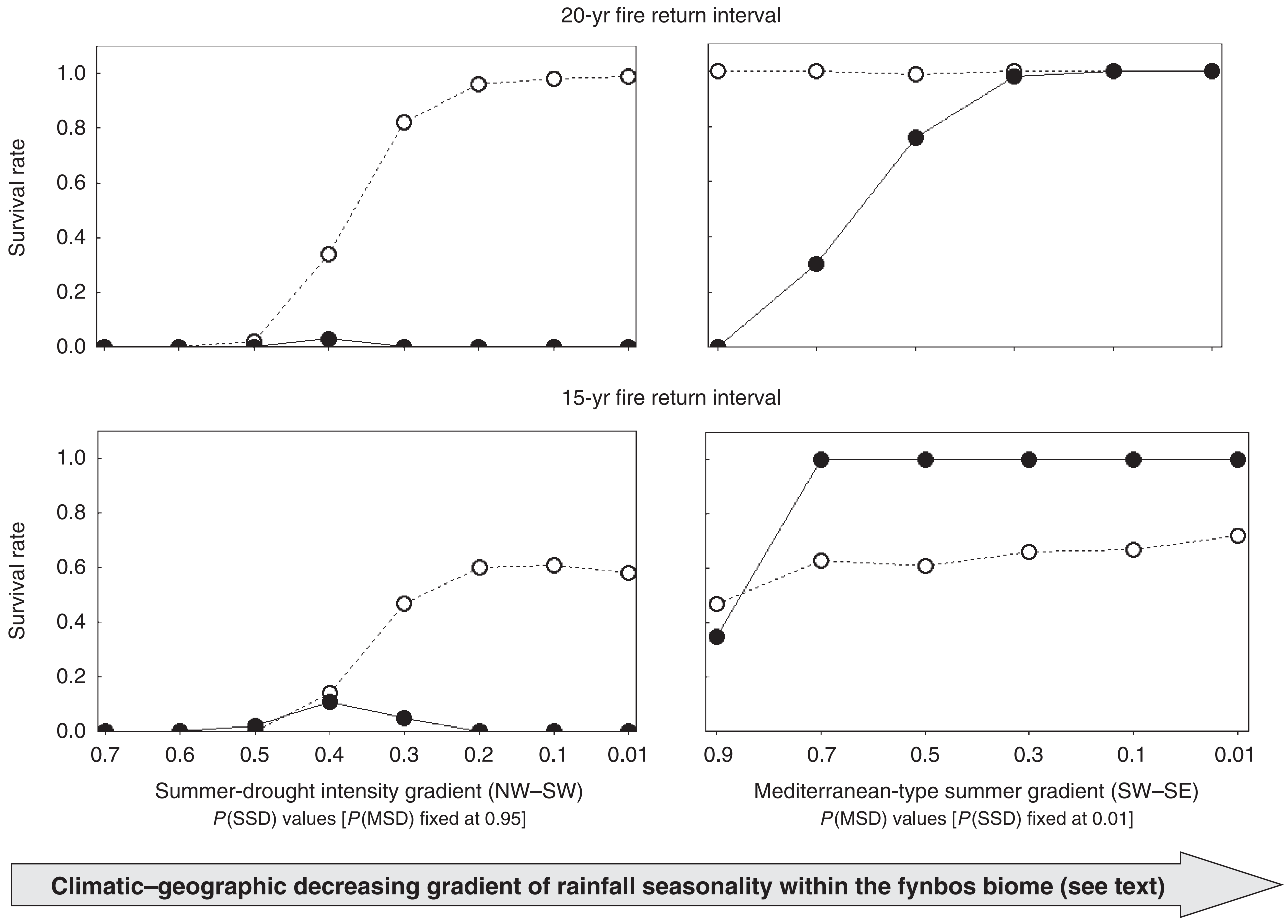

Fig. 5 Survival rate of the 'mutant' resprouter (black circle) and the 'resident' seeder (white circle) life-histories across the summer drought intensity and the mediterranean-type summer gradients at the end of the 2000-yr simulated period in the two fire-return interval scenarios. Probability values were obtained after 100 replicate simulations per each of the 14 rainfall conditions. MSD, moderate summer drought; NW, north-west; SE, south-east; SSD, severe summer drought; SW, south-west.

Under any other situations of the summer-drought and mediterranean-type summer gradients, the 'resident' resprouter population would remain virtually uninvadable. If this holds true, how can it be explained that most Cape *Erica* species are seeder (approx. 90% of more than 600 species; Ojeda, 1998)?

A truly mild-mediterranean rainfall regime is typical of coastal mountains of the south-western Cape region (Linder, 1991; Ojeda, 1998). Fire-prone fynbos in these mountains would not only favour a strong selection of the seeder phenotype against the resprouter if a 'mutant' seeder plant enters a resprouter *Erica* population, but would also buffer those subsequent seeder populations against (local) extinction. Fire-killed (i.e. seeder) lineages are speciation-prone (Wells, 1969; Cowling, 1987; Cowling & Holmes, 1992) but they are also extinction-prone (Zammit & Westoby, 1987; Higgins *et al.*, 2000). However, 'seeder-friendly' ecological conditions (i.e. reliable winter rainfall and short, moderate summer droughts) might support the existence of a shift of the speciation-extinction balance towards speciation in seeder lineages (Cowling & Lombard, 2002), which would thereby account for the recent, massive concentration of seeder *Erica* species in coastal mountains of the south-western Cape (Oliver *et al.*, 1983; Ojeda, 1998; Cowling & Lombard, 2002; Linder, 2003), most of them narrow endemics (Ojeda, 1998).

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