Research review

Evolutionary ecology of resprouting and seeding in fire-prone ecosystems

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Summary

There are two broad mechanisms by which plant populations persist under recurrent disturbances: resprouting from surviving tissues, and seedling recruitment. Species can have one of these mechanisms or both. However, a coherent framework explaining the differential evolutionary pressures driving these regeneration mechanisms is lacking. We propose a bottom-up approach in addressing this question that considers the relative survivorship of adults and juveniles in an evolutionary context, based on two assumptions. First, resprouting and seeding can be interpreted by analogy with annual versus perennial life histories; that is, if we consider disturbance cycles to be analogous to annual cycles, then resprouting species are analogous to the perennial life history with iteroparous reproduction, and obligate seeding species that survive disturbances solely through seed banks are analogous to the annual life history with semelparous reproduction. Secondly, changes in the selective regimes differentially modify the survival rates of adults and juveniles and thus the relative costs and benefits of resprouting versus seeding. Our approach provides a framework for understanding temporal and spatial variation in resprouting and seeding under crown-fire regimes. It accounts for patterns of coexistence and environmental changes that contribute to the evolution of seeding from resprouting ancestors.

Introduction

Recurrent disturbances underpin the dynamics of many ecosystems world-wide and exert a strong evolutionary pressure on plants. Many species have consequently acquired traits and mechanisms that confer fitness benefits in repeatedly disturbed environments. There are two broad mechanisms by which plant populations persist in the face of recurrent disturbances: resprouting from surviving parental tissues and seedling recruitment (Bond & Midgley, 2001; Pausas *et al.*, 2004). Despite attempts to explain the relative roles of these two regeneration mechanisms (Bellingham & Sparrow, 2000; Bond & Midgley, 2001, 2003; Pausas, 2001; Klimesová & Klimes, 2003, 2007; Pausas *et al.*, 2004; Vesk & Westoby, 2004; Knox & Clarke, 2005; Pausas & Bradstock, 2007; Lamont *et al.*, 2011; Clarke *et al.*, 2013), a coherent framework explaining the differential evolutionary pressures driving them is still lacking.

We propose a bottom-up approach to address the relative roles of resprouting and seeding that considers relative survivorship of adults and juveniles in an evolutionary context. We focus on ecosystems where fire is the primary disturbance and frequent enough to act as a strong selective pressure (fire-prone ecosystems), and specifically on ecosystems where fire typically kills all aboveground plant parts (crown-fire ecosystems; Box 1). Our approach is based on two assumptions. The first assumption is that resprouting and seeding can be interpreted by analogy with annual versus perennial life histories. If we consider fire cycles to be analogous to annual cycles, then by analogy obligate seeding species that survive fires solely through seed banks are like annual species with semelparous life histories (Keeley, 1986; Bond & Van Wilgen, 1996; monopyric species; Box 1; Table 1). By contrast, resprouters persist through multiple fire cycles and are analogous to perennial species (polypyric species; Box 1) with typically iteroparous reproduction across multiple cycles (Table 1). Despite occasional reproductive events without fire in some obligate seeding species (Nathan *et al.*, 1999), the bulk of the effective reproduction in these species occurs after a fire when the plant dies, and thus they can effectively be considered semelparous with a single reproductive

form even-aged populations while resprouting species form multiple-cohort populations) and in the genetic variability and the evolutionary potential (obligate seeding species have shorter generation time and faster population turnover). Our second assumption is that changes in the selective regimes differentially modify the survival rates of adults and juveniles and thus the relative costs and benefits of resprouting versus seeding. These changes would drive relaxed selection of one trait (i.e. resprouting), increasing the probability of its loss (Lahti *et al.*, 2009), and the intensification of the selection of another trait (i.e. postfire seedling) previously absent or weakly represented (Lamont *et al.*, 2013).

Charnov & Schaffer (1973) proposed a simple model to explain the evolutionary tradeoffs between annual and perennial life histories, more broadly characterized as semelparity versus iteroparity. Their model contends that life history evolution is driven by differences in adult versus offspring survivorship. The evolution of the perennial life history is expected when the average clutch size of an annual organism is increased by P: C individuals, where P and C are adult and juvenile survivorship, respectively. Thus, when adult survivorship through resprouting is high following a disturbance, and seedling survivorship is relatively low, resprouting should be of greater selective value than seedling recruitment. The seeding strategy is expected when resprouting success is low and seedling success is high (Fig. 1). The advantage of this model is that its multivariate nature allows factors affecting P and C to vary under different environmental conditions (e.g. Fig. 2), and thus under different temporal and spatial settings. This approach to understanding the relative roles of resprouting and seeding is more mechanistic, and more directly linked to key processes that enhance fitness, than previous models based on fire regime gradients.

In developing our model we concentrate on fire because it is a very widespread disturbance agent and has played a key role in plant evolution (Keeley & Rundel, 2005; Pausas & Keeley, 2009; Bond & Scott, 2010; Keeley *et al.*, 2011). Phylogenetic studies provide evidence of fire adaptation appearing at least since the early Paleocene (Crisp *et al.*, 2011; He *et al.*, 2012), and recent micro-evolutionary studies provide evidence of fire as an ongoing evolutionary pressure generating phenotypic divergence among populations (Gómez-González *et al.*, 2011; Pausas *et al.*, 2012; Hernández-Serrano *et al.*, 2013, 2014). All of these studies point to the increasing recognition of fire as an evolutionary force in plants (Pausas & Schwilk, 2012). In addition, fires currently occur in most regions world-wide and are susceptible to global change drivers (Pausas & Ribeiro, 2013; Pausas & Keeley, 2014); thus, fire regimes are changing world-wide. Understanding mechanisms of persistence under recurrent fires is of paramount importance for interpreting the past and predicting the future of our biota.

In the context of fire-prone ecosystems, postfire resprouting and postfire seeding are considered as two independent traits; that is, species living in those ecosystems may have one of the two traits, both, or none (Pausas *et al.*, 2004; see Box 1). This contrasts with other models in which resprouting and seeding are considered as alternative mechanisms of response to disturbance (Bellingham & Sparrow, 2000). One misconception arising from such approaches is to equate resprouting species with nonseeding species. All resprouters produce seeds; however, seeds of obligate

event per fire cycle and mostly with nonoverlaping generations. In fact, there is evidence of selection acting to favor early emergence in postfire seeding species (de Luis *et al.*, 2008). The two life histories have consequences in the cohort structure (obligate seeding species

Table 1 Main differences in life history processes among the three postfire strategies considered: species with one regeneration mechanism (resprouting or seeding) are called obligate postfire resprouters and obligate postfire seeders, respectively; species with both mechanisms are facultative postfire species (Fig. 3; Box 1)

	Obligate resprouters	Facultative seeders	Obligate seeders
Postfire resprouting	Yes	Yes	No
Postfire seeding	No	Yes	Yes
Life cycle	Polypyric (perennial)	Polypyric (perennial)	Monopyric (annual)
Reproduction cycles	Iteroparous[1]	Iteroparous[1]	Semelparous
Generations	Long and overlapping	Long and overlapping	Short and nonoverlapping
Recruitment	Between fires (fire-independent)	After fire (fire-dependent)	After fire (fire-dependent)
Synchrony of recruitment	Mainly asynchronous[2]	Synchronous	Synchronous
Age structure of the population	Multiple cohort[2]	Multiple cohort	Single cohort (even-aged)

We propose the terms 'polypyric' and 'monopyric' life cycles to be analogous to the perennial and annual life cycles but related to fire cycles instead of annual cycles (see main text and Box 1 for details).
[1]Resprouters are commonly iteroparous but there are rare exceptions, such as *Agave* spp., that are semelparous (Schaffer & Schaffer, 1977). There are also some bamboo species that are clonal and semelparous but have a monopyric life cycle (Keeley & Bond, 1999).
[2]Obligate resprouters with strong mast-flowering may show synchronous recruitment and some even-aged cohorts, but their recruitment is still independent of fire.

resprouters are short-lived and establish only during interfire intervals, while facultative seeders regenerate by resprouting and reseeding following fires (Box 1; Keeley, 1998). While in some ecosystems resprouting and postfire seeding may show a negative evolutionary correlation (i.e. the loss of one trait is evolutionarily linked to the acquisition of the other; Pausas & Verdú, 2005), it cannot be assumed as universal (Bond & Midgley, 2003; Pausas *et al.*, 2006). In fact the process of losing the resprouting capacity

is not physiologically (mechanistically) linked to the process of acquiring the capacity of postfire seeding, and thus these two processes require different explanations, even if the final outcome (extant functional strategies) implies a correlation. We suggest that changes in evolutionary pressures that modify adult (*P*) and juvenile (*C*) survival in postfire conditions determine the long-term success of each of the two regeneration mechanisms (Fig. 3). Specifically, we propose the following three hypotheses: (1) resprouting appeared early in plant evolution as a response to disturbance, and fire was an important driver in many lineages; (2) postfire seeding evolved under conditions where fires were
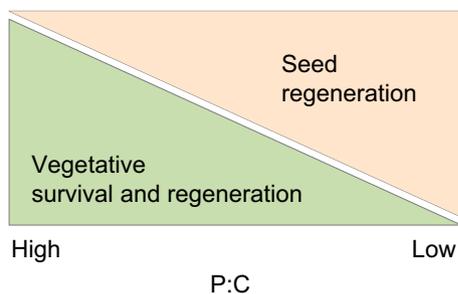
Fig. 1 The relative roles of vegetative and seed regeneration depend on the environmental pressures affecting the adult-to-offspring survival ratio (*P* : *C*).

Fig. 2 Main factors affecting adult (*P*) and offspring seedling (*C*) survival, and thus the *P* : *C* ratio, in fire-prone ecosystems. Black arrows, positive effect; red arrows, negative effect.

Fig. 3 Model of Fig. 1 applied to fire-prone ecosystems. Changes in the probability of resprouting along an adult-to-offspring survival ratio (*P* : *C*) gradient are not linear but show two turning points related to the acquisition of key innovations: the capacity to store a fire-resistant seed bank (postfire seeding), and the loss of resprouting capacity. Changes in the *P* : *C* ratio may be produced by different drivers (Fig. 2) and may have driven the rise of innovations during evolution.

predictable within the life span of the dominant plants and created conditions unfavorable for resprouting; and (3) the intensification of conditions favoring juvenile survival (*C*) and adult mortality (*P*) drove the loss of resprouting ability with the consequence of obligate-seeding species becoming entirely dependent on fire to complete their life cycle, with one generation per fire interval (monopyric life cycle).

Resprouting: an ancient and widespread trait

We define resprouting as the initiation of new shoots, usually from existing plant meristems, following fire or other disturbances that affect the whole plant. Basal resprouting is a nearly universal trait in perennial dicotyledonous plants (Wells, 1969), although in many broad-leaf trees it might be restricted to the sapling stage (Del Tredici, 2001; Shibata *et al.*, 2014). Our analysis of the 2741 species (in 951 genera and 139 families) living in Mediterranean ecosystems in different continents (data from Montenegro *et al.*, 2003; Pausas *et al.*, 2004, 2006; Pausas & Bradstock, 2007; Paula *et al.*, 2009) suggested that 57% have the ability to resprout, and that these resprouting species are distributed in 68% of the genera and in 90% of the families. The widespread taxonomical and phylogenetic distribution of resprouting ability and its presence in old lineages such as in Mesozoic gymnosperms (e.g. *Ephedra*, *Cycas*, *Wollemia nobilis*, *Ginkgo biloba* and *Sequoia sempervirens*; Pausas & Keeley, 2009), and in basal angiosperms (Feild *et al.*, 2004) suggest that it is an ancient trait in woody plants (Keeley *et al.*, 2012, chapter 9).

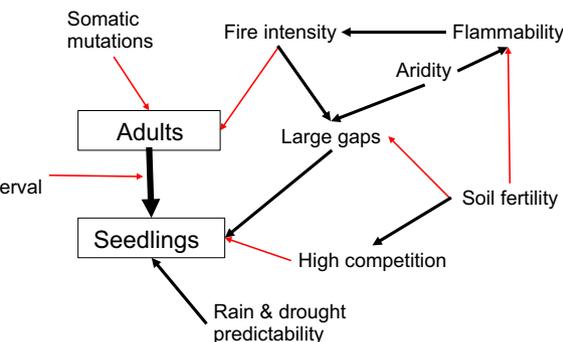Plants resprout following many types of disturbance, and although of apparently adaptive value in fire-prone landscapes, resprouting is common in many vegetation types where fires are rare, such as rainforests or cold temperate ecosystems (Putz & Brokaw, 1989; Kauffman, 1991; Dietze & Clark, 2008; Shibata *et al.*, 2014). Given the long history of fire on Earth (Pausas & Keeley, 2009), it is plausible that in some lineages the evolution of resprouting may have been driven by fire, although this is not likely true for all lineages. Resprouting is not a simple trait and there are several mechanisms (Clarke *et al.*, 2013) that may be tied to different evolutionary frameworks. For instance, while epicormic resprouting can be clearly linked to fire (Crisp *et al.*, 2011), resprouting from roots, rhizomes, or even the root collar is not necessarily linked to fire (Lacey & Johnston, 1990). Resprouting from buds located in specialized and ontogenic structures such as lignotubers is also tied to fire-prone environments (Canadell & Zedler, 1995; Keeley *et al.*, 2012 chapter 3). In addition, some fire regimes may select against resprouting (see 'Loss of resprouting ability' below). Thus, resprouting is a complex functional trait that requires a careful analysis before its origin can be linked to a specific evolutionary pressure (Keeley *et al.*, 2011).

In moist and fertile environments, post-disturbance regeneration is very rapid and resprouting confers a competitive advantage by recapturing space previously occupied by the mature plant. This is because the surviving biomass (often belowground) enables the plant to quickly regenerate the aboveground biomass. In such conditions, seedlings fare poorly in competition with resprouts (Tyler & D'Antonio, 1995), and

thus the sexual reproduction of obligate resprouters is not usually linked to local disturbance, but rather these resprouters focus on strategies for finding appropriate microsites for recruitment (efficient dispersal methods, e.g. vertebrate dispersal). Consequently, such conditions do not select for delayed germination that restricts recruitment to postfire conditions (Keeley, 1998; Keeley *et al.*, 2012).

Given that resprouting is spatially, ecologically, and phylogenetically widespread, a reasonable hypothesis is that it is the ancestral state in most lineages, and that losing resprouting is a derived state (Wells, 1969; Bond & Midgley, 2003; Verdaguer & Ojeda, 2005). This does not discount the possibility of reversals in some lineages where occasionally resprouting species may originate from nonresprouting ancestors (Bond & Midgley, 2003; He *et al.*, 2011; Keeley *et al.*, 2012). In fire-prone ecosystems, a prerequisite for losing resprouting is to have an alternative postfire regeneration strategy, namely postfire seeding (Box 1). Thus, the appearance of postfire seeding should precede (or occur simultaneously with) the loss of resprouting capacity. Consequently, we hypothesize that facultative seeders were derived from resprouters and that nonresprouting obligate seeders were derived from facultative seeders. The loss and acquisition of these traits generate different trait combinations (regeneration strategies; Box 1; Fig. 3) that have very different population dynamics (Pausas, 1999) with strong ecological and evolutionary consequences (Table 1).

The acquisition of postfire seeding

Resprouting is optimal in fertile competitive environments where vigorous and aggressive resprouts rapidly occupy postfire gaps and therefore provide limited opportunities for seedling recruitment. By contrast, under stressful site conditions (such as low soil fertility and severe water deficits), fires may be more predictable, and the growth and the postfire resprouting rate are slower and the gaps with available resources are larger and longer lasting (Keeley & Zedler, 1978; Meentemeyer & Moody, 2002). Such conditions provide a substantial opportunity for recruitment leading to a decrease in *P* : *C* (Fig. 2) and selection for delaying reproduction to a single point in time (i.e. postfire) when more resources are available. By delaying germination to when conditions are optimal, plants also reduce fitness variance across fire cycles. Because fitness is a multiplicative process, it is very sensitive to occasional low values, and thus low fitness variance is selected for – despite the possible cost of increased seed mortality in the seed bank (Childs *et al.*, 2010). Factors that reduce survivorship of resprouting species would also create gaps; for example, fire regimes with recurrent but relatively long fire return intervals could contribute to selection for postfire gaps by accumulating fuels capable of killing resprouters by high-intensity fires (Moreno & Oechel, 1993; Lloret & López-Soria, 1993; Fig. 2). In addition, old-age mortality of resprouters during long interfire periods would also create gaps and opportunities for seeding regeneration of species with long seedbank longevity (Keeley & Zedler, 1978).

Aridity may reduce survivorship of both seedlings and adults; however, restricting reproduction to postfire conditions can enhance seedling survivorship because of the reduced competition

after fire. In addition, increased temperatures in postfire gaps may also accelerate seedling emergence under low water potential (Stevens *et al.*, 2014). There is evidence that the increasing aridification in marginal sites throughout the Tertiary could have driven the rise of the nonresprouting obligate seeding subgenus *Cerastes* in the genus *Ceanothus* (Ackerly *et al.*, 2006; Keeley *et al.*, 2012). The aridification process increased in extent during the Quaternary, and may have increased the diversification of seeder species (Verdú & Pausas, 2013). There is evidence from extant species that obligate seeders are more tolerant of water stress and fluctuations in water availability than resprouters, and exhibit physiological and anatomical traits that favor recruitment in open sites under stressful soil-drought conditions (Box 2). The expansion of drought-prone landscapes during the late Tertiary (Keeley *et al.*, 2012) resulted in an increase in fire size, which could also have favored delayed reproduction (dispersal in time) rather than dispersal in space.

Delaying reproduction until the advent of postfire conditions requires the accumulation of a seed bank during the fire-free interval, and a germination cue to recruit after fire when resources are most available. In different lineages this has been accomplished by various mechanisms such as serotiny and fire-dependent germination (Box 3). A corollary of having postfire seedling recruitment is the increase in population turnover, which increases the possibility of easily acquiring genetic novelties and thus better tracking changes in the environment from generation to generation (Wells, 1969; Raven, 1973; Schwilk & Kerr, 2002). Additionally, seed banks are also a source of genetic variation and novelty, as the aging of seeds and the reduction in viability implies an accumulation of mutations (Levin, 1990). Because resprouters regenerate in place, they are wedded to their environment, and acquiring postfire seeding makes the species better suited for a changing environment. All these factors may explain the high species richness in lineages that have acquired this trait (e.g. Fig. 4).

In addition to delayed reproduction enforced by deep seed dormancy and germination stimulated by heat or smoke, traits expected to be selected in postfire seeders include early emergence and rapid seedling growth. These traits allow seedlings to quickly capture resources and become more competitive, and this can be adaptive for seedlings under crowded postfire conditions where recruitment is concentrated in a single point in time (de Luis *et al.*, 2008). Concomitant with the evolution of postfire seeding, one might also expect selection for traits that enhance flammability. Flammability-enhancing traits could be favored in individuals if the elevated flammability resulted in increased mortality of neighbors, and thus opened space for recruitment opportunities for the flammable individual's offspring (Bond & Midgley, 1995). Modeling studies have suggested different genetic mechanisms for the evolution of flammability (Kerr *et al.*, 1999; Schwilk & Kerr, 2002), and there is some field evidence that recurrent fires increase plant flammability (Pausas & Moreira, 2012; Pausas *et al.*, 2012; Moreira *et al.*, 2014). The correlation between the postfire seeding strategy and flammability across different species provides further evidence for this hypothesis (Keeley & Zedler, 1998; Schwilk & Ackerly, 2001; Saura-Mas *et al.*, 2010; He *et al.*, 2012).

Box 2 Costs of resprouting

Resprouting carries a cost of storing resources to maintain a bud bank and support rapid post-disturbance regrowth. For instance, resprouting populations have higher levels of carbohydrates than nonresprouting species or populations, even at the seedling stage (Pate *et al.*, 1990; Verdaguer & Ojeda, 2002; Schwilk & Ackerly, 2005). This early allocation to buds might also imply reduced seedling growth. Repeated disturbance causes a reduction in root carbohydrates in resprouting species (Canadell *et al.*, 1991), and this reduction limits post-disturbance resprouting and increases mortality (Moreira *et al.*, 2012). To accumulate these resources, seedlings of resprouting plants allocate more resources to belowground storage while seedlings of nonresprouting plants allocate resources mainly to (aboveground) growth and reproduction (Bowen & Pate, 1993; Schutz *et al.*, 2009). The implications of this differential carbon allocation pattern are many, including a higher root : shoot ratio (Pate *et al.*, 1990; Verdaguer & Ojeda, 2002; Schwilk & Ackerly, 2005), lower seedling height growth (Pausas *et al.*, 2004), lower specific root length (Paula & Pausas, 2011), lower resistance to xylem cavitation (Jacobsen *et al.*, 2007; Pratt *et al.*, 2007, 2008; Vilagrosa *et al.*, 2013) and later maturity (Schwilk & Ackerly, 2005) in resprouting than in coexisting nonresprouting seeder species. In addition, seedlings of obligate seeders are often more efficient at conducting water (when it is available) than those of resprouters, and hence they are better adapted to take full advantage of periods with good water availability (Pratt *et al.*, 2010; Hernández *et al.*, 2011; Vilagrosa *et al.*, 2013). An additional implication is the potential differential response to anthropogenic changes in atmospheric CO_2 concentration (Bond & Midgley, 2012). At the landscape scale, the consequence of the differential carbon allocation pattern between postfire strategies is that resprouters tend to dominate in sites with more reliable water (pole-facing slopes, gullies, etc.) while seeders are able to occupy sites with stronger oscillations in water availability (Keeley, 1977; Pausas *et al.*, 1999; Clarke & Knox, 2002; Meentemeyer & Moody, 2002; Pausas & Bradstock, 2007; Coca & Pausas, 2012). Resource allocation models also predict higher storage capacity in high-productivity habitats (Iwasa & Kubo, 1997), and a lack of resprouting when disturbance is high in relation to productivity (Fig. Box 2, below). Despite the high carbon demand of resprouters, it is an omnipresent strategy in plants living in recurrently disturbed environments world-wide; and only in certain conditions in which safe sites are relatively frequent and large, and post-disturbance conditions reliable and predictable (Fig. 2), has the loss of this characteristic been successful (see main text).

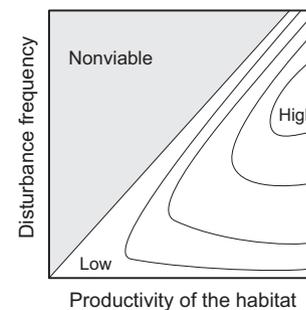**Fig. Box 2** Contours of the ratio of storage to growth allocation for an optimally growing resprouter in the space defined by habitat productivity and disturbance frequency (based on Iwasa & Kubo, 1997).

In our analogy of fire cycles being equivalent to annual cycles, and the loss of resprouting being analogous to a transition from the perennial to annual life history, we have considered the important

role of a decrease in $P:C$ (Charnov & Schaffer, 1973). Semelparity is also favored by a low ratio of maturity age to time-between-reproductive-episodes (Young, 1981), which in our case is the ratio of maturity age to fire interval (Fig. 2; Box 3). Simulation models suggest that the most sensitive component in this process is seedling survival and the subsequent successful establishment as a mature reproductive adult (Bond & Van Wilgen, 1996; Ojeda *et al.*, 2005). Thus, factors contributing to seedling success, such as adaptation to arid sites enhanced by greater numbers of sexual generations, or allocation of resources to growth over storage, may be critical to the evolution of postfire seeding.

Loss of resprouting ability

Trait loss is a common evolutionary phenomenon when environmental change removes or weakens a source of selection that was previously important in maintaining a trait (Lathi *et al.*, 2009). In fire-prone shrublands, increased aridity during the evolutionary history provided the setting for the loss of resprouting in many lineages and for depending entirely on a single postfire pulse of seedlings, and thus becoming monopyric (obligate seeders; Box 1; Fig. 3). Despite resprouting being a good strategy for persisting, it carries costs, such as those related to storing carbohydrates, thickening the bark (in epicormic resprouting species), maintaining the bud bank for postfire regeneration and the associated reduction of both above- and belowground growth and delayed reproduction (Box 2). In addition, there are specific conditions linked to aridity in which adults are negatively affected (e.g. high-intensity fires and postfire droughts) and seedlings are promoted (e.g. increased availability of safe sites; Fig. 2), which facilitate the transition towards obligate seeding (lower $P:C$). Increasing aridity, however, makes postfire seedling recruitment more precarious and has selected for both physiological and anatomical traits that enhance drought tolerance (Box 2).

However, for seedling recruitment to become fully independent of resprouting, there must be a predictable fire regime (i.e. fire return intervals coupled with maturity age, plant longevity, and seed bank longevity; Box 3) and reliable postfire conditions (seasonal climates). While fire return intervals must fall within the life span of the plant (including the seedbank; Box 3), very short fire intervals preclude regeneration of obligate seeders (immaturity risk; Box 3), which explains why this transition has rarely occurred in savannas (fire intervals *c.* 1–5 yr). Examples of loss of resprouting are observed in the different Mediterranean-type ecosystems (where fire intervals vary from decades to centuries), such as the *Cerastes* subgenus of *Ceanothus* in North America, the genus *Cistus* in southern Europe, or the genus *Erica* in South Africa, among others (Fig. 4; Keeley *et al.*, 2012). In addition, there is evidence from extant species of such loss of resprouting resulting from the suppression of bud development responsible for lignotuber formation (Verdaguer & Ojeda, 2005). In fact, factors driving this transition could have been just an intensification of those responsible for the initial acquisition of postfire seeding in resprouters; so the loss of resprouting may have been occurring together with the optimization of the postfire seeding strategy, and factors working against resprouting may have favored postfire

Box 3 Postfire seeding: mechanisms of storing seeds and delaying germination

There are two modes of seed storage in postfire seeders: soil-stored seed banks and canopy-stored seed banks (also called serotiny). **Canopy-stored** seeds remain quiescent in closed woody structures (serotinous cones) for several to many years and seeds are released when the heat of the fire causes cones to open and disperse the seeds into the postfire soil bed (Lamont *et al.*, 1991). **Soil-stored** seeds remain dormant in the soil for decades to centuries and the heat of the fire or the chemicals from the combustion of organic matter break seed dormancy and stimulate germination after fire (i.e. heat-stimulated and smoke-stimulated germination; Keeley & Fotheringham, 2000). These different mechanisms of delaying reproduction correspond to different solutions for a similar 'problem', and may depend on phylogenetic constraints and the availability of pre-existing structures in the corresponding lineages on which natural selection could act. In addition, low-fertility soils may have selected against soil storage in favor of aerial storage because in such ecosystems high-nutrient seeds are subject to more intense predation when exposed on the soil surface (Keeley *et al.*, 2011).

Additionally, different fire regimes may play a critical role as soil-stored seeds can persist under long fire-free intervals whereas serotinous species cannot and thus such species require *a more predictable fire regime* (Fig. Box 3 below; Lamont *et al.*, 1991; Enright *et al.*, 1998; Lamont & Enright, 2000). Although serotinous cones may open with time or when the plant dies, the chance of recruiting without fire is low because of competition with existing vegetation, and when fire occurs the dead individual will not contribute to postfire seedling populations. By contrast, this is not necessarily true in soil seed bank species because seeds may remain in the soil for many years after the death of the parent plant waiting for the appropriate opportunity to germinate. Consequently, plants with soil-stored seed banks are more capable of dealing with higher variability in fire intervals than serotinous plants that require a more predictable fire regime.
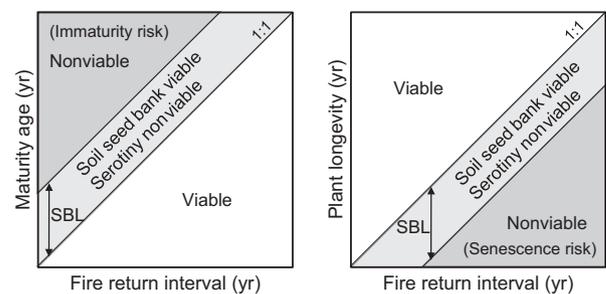
Fig. Box 3 The persistence of obligate postfire seeders is constrained by maturity age (left), plant longevity (right), and seed bank longevity (SBL), in relation to the fire-return interval, and these constrictions are stronger for serotinous seeders than for species with soil seed banks. Obligate postfire seeders are viable when the ratio of maturity age to fire interval is low and the ratio of longevity to fire interval is high. In soil seed bank seeders, these constraints are relaxed by the seed bank longevity. Nonviable conditions are also referred to as 'immaturity risk' (Zedler, 1995) where fire intervals are shorter than the maturity age plus the longevity of the soil seedbank, and 'senescence risk', where fire intervals are longer than plant longevity plus the longevity of the soil seedbank.

seeding. For instance, high-intensity fires negatively affect resprouting by killing vegetative buds (Lloret & López-Soria, 1993; Moreno & Oechel, 1993; Vesk *et al.*, 2004), and postfire droughts

Fig. 4 Examples of spectacular radiations (high number of species per genus) for 15 genera (*y*-axis) living in fire-prone ecosystems of Australia, California, the Cape Region of South Africa, and the Mediterranean Basin. The number 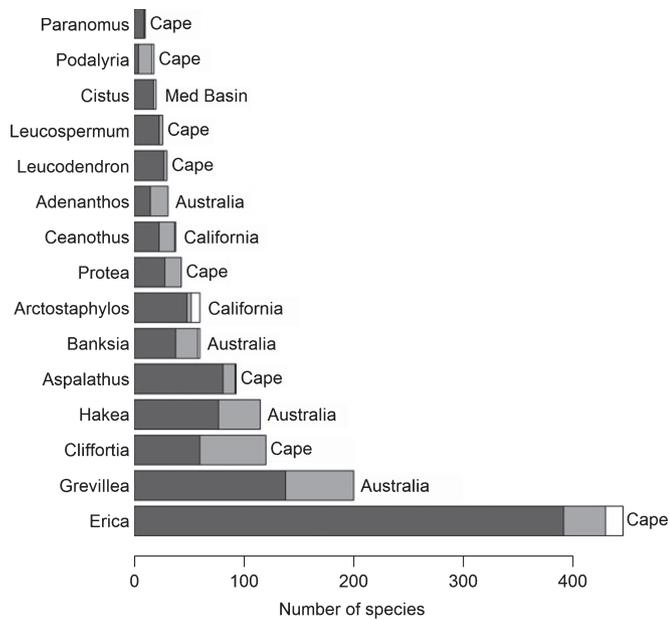of postfire obligate (nonresprouting) seeders (dark gray), the number of postfire resprouters (light gray; mainly facultative species; see Box 1), and the number of species with variability in resprouting ability among populations (white) are shown. Data were compiled by Keeley *et al.* (2012).

reduce resprout success (Pratt *et al.*, 2014); but the increased intensity of fires might have also increased seed resistance to fire and the temperature thresholds for dormancy release (Moreira & Pausas, 2012). Thus, fire intensity favors postfire seeders by simultaneously increasing C and decreasing P (Figs 2, 3).

Another factor against resprouting is that genets may become very old and the potential exists for greater accumulation of deleterious alleles from somatic mutations (Wiens *et al.*, 1987). A high genetic load would potentially result in a reduced seed set (Lamont & Wiens, 2003). This hypothesis could explain the higher seed abortion rate in resprouting than in non-resprouting monocots in Western Australia (Meney *et al.*, 1997), and the anomalously nearly nonexistent seedling recruitment in some resprouters in Cape fynbos (*Retzia* spp.), *Banksia elegans* in Western Australian woodlands (Bond & Midgley, 2003), and *Adenostoma sparsifolium* in California (Wiens *et al.*, 2012). It could also explain the spatial genetic structure of some long-lived resprouters (Premoli & Steinke, 2008).

Selection of the obligate seeder life history would have been enhanced by their short generation time and rapid population turnover (under recurrent fires), which increases recombination-based mutations. In addition, the fact that seeders recruit from an aged seed bank also ensures the generation of genetic novelties (Levin, 1990). All of these processes increase the opportunity for natural selection to act, and thus speed up life history evolution (Wells, 1969; Schwilk & Kerr, 2002). The monopyric life cycle of obligate seeders precludes generational overlapping, which also contributes to increased genetic differentiation among populations and thus enhances evolutionary changes (Wade & McCauley, 1988; Nunney, 1993; Ellner & Hairston, 1994). These fast evolutionary changes should enable the species to better track

changes in the environment from generation to generation and adapt to micro-enviromental conditions (Wells, 1969; Raven, 1973; Schwilk & Kerr, 2002), with the possible consequence of increasing diversification. In fact, the richness of many fire-prone ecosystems has been explained by the high diversification rates associated with the high population turnover in seeder species (Cowling & Pressey, 2001; Wisheu *et al.*, 2000; Barraclough, 2006; Fig. 4), as short generation times are related to high rates of molecular change (Smith & Donoghue, 2008). In this framework, there is some evidence of greater genetic diversity and differentiation in seeder than in resprouter populations of the same species (Segarra-Moragues & Ojeda, 2010), which can be considered an initial step to speciation (Coyne & Orr, 2004). However, diversification studies are still ambiguous in demonstrating a higher diversification of seeders, as other factors such as soil type and spatial heterogeneity may mask the pattern (Verdú *et al.*, 2007; Schnitzler *et al.*, 2011; Litsios *et al.*, 2014), and a broader analysis, including the three fire strategies (Table 1), remains to be carried out.

A successful coexistence

By losing the resprouting ability and acquiring the postfire seeding strategy, plants greatly increase their fitness in ecosystems with predictable fire recurrence, and thus access new ecological conditions causing rapid, and sometimes spectacular, adaptive radiations (Cowling & Pressey, 2001; Fig. 4). These novelties appear in different clades through convergent or parallel evolution (homoplastic novelties; Hunter, 1998) and have been highly successful in ecological and evolutionary terms. Thus, they could be considered as key evolutionary innovations (Hunter, 1998) in crown-fire ecosystems. In fact, most fire-prone ecosystems are included in the list of global biodiversity hotspots (Myers *et al.*, 2000) and the evolutionary pathways shaping fire-related traits may contribute to their diversity. A consequence of the proposed model is that, in lineages that have acquired postfire seeding, this trait is more phylogenetically conserved than resprouting, as has been observed in different Proteaceae lineages (Bond & Midgley, 2003; He *et al.*, 2011) and in *Ceanothus* (Ackerly, 2003).

We have described the main transitions in fire traits driven by the historical increase in aridity and the concomitant increase in the predictable role of fire in some landscapes (Figs 2, 3). Although the primary factors driving these transitions are likely to be similar in fire-prone environments, the timing of the evolution of each of the novelties has varied across different regions and lineages. For example, the widespread and very old infertile soils in southwestern Australia would have assembled flammable vegetation early in the Tertiary (He *et al.*, 2011, 2012; Crisp *et al.*, 2011; Keeley *et al.*, 2012; chapter 10), whereas in other regions, aridity may have played a larger role in diversification at a later point (Verdú & Pausas, 2013). In addition, not all plant lineages were subject to the same transitions because the ecological and evolutionary forces that shaped plants changed in time and space (see box 1 from Keeley *et al.*, 2011), and plants in different regions had different phylogenetic (historic) constraints. Consequently, alternative pathways also exist (Box 4) and thus differing strategies may coexist.

Box 4 Evolutionary transitions

If we note the two traits (resprouting and postfire seeding) as R and P, and the two states of each trait as + and −, the four possible combinations define the four general postfire strategies (Box 1 and Pausas *et al.*, 2004): R+P− (obligate resprouters); R+P+ (facultative species); R−P+ (obligate seeders); and R−P− (without endogenous regeneration, postfire colonizers). By changing the state of one of the traits, species may evolve from one strategy to another. Fig. Box 4 (below) shows some possible evolutionary transitions. For instance (Fig. Box 4 below, clockwise), the acquisition of postfire seeding by obligate resprouters (R+P−, ancestral strategy) might have occurred in *Arctostaphylos* and *Ceanothus* species (Keeley *et al.*, 2012), leading to some facultative species (R+P+) in these genera (Fig. 4). The reversal may have occurred in the Chilean matorral where fire was probably frequent before the rise of the Andes that currently limit the summer storms (Keeley *et al.*, 2012). Loss and acquisition of resprouting in seeders are common in Proteaceae (Bond & Midgley, 2003; Lamont *et al.*, 2013) and Fabaceae (Boatwright *et al.*, 2008); and aberrant resprouting individuals of obligate seeders have been observed in Lamiaceae in the Mediterranean basin (J. G. Pausas, personal observations), in Ericaceae and Fabaceae in the South African Cape region (Schutte *et al.*, 1995; Ojeda, 1998) and in the Australian *Banksia* and *Hakea* (R. Bradstock, pers. comm.). The acquisition of postfire seeding by nonresprouters can be exemplified by the acquisition of serotiny in *Pinus* during the Cretaceous (He *et al.*, 2012). Loss and acquisition of resprouting from the ancestral obligate resprouter seem to have occurred in conifers (*Juniperus* and *Pinus*; He *et al.*, 2012).
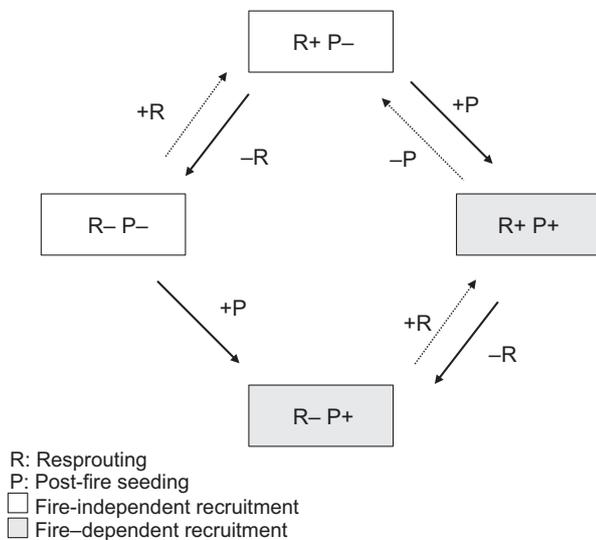

R: Resprouting
P: Post-fire seeding
☐ Fire-independent recruitment
▨ Fire–dependent recruitment

Fig. Box 4 Possible evolutionary transitions between postfire regeneration strategies. Continuous lines indicate more frequent transitions than dotted lines.

niches is one of the mechanisms of coexistence in disturbance-prone ecosystems (Grubb, 1977; Lavorel & Chesson, 1995; Miller & Chesson, 2009), and Mediterranean ecosystems provide examples of such coexistence (Pausas *et al.*, 2004; Keeley *et al.*, 2012; Marais *et al.*, 2014). Spatial models of iteroparity and semelparity dynamics also suggest long-term coexistence when life-history traits (number of offspring and juvenile and adult survival) are variable in time (Ranta *et al.*, 2002). In accordance with the evolutionary tendency of resprouting being lost with aridity and seeders being more capable to recruit in drier conditions (Box 2), there is evidence from many regions world-wide of some spatial landscape segregation between postfire seeders and obligate resprouters, in such a way that the former occupy the parts of the landscape where water is more susceptible to strong oscillations, and the latter occupy parts where water is more reliable (Box 2). The coexistence of species with different regeneration strategies reflects that different combinations of traits can be adaptive in fire-prone ecosystems (Box 4). This is an alternative view to the one considering that strategies with ancestral trait states (such as obligate resprouters) are relict and can only persist thanks to the facilitative effect of species with derived trait states (such as obligate seeders) (sensu Valiente-Banuet *et al.*, 2006). However, simulation studies of population dynamics in variable fire regimes find coexistence possible between any two of the three strategies, but not for all three (Cowan, 2010).

In conclusion, our models based on the relative survivorships of adults and juveniles coupled with the restrictions imposed by fire return intervals provide a useful framework for understanding temporal and spatial variations in resprouting and seeding in ecosystems subjected to crown-fire regimes. This model accounts for patterns of coexistence and environmental changes contributing to the evolution of seeding from resprouting ancestors.

Acknowledgements

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Considering that landscape heterogeneity leads to heterogeneous fire regimes, it is to be expected that evolution would select for diverse life history solutions to fire, including both polypyric and monopyric life cycles (i.e. resprouters and obligate seeders, respectively), and that communities would assemble that include this variety of strategies. In fact, having different regeneration

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