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Fire as a Selective Agent for both Serotiny and Nonserotiny Over Space and Time

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ABSTRACT
Serotiny is the prolonged storage of seeds in closed cones or fruits held within the crown of woody plants. It is widespread throughout fireprone vegetation with a predominantly winter rainfall, especially in Mediterrnanean-type ecosystems (MTEs). Nonstorage is a feature of fireprone vegetation with summer-dominant rainfall or nonfireprone vegetation. Serotiny confers fitness benefits on an individual when fire return intervals fall between age to reproductive maturity and the plant life span. The level of serotiny within and between species varies greatly along a continuum indicating highly plastic responses to different environmental conditions. Here we review how and why the traits that underpin this reproductive syndrome evolved and continue to control the occurrence of species in contemporary landscapes. We documented 1345 serotinous species in fireprone regions of Australia, South Africa, the Mediterranean Basin, North America, and Asia. The length of seed storage varies from a few years (weak serotiny) to >10 years (strong serotiny), with remarkable diversity even within clades. We show how the interplay between postfire and interfire seedling recruitment dictates the expression of serotiny along a strong serotiny/nonserotiny continuum, and that, where strong serotiny is favored, the 'gene support for serotiny' builds up over successive generations. Nonserotiny is favored in the absence of fire or occurs at intervals exceeding plant longevity, but also when the fire is so frequent that only resprouters can survive. We identify 23 traits associated with serotiny/nonserotiny syndromes that are subject to both environmental and phylogenetic constraints. While all are coordinated for maximum fitness, some traits, such as protection from granivores, are only indirectly related to the fire regime. Serotiny has a long history extending back to the Triassic. The rate of serotinous-lineage proliferation has fluctuated greatly over time but peaked over the last 5 million years. Nonserotinous species have evolved from serotinous ancestors in response to increased fire frequency, or as plants migrated to fire-free habitats. We note that contemporary shifts in climate, land-use, and exploitation have had a profound, but disproportionate, effect on the conservation status and evolutionary trajectory of serotinous species in MTEs. Escalating anthropogenic impacts increase the need to understand how and why serotiny is such a prominent feature of some fireprone ecosystems. We highlight avenues for future research and argue for the use of temporally based measures of serotiny to facilitate comparisons between studies.

KEYWORDS
Banksia; canopy seed storage; fire ecology; flammability; *Hakea*; interfire; Mediterranean; *Pinus*; postfire recruitment; *Protea*; resprouters; savanna; seedlings; seed storage; woody fruits

I. Serotiny vs nonserotiny

Serotiny refers to prolonged storage of seeds in cones or fruits retained on the plant. It is part of a major reproductive syndrome among woody shrubs and trees (Box 1) that can be distinguished from seed release at maturity (nonserotiny) and soil storage (geospory). The ecology and evolution of serotiny have been widely studied in Australia, North America, Mediterranean Basin, and South Africa where it is recognized as a key adaptive trait to fire (Lamont and Enright, 2000; Keeley *et al.*, 2011; Treurnicht *et al.*, 2016) with an evolutionary history that extends back to the Triassic (He, Belcher, *et al.*, 2016; Lamont *et al.*, 2019a). The adaptive advantages of serotiny among woody plants center on its ability to increase seed availability above the minimum required for postfire population recovery (Enright *et al.*, 1998a).

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Box 1. The concept of serotiny

The origin of the term serotiny is quite general in meaning: late occurrence of an event (Lamont, 1991), and was first used in 1803 for *Pinus serotina* in reference to the delayed opening of its cones. Strictly one should refer to serotinous fruits or cones (delayed release of seeds) or serotinous seeds (prolonged retention in cones/fruits). However, this rider is hardly ever used, and reference to serotinous individuals and species is taken to imply the prolonged retention of seeds on the mother plant. 'Prolonged' is usually interpreted as retention of some seeds in the presence of at least the next crop of mature seeds (Lamont and Enright, 2000). Cones/fruits, individuals, populations or species can be described as (i) nonserotinous (seeds released at maturity), (ii) weakly serotinous (seeds retained for 1–4 years), (iii) moderately serotinous (5–9 years), or (iv) strongly serotinous (10+ years). Individual plants within a population may be assigned to any of these four categories – this may have a temporal or growing condition component (e.g., most cones/fruits might be open in moribund plants, all cones/fruits might be closed with only 1–2 years crops on them, vigorously growing plants will mostly comprise young, closed cones/fruits). Among pines and proteas, cones are usually either closed (immature, green; older, brown – some may open) or open (old, gray – closed or open). This also applies to species with solitary woody fruits, such as hakeas, with similar color changes apparent. For other clades, with clusters of fruits (eucalypts) or cones (banksias), the fraction of open fruits per cluster/cone may vary in any year's crop (Lamont, Rees, *et al.*, 1994). Severance from their vascular supply, whether induced by fire or not, is sufficient to stimulate the opening of serotinous cones/fruits in most species; rarely, cones/fruits in some species never open in the absence of fire heat even when removed from the parent plant.

The seed-supporting structures of the great majority of species gradually open and release their seeds over time, but often at vastly different rates. As the structures age, so the threshold cue required to stimulate opening becomes less intense, fir example, lower temperatures are needed (Enright and Lamont, 2006), or their vascular supply clogs, and they begin to open spontaneously. The rate (inverse of the slope of the best fit line) at which opening occurs, independent of crop size, determines the 'inherent' level of serotiny (Cowling and Lamont, 1985a). The fraction of cones/fruits that is closed on a plant at a given time is an estimate of 'apparent' serotiny – differences in annual crop size (with their different levels of opening) are not taken into account. Nevertheless, even the slope measure of serotiny will be susceptible to say, increases in mean temperatures due to climate change which have yet to lead to differential survival and adaptation, so that the best estimates of the level of serotiny will still have an environmental component (Hernández-Serrano *et al.*, 2014). Ideally, viability of the seeds should be included in any estimates of inherent serotiny, for example, age of oldest viable seeds retained on the plant (Lamont, 2020), although this is rarely done.

In other contexts, the concept of serotiny has been widened to include seeds retained (i) on a dead ephemeral plant where seed dispersal relies on dislodgement during highly stochastic rainfall events in desert environments (Martínez-Berdeja *et al.*, 2015) or physical dislodgement during movement as a wind-blown 'tumbleweed' (Borger *et al.*, 2007; Long *et al.*, 2015), (ii) within the cladode of certain cacti (*Mammillaria*) that ensures the seeds become 'primed' before dislodgement by rain (Santini and Martorell, 2013), and (iii) on a living plant for up to 9 months beyond the point of reaching maturity with retention of heat-tolerant proteins during that time without any obvious environmental cue for release has been recorded in a few hard-seeded legumes (*Peltophorum*) (Silva *et al.*, 2017). All these examples lack the three attributes that characterize the many hundreds of species that are the subject of this review: (a) on-plant storage of most mature seeds for at least a year, (b) retention of seeds within woody supporting structures, and (c) seed release in response to fire that may have a direct or indirect role in seed release (e.g., melting of binding resins, death of the supporting branch with associated desiccation processes).

The relative benefits of different levels of serotiny revolve around the opportunities for interfire recruitment compared with postfire recruitment (Cowling and Lamont, 1985a; Enright *et al.*, 1998a). Adaptive changes in the level of serotiny are expected when a) a species attempts to invade an area whose fire regime is different from the current one, or b) the fire regime changes in its native habitat (Ne'eman *et al.*, 2004; Lamont *et al.*, 2013). Thus, nonserotiny can be expected in nonfireprone habitats where postfire germination is not possible (Lamont *et al.*, 2019b). Less well-appreciated is the fact that high fire frequency may also induce nonserotiny, or more generally, nonstorage (Buma *et al.*, 2013; Lamont, He, *et al.*, 2017). When fire is likely in most years, as in (sub)tropical savannas, there is little opportunity for, nor benefit in, the accumulation of seeds, and, in fact, flames from surface fires do not reach the crown of trees anyway. Thus, both extremes of fire frequency promote nonserotiny, and the processes responsible are discussed here.

The purpose of this review is to explore the environmental factors associated with fire (or its absence) that promote or inhibit the evolution of serotiny spatially (different fire regimes and growing conditions), at different levels of organization (within and between populations, species, genera and broader clades), and at different temporal scales [currently (microevolution) and over geological time (macroevolution)]. We begin by describing the serotinous structures that protect their stored seeds and their taxonomic and geographic distribution. Consideration of the syndrome of traits associated with on-plant seed storage, seed release, and seedling recruitment follows. What is the genetic basis for these fire-adapted traits? The relevant genes and alleles arise from somatic or meiotic mutations (Benca *et al.*, 2018; He and Lamont, 2018) and we assume that they already exist at low frequencies among some genotypes. Prior adaptive responses to other survival hazards, such as herbivory, seasonal drought or other disturbances/stresses (in this review, *x*/*y* means '*x* and/or *y*') may play some role but fire usually precedes them as a selective agent (Lamont *et al.*, 2019b). We concentrate on the selection process because little is known about the initiation of genetic mutations while the role of fire as a selective agent is well established (Castellanos *et al.*, 2015). Next considered are impacts of the population dynamics on interfire and postfire recruitment and phenotypic selection, followed by the possible genetic mechanisms that increase or decrease the gene 'support' for serotinous traits. We then review actual examples of the outcome of the selection processes described above, first at the intraspecific scale and then at the interspecific, intrageneric and intracladal scales. These highlight different responses between populations and taxa to different constraints, and different responses to the same constraints by different taxa. We then document changes in the occurrence of serotiny and nonserotiny through geological time. Finally, we consider issues for conservation and priorities for future research.

II. Morphology, taxonomy, and distribution of serotinous structures

There is a great diversity of serotinous structures (Figure 1) among the 1345 species, distributed across 55 genera in 12 families (Figure 2), documented in this review. All seed-bearing structures, but two types with fleshy sepals, are dry and variously woody, and all are dehiscent at the level of the cone (that releases seeds or indehiscent fruits) or fruit (that releases seeds) (Table S1). The data for species yet to be examined indicate that the total listed here is a little more than half of the likely total number (~2500). Seven genera are currently recorded with ≥50 serotinous species (*Eucalyptus* to *Callistemon* in Figure 2). Among serotinous clades, 21 (38%) of the largest genera also contain nonserotinous species, while 53% are solely serotinous. Regionally, 87.5% of records are for Australia, with 75% of these in SW Australia (that occupies only 4% area of the continent). South Africa accounts for 10.5% of species, with 1.5% in North America and 0.5% in the Mediterranean Basin, and two species in Asia (*Pinus yunnanensis*, *Larix gmilinii*). Overall, about 85% of species occur under predominantly winter-rainfall climates corresponding to the world's Mediterranean-type ecosystems (Esler *et al.*, 2018). The rest occur in uniform-rainfall regions with summer-rainfall regions notable for the absence of serotinous species (Lamont *et al.*, 2013). The incidence of serotiny declines as the fraction of rainfall in summer increases (Hernández-Serrano *et al.*, 2013; de Gouvenain *et al.*, 2019). All occur in fire-prone, sclerophyll shrublands, woodlands or forests.

Regarding serotinous structures, 43% are isolated or loosely clustered fruits (axillary or terminal), 30% are cones (terminal) with indehiscent fruits, 25% are aggregated fruits (axillary, except for *Syncarpia*) and 4% are cones with seeds (terminal), all pictured in Figure 1 and described in Table S1. Homology exists within the fruit type (follicle, capsule, achene) and within conflorescence type (solitary, umbel, capitulum, cyme) but not between them (homoplasy). Pinaceae, Casuarinaceae, and the two major subfamilies of Proteaceae (Proteoideae, *Banksia* in Grevilleoideae) have quite different cone types structurally. The first stores naked seeds supported by fused scales (bracteoles), the second has fruits immersed between two woody scales, the Proteoideae has one woody scale pressing the fruit against the rachis, whereas *Banksia* has protruding fruits immersed in a mantle of fibrous bracts per two florets each with its own fibrous bracteole (George, 1981). As for the dispersal units, 70% are air buoyant with 51% having winged seeds, 19% with winged, hairy or otherwise buoyant fruits, 29% with small (<2 mm long), wingless seeds, and 1.5% with wingless fruits (*Leucadendron*). All these structures appear to have evolved independently although subjected to the same forces of selection (discussed later).

III. Traits that control serotiny, seed release, and recruitment

If we are to consider fire as a selective agent for the evolution of serotiny/seed-release or their reverse, then we need to identify what traits fire must act upon for adaptive changes to occur. The first three of six stages are common to plants in general (Figure 3). Species possess a syndrome of traits that are adapted to three constraint dimensions – the prevailing abiotic environment (climate, soils, topography), the prevailing biotic environment (pollinators, herbivores, granivores, pathogens, symbionts, dispersers) and disturbance, principally fire (Pausas and Lamont, 2018; Lamont *et al.*, 2019b). Thus, the preexistence of adaptations (genetically based traits selected for over time) to the abiotic and biotic environments and fire regime occupied are prerequisites. Serotiny (vs nonserotiny) are the initial components of

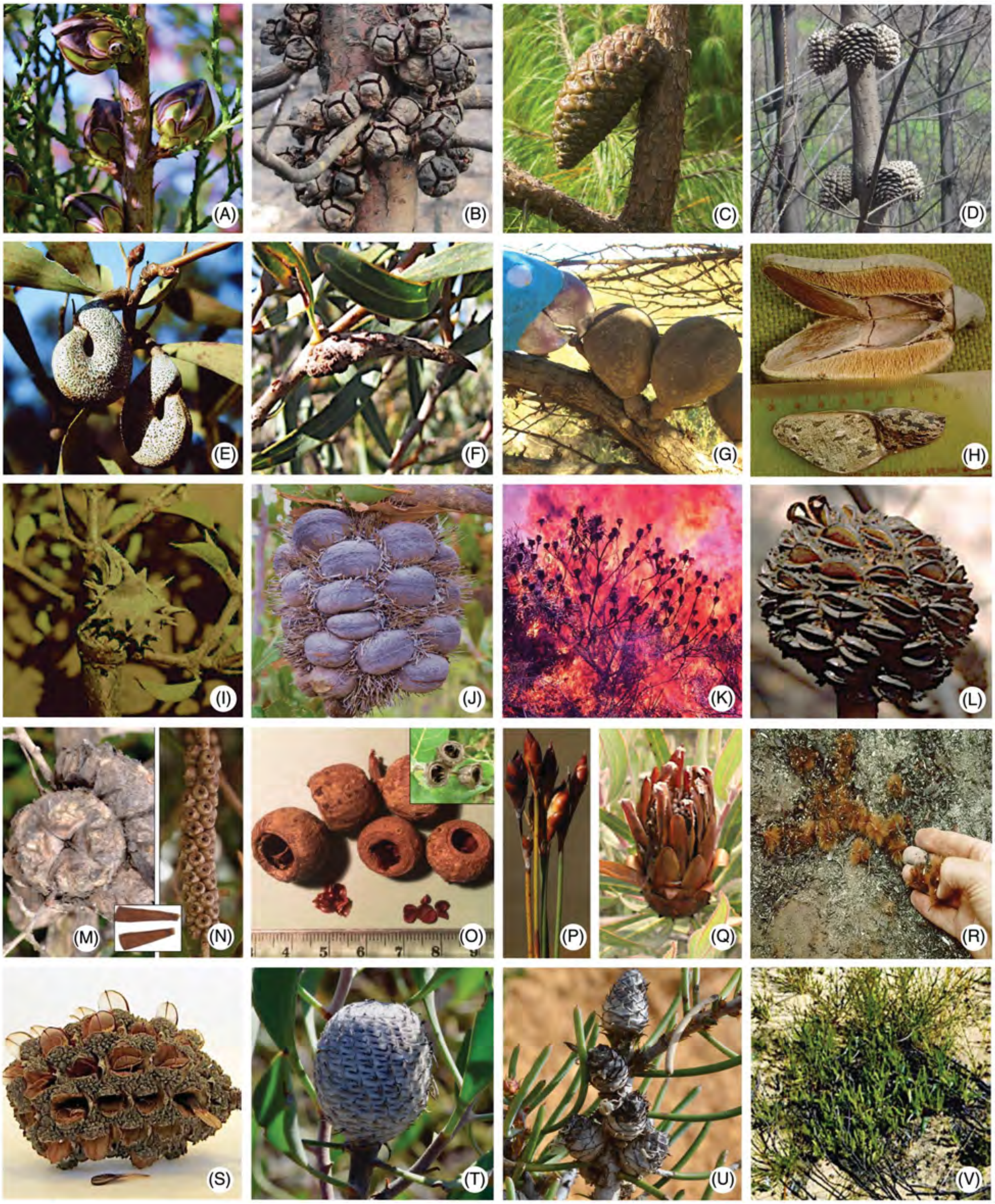

Figure 1. Selection of serotinous structures and their association with postfire seed release and seedling establishment. (from left to right, top to bottom). (A) Pyramidal cones (strobili) of *Callitris* (*Actinostrobus*) *pyramidalis* (Cupressaceae) (15 mm long); (B) Postfire globular cones of *Cupressus sempervirens* (Cupressaceae) (30 mm diameter) in Spain with scale complexes beginning to separate in order to release seeds; (C) Ovoid cone of *Pinus patula* (13 cm long) in Mexico, note fibrous bark and retention of foliage that would enhance flammability around the cone; (D) Postfire ovoid cones of *P. radiata* (10 cm long) from California, with reflexed scales that have allowed the release of their seeds, note how the annual clustering of cones enables their age to be determined; (E) Two follicles, 40 mm long, of *Hakea cyclocarpa* (Proteaceae), whose recurvature prevents the ovipositor of insect granivores from penetrating the thinnest part of the fruit; (F) *Hakea stenocarpa* follicle (35 mm long) mimicking branchlet (warts and all!); (G) three follicles of *Hakea platysperma* (65 mm long), the largest fruits of all 170 *Hakea* species, whose size and globular shape resist penetration by the main granivore of hakeas, the black cockatoo (reconstructed head on left);

Figure 1. (*Continued*)
(H) *Xylomelum angustifolium* (Proteaceae) follicle, the heaviest among all species with woody fruits, with one of its two seeds showing mottling that might serve a cryptic function postfire; (I) *Lambertia echinata* (Proteaceae) follicle (15 mm wide) with sharp spines not unlike surrounding foliage; (J) Globular cone of *Banksia lemanniana* (Proteaceae) with 12 follicles (35 mm wide) visible among persistent dead florets and leaves that enhance flammability; (K) *Banksia hookeriana* (2 m tall) burning, showing scores of floret-covered cones alight but which survive the heat; (L) Postfire *Banksia leptophylla* cone (85 mm diameter) showing split separator pulling two winged seeds out of a ruptured follicle; M) Cluster of corky, cup-shaped capsules (20 mm wide) of *Leptospermum spinescens* (Myrtaceae), Inset: two seeds of *Callistemon* (*Melaleuca*) *teretifolius* (1 mm long) [South Australian Seed Conservation Center]; (N) Elongated, spiral-arranged cluster of sessile capsules of *Callistemon citrinus* (Myrtaceae) (80 mm long) in NSW, Victoria [Fir0002/Flagstaffotos, GFDL v1.2]; (O) Five woody capsules of *Eucalyptus todtiana* (Myrtaceae) that have released their contents on drying out postfire, three fertile seeds on the left and six aborted seeds on the right, Inset: capsules of *Angophora hispida* (Myrtaceae), 8 mm wide, already released their seeds even though subtended by current season's leaves (nonserotinous), in NSW [http://www.friendsoflanecovenationalpark.org.au/Angophora_hispida.htm]; (P) 5 spikes of *Connomois parviflora* (Restionaceae) (12 mm long) each bearing one nutlet in W Cape, [Tony Rebelo, https://www.inaturalist.org/photos/15419835]; (Q) *Protea burchellii* (Proteaceae) in W Cape with loose cone of dry bracts and florets (100 mm long) that burn off when ignited [Elana Mostert, iSpot]; (R) fruits of *Protea burchellii*, with tufts of brown hairs (15 mm diameter), released onto an ashbed after fire; (S) Cone of *Allocasuarina torulosus* (Casuarinaceae) (30 mm long) with scores of samaras emerging from pairs of woody valves when left to dry out on a bench [Ian T. Riley, with permission]; (T) Globular-ovoid cone of *Isopogon trilobus* (Proteaceae) (35 mm long) with 150 tightly bound scales (bracteoles) with only a few bearing flattened, fertile nuts; (U) Loosely clustered, ovoid cones of *Petrophile brevifolia* (Proceaceae) (20 mm long), sparsely scaled and bearing few nuts; (V) Seedlings (5-12 cm tall) from serotinous *Hakea polyanthema*, *Banksia attenuata* and *Banksia hookeriana* in litter microsite (see Lamont *et al.*, 1993). Plants native to SW Australia unless otherwise indicated. (E–I, L, N, O) photographed by B. Lamont; (B–D) by J. Pausas; (A, J, M, T, and U) by T. He.

two reproductive syndromes that consist of (a) accumulation of an aerial seed bank (vs release at maturity), (b) release of seeds in response to fire heat (vs release in the absence of fire), and (c) germination and recruitment of seedlings *en masse* postfire (vs continuous recruitment in the absence of fire) (Figure 3). Analysis of one component without reference to the other two will underplay the ecological significance of serotiny. Thus, prolonged storage traits are promoted in an ultimate sense because (a) annual seed production is inadequate for self-replacement should a fire occur in that year, (b) optimal recruitment conditions only exist immediately post-release as a result of fire, and (c) seeds released interfire are no longer available to contribute to the next generation (Lamont *et al.*, 1991; Enright *et al.*, 1998a; 1998b). On-plant storage also gives extra time for seed mass and nutrient content to build up, of particular value for seedling recruitment in nutrient-impoverished, seasonally dry soils where the incidence of serotiny reaches its peak abundance (Lamont and Groom, 2013) and so is related to point (a) above. This solution to the need for nutrient-enriched seeds would still not favor serotiny were it not tied to fire-stimulated seed release under superior conditions for recruitment afforded by the postfire habitat.

We now discuss 23 traits identified from the literature and associated with these three components that are under genetic control and environmental selection, as tempered by phylogenetic constraints (Table 1). Several processes are related directly to storage: the propensity to produce enclosure sealants, a vascular system that prevents premature drying out of the storage tissues, and seed viability that matches the length of storage. Equally, for nonstorage, an efficient abscission mechanism is required that may involve rapid occlusion of the xylem once maturity is reached (Moya *et al.*, 2008). Effective serotiny entails (a) protection of seeds from the 'elements' over some years in the absence of fire and (b) corresponding longevity of the protected seeds. However, the supporting structures invariably stay closed for longer than their seeds remain viable. Thus, 85% of 10 to 12-year-old follicles and seeds of *Banksia cuneata* remain intact, but seed viability is <35% compared with 85% for 1-year-old cones (Lamont *et al.*, 1991). Death of embryos can be due to postzygotic-acting deleterious alleles, consumption by insect larvae, granivorous birds or rodents, the action of pathogenic fungi or bacteria, desiccation, waterlogging or gradual senescence. Some pine cones have tough, spiny apophyses apparently directed at squirrels or corvids (Elliott, 1974; Benkman *et al.*, 2003; Siepielski and Benkman, 2004); some banksias have a dense mantle of persistent florets that not only increase flammability and ensure seed release (Enright and Lamont, 2006), but also serve to conceal the fruits from granivores; some hakeas have elaborate woody rims over the thinnest, weakest part of the fruit (suture line) deterring granivores, especially cockatoos and ovipositing insects, from reaching the seeds (Midgley *et al.*, 1991; Groom and Lamont, 2015; Figure 3). All these protective mechanisms will have different genetic bases that vary greatly between different plant taxa.

As seed release is essentially a desiccation phenomenon, any drying out of the seed-supporting structures

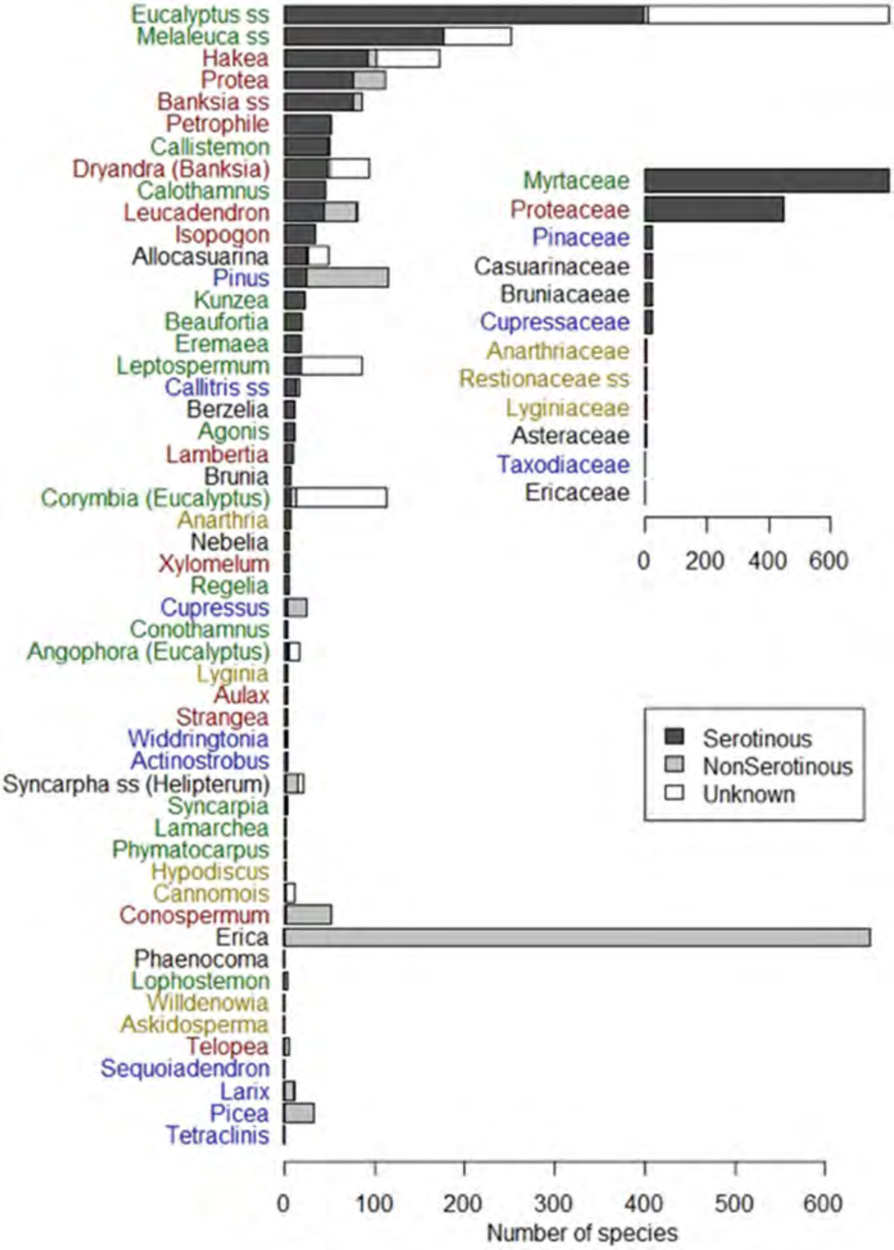

Figure 2. Taxonomic distribution of serotiny (dark gray), and nonserotiny (light gray) in clades that include serotinous species, plus numbers of species yet to be examined in the clade (white). The large graph is at genus level and the inset is at family level. Conifers are given in blue, monocots in gold, and the rest are dicots: Myrtaceae is given in green, Proteaceae in red, and the smaller groups in black. See Table S1 for details on their geography, morphology, habitats and supporting references.

can lead to seed release (dos Santos *et al.*, 2015), given the general term desiscence – release in response to desiccation (Lamont 1991). Only fire heat causes *en masse* cone/fruit opening and seed release, known as pyriscence. Interfire dehiscence can be the result of plant death or local necrosis of the supporting branches or even of individual fruits or cones (necriscence), usually through failure of the vascular system to maintain water supply to the maternal tissues (Cramer and Midgley, 2009). Direct insolation (soliscence), hot weather and dry winds (xeriscence – Nathan *et al.*, 1999) can also lead to the weakening of the binding resins and desiccation, while these effects can occur simply with the passage of time. Weakly serotinous structures are more likely to open at ambient temperatures and milder fire heat than strongly serotinous structures (Enright and Lamont, 2006; Huss *et al.*, 2018) so that they are more likely to release their seeds between fires.

That serotiny is usually terminated by fire heat has implications for the selection of a number of traits (Table 1). Of paramount importance is the insulation

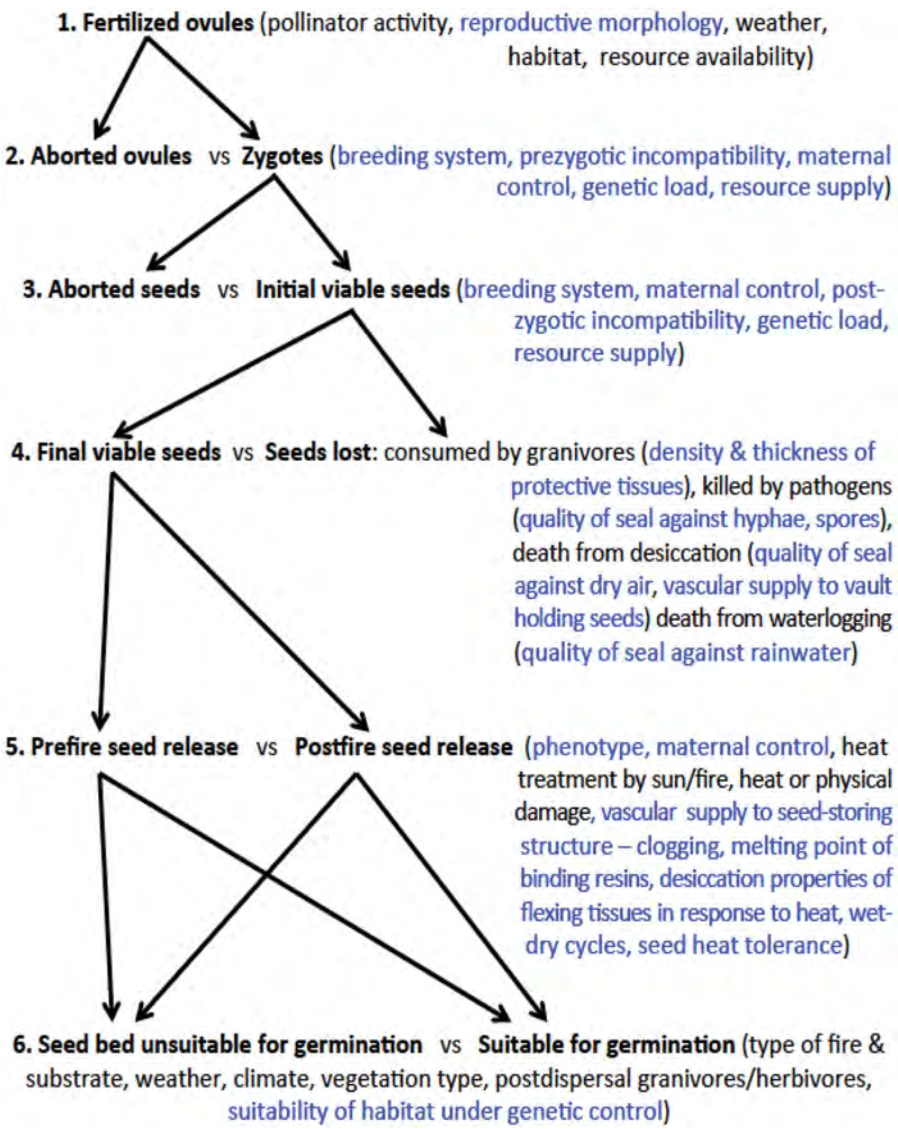

Figure 3. Sequence of events involved in the success or otherwise of on-plant seed storage and release with the options at each step highlighted in bold. The constraints at each step are given in parentheses and those subject to genetic control are highlighted in blue. Support obtained from Ledig and Little (1979), Lamont, Rees, *et al.* (1994), Lamont, Whitten, *et al.* (1994), Groom and Lamont (1997), Lamont and Enright (2000), Lamont and Wiens (2003), Cramer and Midgley (2009), Parchman *et al.* (2012), Hernández-Serrano *et al.* (2013), Talluto and Benkman (2013), Budde *et al.* (2014), Causley *et al.* (2016), Huss *et al.* (2018; 2019), Tangney *et al.* (2019).

of seeds from fire heat that requires the genetic propensity to synthesize nonflammable, woody/corky tissues. As it turns out, many species are 'over adapted' for fire resistance as protection from granivores requires even thicker and denser tissues. Further, seeds of many species have high heat tolerances (up to 170 °C for 2 min, Lovreglio *et al.*, 2007; Tangney *et al.*, 2019), equivalent to those of soil-stored, 'hard' seeds, whereas the germination of some others is optimized by temperature pretreatments not expected in the absence of fire (60-80 °C, Hanley and Lamont, 2000), showing that fire has acted as a selective agent even at the prerelease stage. Nevertheless, old, partly open cones (Lamont and Barker, 1988) or dry cones/fruits on dead plants (Lamont and Groom, 1998) are more likely to be incinerated even where viable seeds remain stored on dead branches or plants. Thus, some traits are directed at storage as an end in itself unrelated to the inevitability of fire events, some protect against heat as well as granivores (multifunctional), while others control the heat-induced, seed-release mechanism. All of these should be controlled by different parts of the genome.

The cueing of seed release by fire involves a complex mechanism, which must be controlled by numerous genes and alleles, that may include (a) the

Table 1. Traits within the serotiny syndrome (seed storage, pyriscence, postfire recruitment) or nonserotiny syndrome (seed release at maturity, interfire recruitment) and how these are affected by environmental and phylogenetic constraints, and whether the effect of the trait on each of the three components is positive or negative, direct or indirect, with generic examples and supporting references.

Component (alternatives)	Trait subject to selection	Environmental constraint	Phylogenetic constraint	Effect on component	Generic examples	References
1. On-plant seed storage vs non-storage	Seed/fruit completely enclosed within a sealed supporting structure but has zone of weakness for enabling dehiscence	Growing conditions sufficient to ensure complete development of seed storage complex	Ability of surrounding structures to support and wrap around seed/fruit yet be dehiscent; propensity to produce enclosure sealants (resins) vs physical resistance limits of potentially flexing tissues	Direct	*Banksia*	Enright and Lamont, 2006; Huss *et al.*, 2018; 2019
	Cone/fruit maintained in closed condition	Water and nutrient availability – rainfall, seasonal drought	Ability of vascular system to resist clogging, embolism	Direct	*Aulax*, *Hakea*, *Leucadendron*	Cramer and Midgley, 2009
	Decline in seed longevity matches rate of cone/ fruit opening	Invasion by pathogens, granivores, rainwater, dry air	Propensity of enclosure to remain closed over time, inherent seed dormancy limits	Direct	*Eucalyptus*, *Melaleuca*, *Banksia*	Pannell and Myerscough, 1993; Lamont and Enright, 2000; Crawford *et al.*, 2011; Figure 1
	Insulation of seeds from heat (unrelated to fire)/cold – even if nonserotinous	Exposure to sunlight, hot/cold air currents, snow	Metabolic and anatomical properties of supporting structure	Indirect (insulation from the 'elements')	*Pinus*, *Banksia*, *Hakea*	Personal observations of fruits opening on sunny side of plant; see Table 3
	Fruit thick, woody, corky	Granivore pressure (ovipositing insects; parrots – cockatoos)	Metabolic and morphological properties of leaves (to supply carbohydrates) and supporting enclosure	Indirect (granivory)	*Hakea*	Groom and Lamont, 1997; Lamont, Hanley *et al.*, 2016
	Cone scale complex thick, woody, spiny	Granivore pressure (crossbill corvids, squirrels)	Metabolic and morphological properties of leaves and supporting enclosure, propensity to develop spines	Indirect (granivory)	*Pinus*	Elliott, 1974; Moya *et al.*, 2008
	Enclosure sealed off from atmosphere, water repellent	Exposure to water held in crevices, pathogens, dry air, air pollutants	Metabolic and anatomical properties of supporting enclosure	Indirect (waterlogging, pathogenesis, desiccation, pollutants)	*Banksia*	Lamont *et al.*, 1991; Moya *et al.*, 2008
	Accumulation by seed of nutrients vital for seedling recruitment in impoverished soils	Soil nutrient availability	Metabolic and vascular limits to supply nutrients to embryo over an extended period	Indirect*	*Hakea*	Lamont and Groom, 2013
	Propensity of cone to open at maturity (nonserotinous)	(Sub)tropical grassland/savanna, frequent fire, summer rainfall	Efficiency of dehiscence mechanism	Indirect (flame not reach crown)	*Banksia* (*dentata*), *Protea*, *Pinus*, *Larix*, *Hakea*	See Tables 4 and 5, and Figure 6
	Propensity of cone to open at maturity	Habitat non-fireprone	Efficiency of dehiscence mechanism	Direct	*Banksia*, *Protea*, *Pinus*, *Hakea*	See Tables 4 and 5
2. Pyriscence vs seed release at maturity	Fire-sourced heat able to stimulate operation of seed release mechanism directly or via death of supporting stem and thus supporting structure	Flammability of surrounding foliage and litter (fire of sufficient intensity)	Location of crown in relation to heat source (inherent plant growth rate), for example, tree crown may escape heat from grass fires but prostrate plants will be burnt	Direct	*Banksia*, *Pinus*, *Eucalyptus*	Cowling and Lamont, 1985b; Enright and Lamont, 2006; Habrouk *et al.*, 1999; Lamont and Enright, 2000; dos Santos *et al.*, 2015
	Insulation of seed from fire heat	Intensity of fires	Insulation and non-flammability properties of supporting tissues	Direct	*Pinus*, *Banksia*, leptospermoid Myrtaceae	Judd, 1994; Habrouk *et al.*, 1999; Lovreglio *et al.*, 2007; Moya *et al.*, 2008; Salvatore

(*Continued*)

Table 1. Continued.

Component (alternatives)	Trait subject to selection	Environmental constraint	Phylogenetic constraint	Effect on component	Generic examples	References
						et al; 2010; Lamont, Whitten, *et al.*, 1994
	Tolerance of seed to fire heat	Intensity of fires	Heat-tolerant limits of dormant seed	Direct	*Calothamnus*, *Banksia*, *Hakea*, *Pinus*, *Dryandra*, *Allocasuarina*, *Eucalyptus*, *Melaleuca*	Habrouk *et al.*, 1999; Hanley and Lamont, 2000; Goubitz *et al.*, 2003; Lovreglio *et al.*, 2007; Tangney *et al.*, 2019
	High melting point of binding resins (opening mechanism)	Intensity of fires	Propensity for terpenoid synthesis	Direct	*Banksia*, *Pinus*	Enright and Lamont, 2006; Tapias *et al.*, 2001
	Fruit/scale/bract reflexation (opening mechanism)	Intensity of fires	Tissue arrangement, secondary metabolism and anatomy relative to flexing requirements	Direct	*Banksia*, *Pinus*	Moya *et al.*, 2008; Huss *et al.*, 2018; 2019
	Central plate pulls seeds out of enclosure (seed release mechanism)	Intensity of fires	Propensity to produce a central plate (decipium) that can grasp seeds and reflex to pull seed out of fruit	Direct	*Banksia*, *Dryandra*	Cowling and Lamont, 1985b
	Wet-dry cycles required to ease seeds out of the supporting structure	Intensity of fires (redundant if flame temperature is high enough), postfire weather	Tissue arrangement, secondary metabolism and anatomy relative to flexing requirements	Direct	*Banksia*, *Dryandra*	Cowling and Lamont, 1985b; Lamont and Barker, 1988; Lamont and Enright, 2000
	Mantle of dead florets (high flammability)	Flame source	Ability to retard abscission layer development at base of florets	Direct	*Banksia*	Lamont and Cowling, 1984
	Dead leaf retention (high flammability)	Flame source	Ability to retard abscission layer development at base of leaves	Direct	*Banksia*	He, Lamont and Downes, 2011
	Dead branch retention (transports flames to crown)	Flame source	Ability to retain dead branches that serve to propagate flames	Direct	*Pinus*	Schwilk and Ackerly, 2001; He *et al.*, 2012
	Heat not required to stimulate seed release mechanism (occurs at maturity or in response to other cues or gradual desiccation)	Interfire release (absence of fire)	Efficiency of dehiscence mechanism on reaching maturity	Direct	Species in otherwise serotinous genera can be nonserotinous	Lamont *et al.*, 2019b
	Predispersal granivore avoidance	Interfire release (absence of fire)	Efficiency of dehiscence mechanism on reaching maturity	Direct	*Pinus*	Talluto and Benkman, 2013
3. Recruitment – postfire vs interfire	Heat-stimulated (predispersal) germination	Postfire release (fire occurrence)	Physiological limits of seeds to high-temperature tolerance	Direct	*Pinus*, *Allocasuarina*	Habrouk *et al.* 1999; Hanley and Lamont, 2000; Lovreglio *et al.*, 2007
	Postdispersal seed ash/charcoal/burial tolerance	Postfire release (fire occurrence)	Physiological/morphological limits of seeds re alkali/burial tolerance	Direct (minor)	*Banksia*, *Hakea*, *Pinus*, *Petrophile*	Lamont *et al.*, 1993; Goubitz *et al.*, 2003
	Postdispersal seed tolerance of alkaline soil	Interfire release (absence of fire)	Physiological limits of seeds re alkali tolerance	Inverse (minor)	*Pinus*	Goubitz *et al.*, 2003
	Postdispersal seed high-temperature tolerance	Postfire release (fire occurrence)	Physiological limits of seeds re high temperature tolerance	Inverse (minor)	*Pinus*	Moya *et al.*, 2008
	Postdispersal seed high-temperature tolerance	Interfire release (absence of fire)	Physiological limits of seeds re high temperature tolerance	Direct (minor)	*Pinus*	Moya *et al.*, 2008
	Smoke-stimulated germination	Fire occurrence	If released interfire, ability to survive soil storage and fire	Direct (minor)	*Leucadendron*	Brown and Botha, 2004

		(smoke) required for germination			
Full-sun-tolerant seedlings	Postfire release (fire occurrence)	Drought/full-sun/heat tolerance of seedlings	Inverse	*Banksia*, *Hakea*, *Dryandra*	Causley *et al.*, 2016
Drought/shade-tolerant seedlings	Interfire release (absence of fire)	Drought/shade tolerance of seedlings, for example, via large seeds	Direct	*Banksia*, *Dryandra*, *Hakea*, *Pinus*	Hanley and Lamont, 2001
Postdispersal granivory minimization by synchronized seed release[#], mimicry	Postfire release (fire occurrence)	Limit to number and size of seeds that can be produced to satiate granivores	Direct	*Banksia*, *Pinus*	Lamont *et al.*, 1991; Saracino *et al.*, 1997
Postdispersal herbivory minimization by synchronized seedling emergence[#]	Postfire release (fire occurrence)	Limit to number and size of seedlings that can be produced to satiate herbivores	Direct	*Banksia*	Lamont *et al.*, 1993
Strong heterospecific-competition tolerance	Postfire release (fire occurrence)	Limit to number and size of seedlings that can be produced	Direct	*Banksia*, *Hakea*, *Petrophile*	Lamont *et al.*, 1993
Strong conspecific-competition tolerance	Interfire release (absence of fire)	Limit to number and size of seedlings that can be produced	Direct	*Banksia*, *Dryandra*, *Hakea*	Hanley and Lamont, 2001

*Needs strong root system for recruitment. [#]Trait may be ineffective as burnt sites with abundant seeds and seedlings also attract granivores and herbivores.

presence and melting of binding resins at the suture line, then (b) the presence of specialized tissues that cause reflexing of the enclosures as they desiccate, sometimes aided by wet-dry cycles. The mechanism is particularly elaborate among banksias and dryandras where a winged central plate gradually pulls the two seeds out of the follicle – it seems that this 'separator' also serves to deter granivorous birds, which descend on the cones as soon as the fire passes, from accessing the seeds (Cowling and Lamont, 1987). If this is the result of selection then its current morphology might be relatively recent as cockatoos only arose ~20 million years ago (Ma) whereas this clade emerged >60 Ma (He *et al.*, 2011). At about the same time, other traits arose that enhance the flammability of the region around the cones/fruits and ensure the critical temperature for resin melting is reached – retention of dead florets, leaves, and twigs. Serotiny in pines is tied to the retention of dead branches that enable propagation of flames from the ground to the crown (the 'ladder' effect) where the closed cones are located (Schwilk and Ackerly, 2001; Pausas, 2015a).

Where nonserotiny is beneficial, all that is required in the absence of fire is an efficient dehiscence mechanism of the cones/fruits that is cued once they reach maturity. Note that nonserotiny does not necessarily imply the absence of fire adaptations. For example, it is coupled with thick bark (trees, Pausas, 2015b) and/or resprouting (shrubs – subshrub geoxyles) among plants in low vegetation where fires are very frequent (savannas) (Lamont, He, *et al.*, 2017).

Selection will also occur at the seedling phase: germination will be promoted and young plants of nonserotinous taxa should thrive interfire, whereas serotinous taxa should thrive postfire (Table 1, Figure 3). Selected traits linked to serotiny include heat-stimulated germination, tolerance of high pH (ash), charates, and soil/litter burial (as a result of postfire shifting of seeds and debris by wind and rain), high light and intra/inter-specific-competition tolerance (Table 1). Weakly or nonserotinous taxa display the reverse traits. Rarely, the germination of seeds of some species is promoted by smoke (Brown and Botha, 2004) that coincides with the postfire environment, though it is usually confined to soil-stored seeds. The abundance of postfire litter microsites packed with seeds and seedlings is a two-edged sword: they both attract and satiate granivores and herbivores so that the effect on net recruitment needs to be considered. Nevertheless, recruitment in the burnt sites always exceeds that in the unburnt (Cowling and Lamont, 1987; Hanley and Lamont, 2000; Causley *et al.*, 2016). Many serotinous seeds are black, brown, mottled, or pale that implies a mimicry function against the postfire ash or charcoal-filled litter beds (Figure 1H). Postfire released seeds can merge with the soil surface background to potentially deter vertebrate granivores from consuming the seeds (Saracino *et al.*, 2004; Lev-Yadun and Ne'eman, 2013; Midgley, in press). To what extent these colors and patterns differ from nonserotinous seeds in the same taxon (Lev-Yadun and Ne'eman, 2013) or in different taxa, or are more effective at reducing granivory, awaits detailed study.

IV. Genetic control of serotiny

There is much interest in the genetic versus environmental control of serotiny with the evidence so far varying from strongly to negligibly heritable (Parchman *et al.*, 2012; Budde *et al.*, 2014; Vincenzi and Piotti, 2014; Castellanos *et al.*, 2015; Feduck *et al.*, 2015). Part of the explanation for such variable results is that in most of these studies serotiny is gauged as the fraction of cones that is closed, which clearly has an age/size/growing-condition component. Thus, younger/faster-growing plants will have a greater percentage of young (closed) cones and register a higher level of serotiny unrelated to any genetic basis. Equally, old plants may predominantly possess open fruits/cones and thus their serotiny level is underestimated. This problem is overcome by using the slope measure of serotiny that is unaffected by annual crop size and ignores years once cones/fruits are fully open (Cowling and Lamont, 1985a, Lamont, 2020) – this distinguishes the 'apparent' level of serotiny (the fraction of cones/fruits that is closed at a given point in time) from the 'inherent' level of serotiny (the rate at which cones/fruits open over some years).

Common-garden trials are an alternative approach with much to commend them as they dispense with differential environmental effects (multiple garden locations provide even more information on the expression of the trait). Harris (2002) assessed the current crop of capsules in 2.5-year-old shrubs of *Leptospermum scoparium* (Myrtaceae), grown in an experimental garden at Canterbury, New Zealand, which had split to release their seeds. Populations differed by ten-fold in the level of splitting, confirming that serotiny has a strong genetic basis and implying rapid adaptive intraspecific responses to different fire regimes. Heritability could not be determined as within-population variability was not assessed. Ideally, the assessment would be applied over a number of years in such trials to reduce seasonal variability effects.

An elegant study by Hernández-Serrano *et al.*, (2014) reported a 17-fold difference in closed to total cones for 29 provenances of *Pinus halepensis*. This variation could be equated with the level of summer drought as a surrogate for fire intensity (likelihood of fire reaching crowns of the trees). Care was taken to omit the youngest cones as these are immature while the trees were at an active stage of growth having produced cones for 10-14 years. Since cones can remain closed for 15 y the problem of fully open crops was avoided. Heritability (h^2) was moderate at 0.20. Since total or annual cone production was not used as covariates, the possibility that differences among these attributes accounted for some of the variation in serotiny remains. Using single nucleotide polymorphisms (SNP) markers for estimating relatedness among individuals in wild populations of this species, Castellanos *et al.*, (2015) obtained a lower h^2 of 0.10, which confirms that this measure of serotiny responds to both environmental and genetic effects.

Further support for the strong genetic basis of serotiny has come from genome-wide association studies for the variably serotinous shrub/tree, *Banksia attenuata*. Among the 382,287 genome-wide single nucleotide polymorphisms (SNPs) obtained, 220 were associated with the level of serotiny at $p < 0.010$ (Figure S1), possibly representing 20–30 genes (Nock *et al.* 2016). It is not clear what genes are involved in controlling serotiny in *B. attenuata*, as the *Banksia* reference genome has not yet been annotated. The detection of such a large number of SNPs associated with serotiny indicates that on-plant seed storage is genetically controlled, and therefore strongly heritable in this species.

Individual trees of some *Pinus* species may be serotinous or nonserotinous (Teich, 1970, Givnish, 1981; Talluto and Benkman, 2013) indicating that this trait may be under simple Mendelian control. However, for the great majority of serotinous species, including most pines, serotiny is a question of degree, depending on the thickness and density of the protective tissues, the constitution of the binding resins, and the like (Figure 3, Table 1). This implies that many genes control the different traits described above and there are many alleles for the same trait (Budde *et al.*, 2014; Parchman *et al.*, 2012; Hernández-Serrano *et al.*, 2014). The effects will be additive or synergistic, including heterosis and epistasis. As alleles controlling serotiny/pyriscence (seed store and the fire cue for seed release respectively) accumulate, so serotiny will

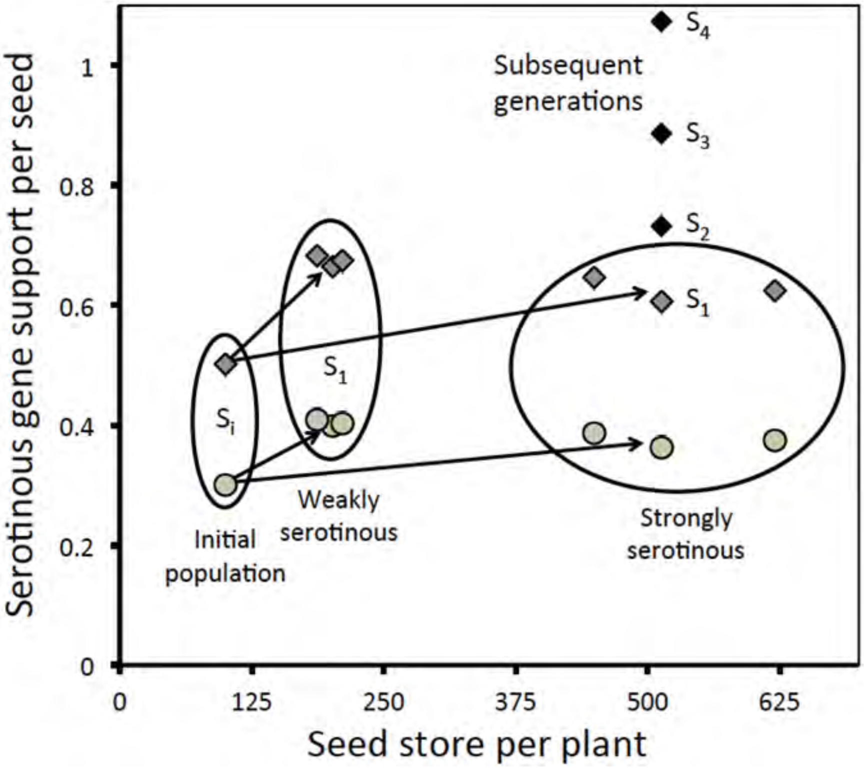

Figure 4. Model outcomes for the impact of initial level of serotiny and increasing gene support for serotiny per seed (S) at two initial levels [$S_i = 0.3$ (circles), 0.5 (diamonds)] on seed storage and gene support for the next postfire generation. The hypothetical plant produces 100 seeds in the initial season and may store seeds for up to 4 years (weak serotiny) or 12 years (strong serotiny) with seeds released at a steady rate from zero at year 1 (the slope measure of serotiny, Cowling and Lamont, 1985b). Three scenarios are modeled: decreasing (left hand values circled), increasing (right hand) or constant (middle) annual seed production over the ensuing 10 years. The arrows show how both sets of S_1 values (circled) increase when genetically nonserotinous seeds are released by individuals preferentially interfire. Note that S increases in each postfire population that replaces the prefire population (S_1 to S_4) – illustrated here for the strongly serotinous population with increasing seed production up to the current year, but the same trend applies to all scenarios.

strengthen, and seed release is increasingly tied to fire events. A consideration of how these two options become expressed through successive generations now follows using worked examples:

1. *One gene control of serotiny*. If *A* is the new dominant allele for serotiny and the plants are self-compatible then 50% of seeds produced will be phenotypically serotinous. If *aa* (nonserotinous) are the only ones released interfire (Hernández-Serrano *et al.*, 2013; 2014) and these perish as recruitment or maturation are now only possible if seeds germinate postfire, then 75% of seeds produced by the replacement population will be serotinous. Similarly, 88.9% of seeds produced in the next postfire generation will be serotinous ($AA{:}2Aa \times AA{:}2Aa$). By the next generation, it will be 97.5% of seeds. Note that *aa* is never completely lost and can enable the population to recover nonserotiny if interfire recruitment or weak serotiny become favored. While current research indicates that this simple mechanism is unlikely since serotiny/pyriscence involves multiple, coordinated traits, the same principle of progressive dilution of certain alleles via selection can be applied to multigene, quantitative allelic systems.
2. *Multiple gene control of serotiny*. To illustrate likely outcomes when serotiny is favored, we estimated annual seed production, release and viability of retained seeds for a representative tree or shrub over 10 y since it reached maturity based on empirical trends for banksias (Lamont, Rees, *et al.*, 1994; Lamont and Enright, 2000). The level of serotiny is controlled by the type of alleles present at a number of gene loci that we refer to as the ‘gene support for serotiny’, *S*, representing the fraction of the genome devoted to supporting serotiny that is ‘saturated’ at $S = 1$ (Figure 4). Two initial gene supports for serotiny were used,

0.3 and 0.5 (30 and 50% of genes for serotiny are in a homozygous state). Two degrees of serotiny were used, 4.0 (seeds held for up to 4 years) and 12.0 (seeds held for up to 12 years), based on 100/*b* where *b* is the linear slope of fraction of seeds retained or fruits/cones closed per year (Cowling and Lamont, 1985a; Lamont, 2020). Progressive seed store, $H = \sum_1^x$ (seeds produced × fraction of seeds retained × viability) where x is the number of years prior to, but including, the current year, and progressive total gene support, $G = \sum_1^x$ (seeds produced × S × viability). It is assumed that seeds released are genetically nonserotinous (Hernández-Serrano *et al.*, 2013, 2014) so that G gets reallocated to the retained seeds. The exceptions are when the fraction of seeds retained (R) is less than S when the genetic support is reduced to the value of R as some of S would have been lost in the released seeds. Mean S_x per seed = G/H over the nominated time period x. An example of the procedure and outcomes is given in Table S2. The process was repeated for three successive postfire generations burnt bearing a 10-year crop (strongly serotinous) to obtain new estimates of S_x.

Results show that serotinous phenotypes possess 4.5-6.2 times as many seeds as the current season's at the time of fire if retained for up to 10 years and 1.9-2.1 times as many if held for up to 4 years, depending on whether seed production is increasing, decreasing or steady (Figure 4). If the recruitment is a weighted lottery process (Lamont and Witkowski, 1995), then there would be 2.4-2.9 as many strongly serotinous recruits as weakly serotinous. Assuming that the seeds released interfire are genetically nonserotinous (and fail to contribute to the next generation following a fire), then the gene support for serotiny gradually increases in the seeds retained so that S of the stored seeds is greater than the current season's crop (Table S2, Figure 4). S increases per seed by 1.21-1.29 times for the strongly serotinous plants and 1.33-1.36 times for the weakly serotinous plants. The reason that the weakly serotinous have a slightly higher S than the strongly serotinous is because of the greater rate of interfire seed release meaning that the seeds remaining are more likely to be phenotypically serotinous, even though the rate among old seeds may be so high that even some serotinous structures release their seeds. While this mean rate of increase does not appear high, it escalates with each postfire generation so that only four generations are required for S to pass from 0.5 to 1.0 (when in theory the species is completely serotinous at least for that trait). Thus, once a serotinous mutant appears and serotiny is adaptive, then that allele is rapidly incorporated into each successive postfire generation. Here, selection essentially operates at the interfire stage, where already released seeds are 'wasted', not at the postfire stage that ensures the phenotypes present, which are increasingly serotinous, contribute to the new generation as a function of their contribution to the gene support. The reverse arguments hold for environments where serotiny is nonadaptive, such as fire-free habitats and frequently burnt savannas (Lamont *et al.*, 2019b).

V. Fire-induced selection for or against serotiny

Having demonstrated that serotiny and nonserotiny are syndromes of heritable traits, the task now is to show how the selection process works at the gene level. We assume from the outset that the fire return interval (FRI) exceeds the age to reach maturity, and, consequently, both seed set and serotiny are possible (Figure 5A). If it is otherwise (immaturity risk), then the species is nonviable under those conditions (it cannot reproduce) and serotiny becomes irrelevant. Where the typical FRI is shorter than individual longevity, then serotiny is a viable option; if it is the reverse (senescence risk), then interfire recruitment is the only option and serotiny will not evolve. Thus, serotiny is promoted when the fire is at moderate intervals relative to the timing of vital life-history traits of a species (Figure 5B). The meaning of 'moderate' varies with longevity of the component species: nonsprouting shrubs usually complete their life cycle within <50 years and often <15 years, conifers and resprouting eucalypts may survive for >500 years, while clonal species may survive indefinitely (Lamont and Wiens, 2003). Where there are extreme FRI fluctuations about the mean in space or time, this may provide an opportunity for resprouters to establish even though the mean FRI is less than their age to maturity; these species will be nonserotinous. Within this time frame, whether serotiny or nonserotiny is favored depends on (a) whether or not the species can release its seeds in response to fire, (b) whether the ratio of successful postfire to interfire recruits exceeds 1, and (c) whether serotiny is required to build up the numbers of seeds sufficiently to ensure population viability in response to fire.

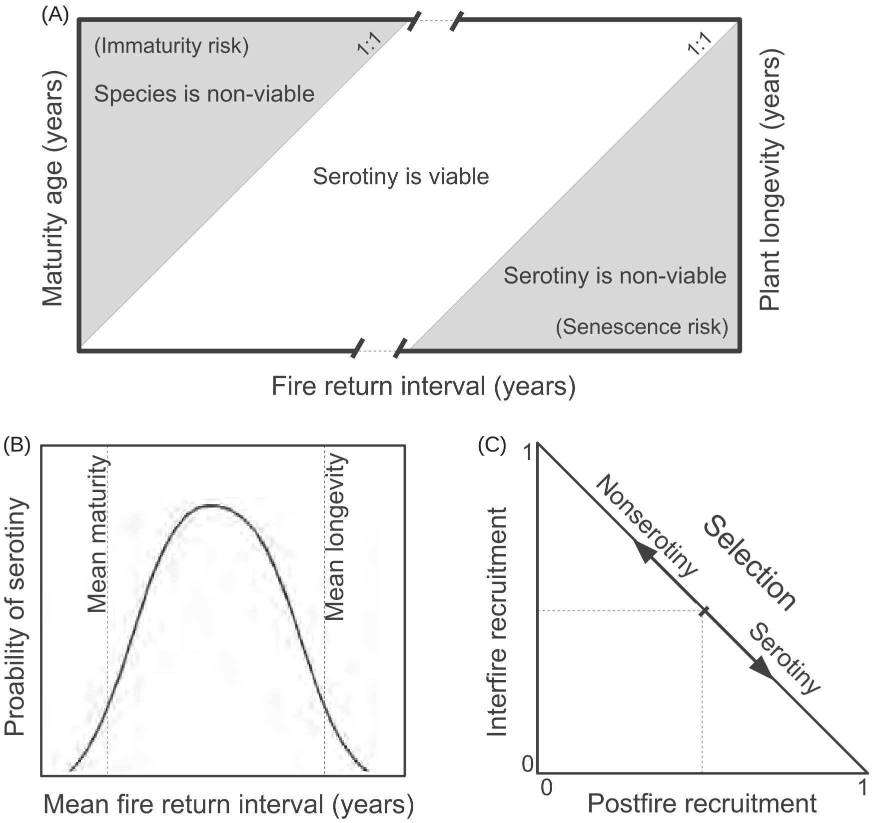

Figure 5. Models of the effects of varying fire return intervals (FRI) and ratio of postfire to interfire recruitment success on serotiny as a viable option. (A) Species and serotiny viability for FRI relative to time to reach plant maturity and plant longevity (model based on Pausas and Keeley, 2014). (B) Selection for serotiny is suppressed as mean FRI approaches or is less than mean age to maturity and approaches or is greater than mean plant longevity. (C) The ratio of successful postfire to interfire seedling recruitment determines whether serotiny or nonserotiny are selected for (expanded in Figure 6).

Three scenarios (sets of conditions and population dynamics) can be identified that promote strong or weak serotiny or the loss/absence of serotiny in the presence of fire (Table 2). These revolve around fire frequency (mean and variability of fire intervals) compared with plant life span and the relative contribution of seeds released interfire vs postfire to the next generation (Figure 5). The selection process begins with the release of the less serotinous seeds interfire. The pattern of interfire seed release can operate at three genetic scales (Box 1): (a) individuals within a population are not uniformly serotinous, with some releasing their seeds early and others late (Givnish, 1981; Gauthier *et al.*, 1996; Hernández-Serrano *et al.*, 2013), (b) the level of serotiny varies between whole cones or fruits within individual plants such that they open at different rates (Goubitz *et al.*, 2003; Lovreglio *et al.*, 2007), and (c) individual seeds are released at different rates within a given cone that collectively opens at a certain rate (Cowling and Lamont, 1985b). Whole-plant differences in levels of serotiny have an obvious genetic basis (Hernández-Serrano *et al.*, 2014) and must represent the dominant source of variation within populations. A genetic basis for within-plant and within-cone differences in the timing of seed release seems much less likely as somatic mutations are rare even among old plants (Lamont and Wiens, 2003; Herrera, 2017).

Maternal control that might involve recognition of differences in offspring genotypes is possible, although this mechanism has received little direct study (Hudson *et al.*, 2015). Epigenetic effects that might be related to position or production sequence aspects are also possible where late seed release might imply a more serotinous genotype via epigenetic inheritance (Lind and Spagopoulou, 2018). Alternatively, the position of the cone within the plant, or fruit within the cone, might affect its vascular supply or exposure to the ‘elements’ and thus its tendency to open (congenital basis). Nevertheless, assuming that the method of estimating serotiny is sound (Lamont, 2020), there are many findings that (a) the postfire population is often more serotinous than the prefire population (Goubitz *et al.*, 2004; Raffaele *et al.*, 2016) and (b) offspring from different populations show very different levels of serotiny (previous section). These imply rapid

Table 2. Three scenarios of varying fire regimes and contrasting interfire/postfire conditions, leading to three contrasting levels of serotiny through differential selection of the serotinous and nonserotinous phenotypes.

Fire-related trait	Interfire events	Postfire events	Long-term outcome
Strong serotiny (moderate fire frequency, poor interfire recruitment conditions)	Minor nonserotinous seed release, little seedling establishment, recruits rare and their fecundity low, massive serotinous seed buildup (nonserotinous phenotypes selected against as they do not contribute to the next generation)	Fire-caused death of at least some parents and interfire recruits, *en masse* release of serotinous seeds and seedling establishment, extensive seedling/juvenile death but many recruits still reach adulthood (fire promotes selection of serotinous phenotypes)	Buildup of increasingly serotinous adults with negligible interfire recruitment (of less serotinous adults), with increasingly even-aged stands (unless resprouts) (serotinous phenotypes much fitter than nonserotinous phenotypes)
Weak serotiny (low/highly variable fire frequency, interfire recruitment conditions almost as good as postfire)	Continuous release of nonserotinous seeds with weak buildup of serotinous seed store, pulses of recruitment, with different age classes contributing most to population size, many recruits reach maturity as vegetation gaps available for colonization and possess seeds at time of fire (serotinous phenotypes selected against as do not recruit interfire)	Fire-caused death of at least some parents and interfire recruits, *en masse* release of both seed types and seedling establishment, extensive seedling/juvenile death but many recruits still reach adulthood, more than interfire (fire promotes selection of both phenotypes)	Buildup of both serotinous and nonserotinous adults with interfire recruits contributing substantially to successive generations with increasingly multi-aged stands (including resprouts) (serotinous phenotypes only marginally fitter than nonserotinous phenotypes)
No serotiny (high fire frequency, interfire recruitment conditions as good as, or better than, postfire)	Nonserotinous seed release, recruits rare but quickly attain resprouting capacity, insufficient time and resources for serotinous seed buildup (serotinous phenotypes selected against as cannot recruit interfire)	Fire survival of parents and older recruits, or survival in non-fireprone pockets, no more seeds released than annually interfire, recruitment no more likely than interfire if say a dry year (fire does not promote selection of either phenotype)	Buildup of nonserotinous, resprouting adults with interfire recruits contributing most to successive generations with increasingly multi-aged stands (nonserotinous phenotypes fitter than serotinous phenotypes)

See Figure 7 for supporting references.

genetic change between generations, even though little is known about the genetic mechanisms.

If recruitment conditions are poor through lack of gaps in the vegetation then these seeds are wasted (Causley *et al.*, 2016). Even if recruits survive they will be depauperate, as they are often beneath adult plants and poor competitors for scarce resources and vulnerable to herbivores, so rarely contribute seeds to the next generation (Hanley and Lamont, 2001; Figure 6). Besides, they will be younger than the parents when a fire does occur so that their seed store is minimal even if they have reached maturity by then. Strongly serotinous seeds are retained on the plant and are thus more likely to survive fire, and contribute more seeds to the next generation under the superior postfire recruitment and growing conditions (Goubitz *et al.*, 2003; Causley *et al.*, 2016). Increased serotiny in the new stand stems from the facts that (a) seeds from less serotinous cones/fruits or individuals are released interfire so are not available to establish in the postfire microsites, and (b) seeds released postfire from the more serotinous cones/fruits or individuals are more likely to yield fecund recruits. Thus, the new cohort will be more serotinous than its parents.

When fires are rare, most seeds in serotinous cones/fruits are retained by their parent plants so that they will not be available to germinate interfire, whereas seeds released from nonserotinous structures will be able to germinate (even if seedling recruitment is low). Selection may be toward such traits as seeds that can penetrate litter, germinate quicker or have greater heat tolerances that facilitate the establishment in vegetation gaps or shade (Susko, and Lovett-Doust, 2000; Hanley and Lamont, 2001; Calvo *et al.*, 2016). These populations will trend toward weak serotiny. Where fires are expected every 1–5 years among fire-tolerant resprouters (Table 2), there is little difference in germination and recruitment conditions between years, and the optimum may even shift from postfire to those years of, say, above-average rainfall, independent of the fire event. Here, serotiny is nonadaptive, and may even be maladaptive if it involves physiological and antigranivory costs (Lamont and Enright, 2000; Cramer and Midgley, 2009; Tonnabel *et al.*, 2012; Talluto and Benkman, 2013). Individuals that only release seeds postfire will be selected against while selection will favor seed release at maturity, rapid germination (no dormancy), and fast growth rates, including the rapid development of belowground, bud-storing structures (Pausas *et al.*, 2018). Thus, with ongoing population turnover, strongly serotinous individuals are replaced by (genetically) nonserotinous individuals. By understanding the fire regime, life-history traits, and relative interfire/postfire

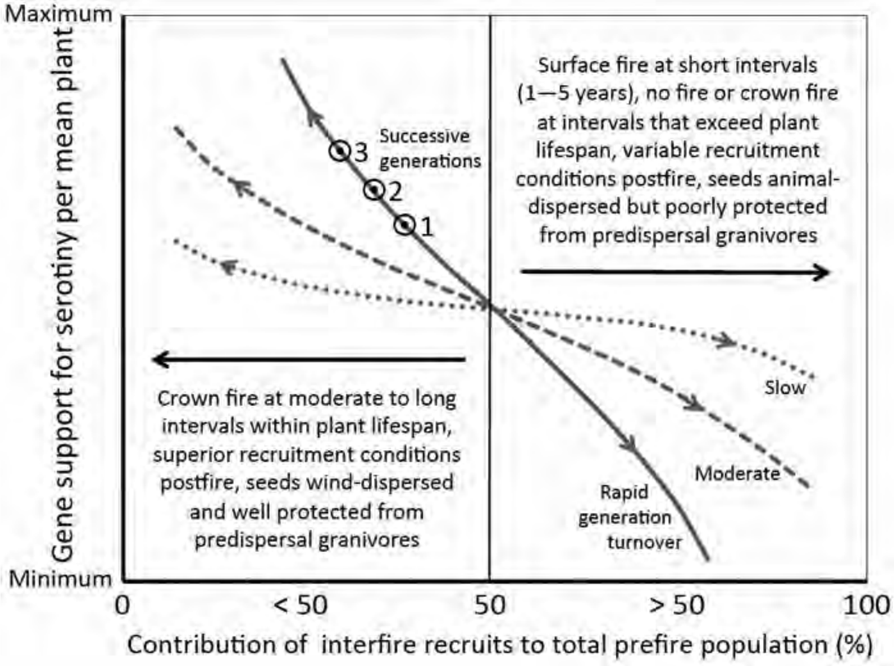

Figure 6. Idealized relationship between gene support for serotiny per mean plant (*S*) and contribution of interfire (inter) recruits to the total, interfire + postfire (post), population at three rates of population turnover (*R*), slow, moderate or rapid. $S = R \times (S_i \pm S_i \times \text{inter/post})$ at time *i*. Prefire conditions are either less (left of the 50% line) or more (right of the line) favorable for recruitment over postfire. Thus, postfire-released seeds carry greater gene support for serotiny than those released prefire. Equally, prefire released seeds carry greater gene support for nonserotiny. With each successive generation, the level of serotiny will accelerate ($+S_i \times$ post/inter ratio) or decelerate ($-S_i \times$ inter/post ratio) depending on the rate of generation turnover until an optimum is reached. Modeled on data in Givnish (1981), Cowling and Lamont (1985a), Lamont *et al.* (1991), Gauthier *et al.* (1996), Enright *et al.* (1998a, 1998b), Lamont and Enright (2000), Goubitz *et al.* (2003), Parchman *et al.* (2012), Talluto and Benkman (2013), Hernández-Serrano *et al.* (2013; 2014), Budde *et al.* (2014), Calvo *et al.* (2016), Battersby *et al.* (2017), Table 2.

recruitment conditions, we can see how fire may select for either serotiny or nonserotiny under different circumstances (Figure 5).

These processes are modeled in Figure 6 in terms of the contribution of interfire recruits to the total population just before the fire (from 0 to 100%). At 50%, there are as many interfire recruits as postfire with no selection for or against serotiny (Figure 5C). The level of serotiny is controlled by the type of alleles present at a number of gene loci (gene support for serotiny) and at this point the support is moderate. Selection for increased serotiny might now be imposed on this population. The key step is changes in the fraction of interfire to total individuals. Essential are the presence of crown fires at low frequency (but within the plant life span), superior recruitment conditions postfire, and the relevant genes and alleles for on-plant seed storage, protection, and fire-cued release (though not yet in a homozygous state). The contribution of interfire recruits then falls and the gene support for serotiny escalates with each successive generation. The rapidity of this change depends on the rate of generation turnover. The converse involves the presence of frequent fires, fire tolerance or avoidance by the incumbent plants, optimal recruitment conditions not necessarily immediately postfire, and the relevant genes and alleles for seed release at maturity. The contribution of interfire recruits then increases and the gene support for serotiny decelerates with each successive generation. Under opposing selection conditions, the traits move in opposite directions as they gradually attain a homozygous condition until a new equilibrium with the selective environment is reached or the gene support is saturated in the absence of further beneficial mutations. Note that the changes in gene support did not need to involve further beneficial mutations (though this would hasten the process) – it is essentially a case of phenotypic selection.

Figure 7 summarizes the sequence of steps and associated selective forces operating at each step over the life cycle of a given species. Note how the traits listed in Table 1 are integrated here to produce an adaptive reproductive syndrome centered on serotiny or nonserotiny. The cycle can be repeated when interfire recruitment is favored and followed by strong interfire seed production and release in the absence of fire that eventually leads to nonserotiny. Alternatively,

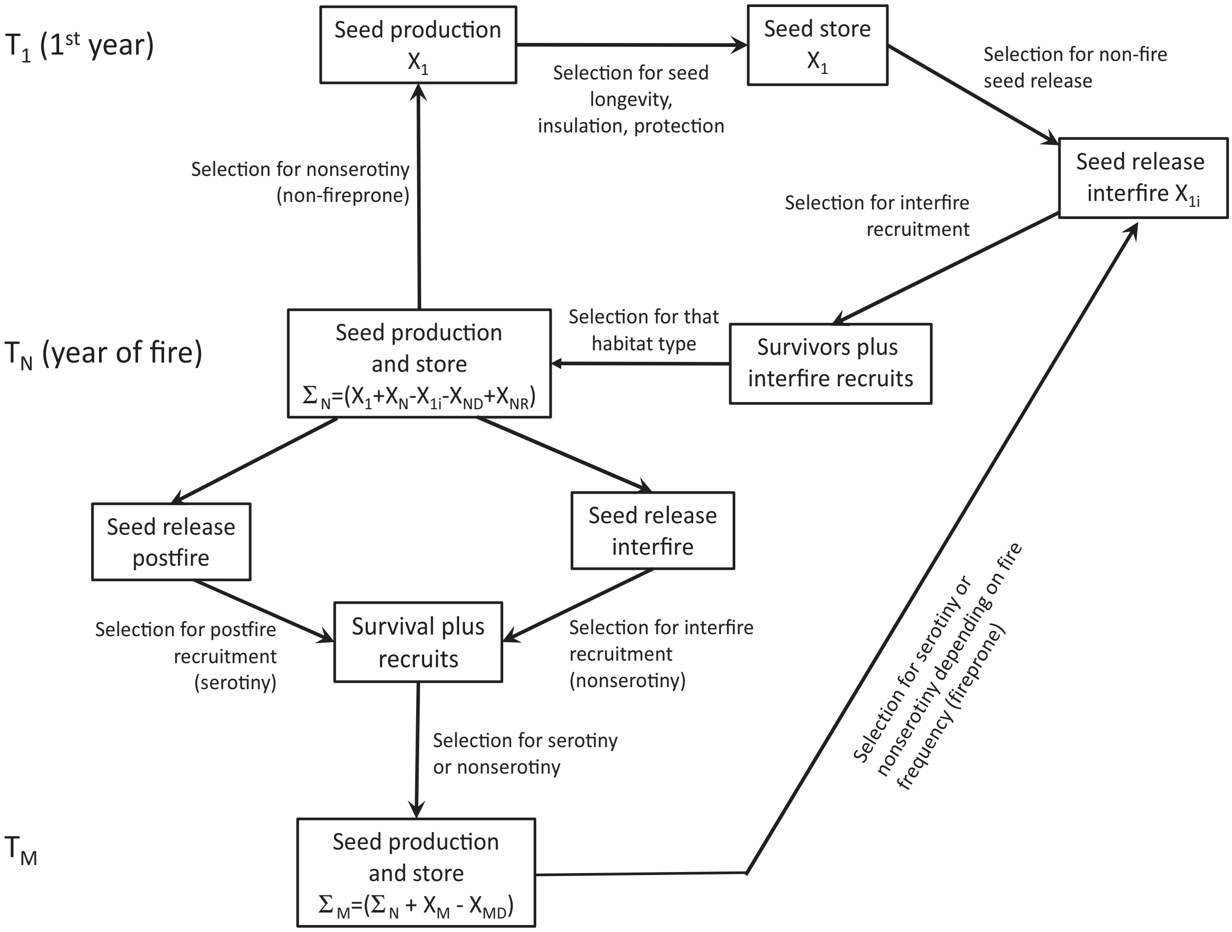

Figure 7. Flow chart of the steps (boxed) and types of selection occurring between these stages (arrowed) involved in accounting for the evolution of particular levels of serotiny, or nonserotiny, at the population scale. The single interfire/fire cycle given here is repeated many times [T_M (year M) back to T_1] until an adaptive equilibrium is reached. X = number of seeds, *i* = interfire, Σ = total seed store, D = nonviable (dead) seeds, R = recruits. The fire occurs in year N – seed release interfire includes seeds released up to the time of the fire. Depending on their relative survival and fecundity in relation to the fire regime, strongly or weakly serotinous or nonserotinous individuals build up in the population. Summarized from Tables 1 and 2, and Figures 3, 5, and 6.

seeds are released both postfire and interfire and depending on the ratio of postfire/interfire success rate of individuals in each phase so the trend is toward strong serotiny (high ratio) or weak serotiny (moderate ratio) or nonserotiny (low ratio). With each cycle, the genetic support for serotiny or nonserotiny and associated traits build up (Figure 7) until an equilibrium is reached for those particular growing conditions and fire regime, where the relevant loci are in a homozygous condition and no further mutants are available for genetic change and fixation. The rate of change depends on the alleles available for fixation and the rate of generation turnover. Thus, Ne'eman *et al.* (2004) argued that, even if fires were rare prior to occupation of the Mediterranean Basin by modern humans 6000 years ago, this was more than sufficient time for *Pinus halepensis*, at 125-year life cycles, to develop the fire adaptive traits, such as moderate serotiny, that it displays today.

The extra protection associated with serotiny indicates that there may be physiological, and thus ultimately fitness, 'costs' that need to be taken into account when assessing the level of serotiny that eventuates from selection by fire (Lamont and Enright, 2000). These involve extra water, carbohydrates, and mineral nutrients but the increased demand has been shown to be minor or nonlimiting (Cramer and Midgley, 2009). More generally, the costs of alternative options, such as soil storage, are unknown, the supporting structures may be multifunctional, for example, woody fruits can photosynthesize when young and they are a source of mineral nutrients for the developing seeds (Groom and Lamont, 2010) so that their net cost is unclear, and the identity of the limiting resource that needs to be measured as a cost is unknown (Lamont, Hanley, *et al.*, 2016). One approach would be to determine experimentally the number of seeds sacrificed to achieve a certain level of serotiny, since increasing seed availability is the ultimate function of serotiny. This has only been undertaken at the simulation modeling level so far (Enright *et al.*, 1998a; Tonnabel *et al.*, 2012). The apparent costs of serotiny pale by comparison with the resources 'wasted' through the failure of seeds released interfire to contribute to the next generation or the gradual attrition of postfire individuals through adverse growing conditions. Thus, it may take up to 200 fire-released seeds to replace a single prefire adult *Banksia hookeriana* at 15 years (Lamont *et al.*, 2001).

VI. Spatial aspects

A. Intraspecific variation in serotiny

We now consider actual examples of the outcome of the selection processes described above, first at the intraspecific scale and then at the interspecific, intracladal (essentially intrageneric) and finally, global, scales. Geographic location effects on intraspecific serotiny are highlighted in Table 3. Here, the stature of two *Banksia* species varies greatly between mesic sites, where most trees are tall and open and often escape ignition from surface fires, and xeric sites, where plants are shrubbier and denser and their crowns are invariably burnt by all fires. Plants at the xeric sites produce and store many more seeds and their degrees of serotiny are 50% greater. This is a genetic (ultimate) response resulting from a long history of selection, consistent with the reduced likelihood of successful interfire recruitment in the drier region and greater chance of fire-caused death of adults. In each region, when growing at the edge of roadways, where water and nutrient availabilities are higher, their size and seed stores are similarly greater than those deep in the undisturbed parts of the reserve. This is a physiological (proximate) response without selection that results in more seeds available for recruitment in both regions. However, serotiny levels (based on 100/*b*) are unaffected by these differences in growing conditions, attesting to the stability of the index and genetic basis of the level of serotiny there. Note that seeds stored as a fraction of seeds produced are greater under the better growing conditions because seed production is increasing at a faster rate such that younger (yet to be released) seeds contribute more to the total crop. Similarly, two species of pine at the mesic and xeric extremes of their climatic range have different levels of serotiny (Table 3). Here, the age of the oldest closed cone is used as the

Table 3. Mean effect of regional location (*S*, mesic vs xeric) and growing conditions (*G*, good vs poor) on plant size, fecundity, nutrient content, level of serotiny and fire-caused mortality among populations of two *Banksia* species in SW Australia and two *Pinus* species in Spain, both with Mediterranean-type climates.

		Mesic sites, low crown fire frequency (surface fire)		Xeric sites, moderate crown fire frequency		Statistical tests		
Species	Attribute or growing conditions	Poor	Good	Poor	Good	Site (S)	Grow (G)	$S \times G$
Banksia menziesii	Length growing season (months)	6.2	>6.2	4.2	>4.2			
	Height (m)	4.2	4.8	2.9	3.6	***	**	NS
	Crown size (m^3)	14.6	35.4	7.8	20.0	**	***	NS
	Shoot N (mg/g)	4.6	8.0	5.1	10.9	NS	*	NS
	Shoot P (mg/g)	0.2	0.5	0.3	0.6	NS	**	NS
	Shoot K (mg/g)	2.6	5.4	3.5	7.6	**	**	NS
	Seeds retained (%)	16.8	38.0	53.8	63.9	***	***	NS
	Seeds stored/plant	6.4	22.7	54.3	202.2	***	***	NS
	Serotiny (100/*b*)	6.6	5.6	9.4	8.3	**	**NS**	NS
	Fire-caused mortality (%)	5.5		21.3		**		
Banksia hookeriana	Height (m)			1.54	2.02		***	
	Crown size (m^3)			2.92	6.83		***	
	Seeds stored/plant			952	3483		***	
	Serotiny (100/*b*)			18.3	19.2		**NS**	
	Fire-caused mortality (%)			100#	100#			
Pinus pinaster (infertile soils), *Pinus halepensis* (fertile soils)	Mean annual temperature (°C)	12.4	13.0	14.7	15.3			
	DBH (cm)	31.5	28.2	25.8	27.5	NS	NS	NS
	Closed cones (%)	11.3	26.5	32.6	45.5	***	***(sp)	*
	Serotiny (max. age closed cones, y)	3.47	3.87	8.27	6.73	***	***(sp)	***
	Fire-caused mortality (%)	?$	?$	100#	100#			

$Surface fires do not reach the crown to cause death. #Observations at numerous sites.

Statistical error terms are given in original papers. Note *Pinus pinaster* (on infertile siliceous substrates) and *Pinus halepensis* (mostly on more fertile calcareous substrates) are placed under poor and good growing conditions [sp(ecies) effect] to assist comparisons. NS: $p > 0.05$; *$p < 0.05$; **$p = 0.05 - 0.01$; ***$p < 0.001$. NS in bold highlights the lack of effect of growing conditions on the level of serotiny in contrast to regional effects. Data for banksias from Cowling and Lamont (1985a), Lamont, Rees, *et al.* (1994), Lamont, Whitten, *et al.* (1994), Groom and Lamont (2011) and for pines from Hernández-Serrano *et al.* (2013), including their Table S2.

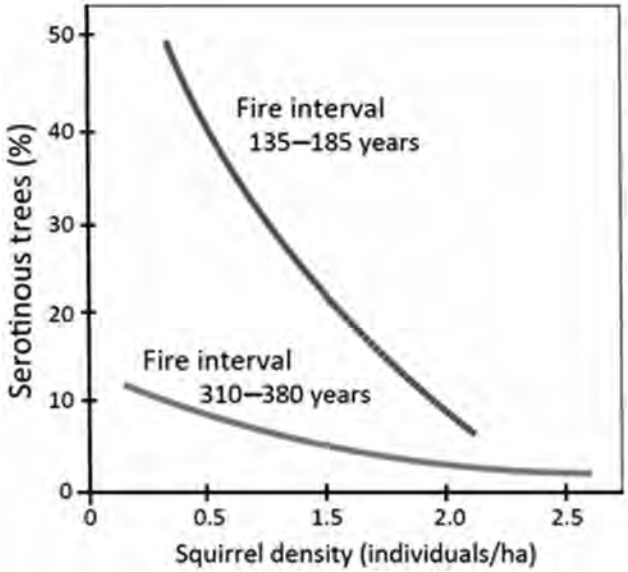

Figure 8. Relationship between squirrel abundance (as an index of seed granivory) and level of serotiny (best fit lines to frequency of serotinous trees) among *Pinus contorta* subsp. *latifolia* stands at two mean fire intervals. Simplified and redrawn from Talluto and Benkman (2014).

index, with serotiny at the warmer coastal sites subject to crown fires at twice the frequency of that at the more elevated, cooler sites.

Biotic as well as abiotic interactions may affect the level of serotiny at the intraspecific level. For example, the red squirrel, *Tamiasciurus hudsonsicus*, in North Americas modifies the level of serotiny among disparate stands of *Pinus contorta* subsp. *latifolia* (Figure 8). The squirrels are most attracted to serotinous cones as they are always available; they remove the cones and store them intact preventing their seed release and dispersal in response to fire (Talluto and Benkman, 2013). Thus, selection works against the expression of serotiny and this pressure increases with a greater abundance of the squirrel. Relatively young trees are more likely to produce serotinous cones so that 50% of trees can be serotinous in the absence of this granivore but <10% when it is abundant. Old trees bear few serotinous cones as most will have released their seeds so that their effective level of serotiny is low and removal by squirrels has only a minor impact on this level. Thus, there is support for an adaptive response by this pine toward weaker serotiny and the early release of seeds, reducing the opportunities for hoarding and consumption of seeds by this major granivore. This assumes that the genetic mechanism operates at the scale of individual trees and trees recorded as nonserotinous did not, in fact, result from earlier removal of all serotinous cones by squirrels. Weak serotiny will be adaptive here as substantial interfire recruitment is possible. Where it is not, then the local extinction of heavily predated populations becomes a risk.

B. Interspecific variation in serotiny

We have demonstrated site effects (differing fire regimes and levels of granivory) on selection for serotiny within a species. The differential response of individual species to the same level of selection is even more marked. Thus, the root-suckering *Banksia elegans*, whose follicles almost never open even when removed from the parent plant (Lamont, 1988), co-occurs with the fire-killed *B. prionotes* that forms a multi-aged woodland at Lake Indoon, SW Australia (>85 times difference in the degree of serotiny between them; Enright and Lamont, 2006). This involves inherent disparities between spontaneous interfire seed release (both show complete follicle opening in the presence of fire heat), and interfire recruitment patterns. Thus, weakly serotinous species show almost annual recruitment [with the peak age classes varying markedly between species and sites (Figure 9), possibly representing differential responses to wetter and drier years, especially summer rainfall (Enright and Lamont, 1992)]. This is a function of both the greater availability of seeds annually compared with the strongly serotinous species and biological differences such as smaller seeds able to penetrate the litter and greater drought tolerances (Hanley and Lamont, 2001). Even so, interfire recruits remain subordinate to postfire recruits in this system and contribute few seeds to the postfire generation that is compensated for by the fact that annual production by the postfire plants is high. Weak serotiny is only an effective ‘bet-hedging’ strategy when some fires occur at intervals exceeding the life span of the species (Enright *et al.*, 1998a). Alternatively, some seeds can deposit in unvegetated gaps through spatial heterogeneity of the plant cover that assists their recruitment. This remains much more likely after the fire (Lamont, Witkowski, *et al.*, 1993) as most interfire seeds disperse around their parents and compete directly with them (personal observations).

Various habitat-vegetation types dictate the fire frequency, fire type, interfire and postfire recruitment opportunities, and maximum plant life span that is possible (Table 2). Thus, particular species are constrained to specific habitat types. It is remarkable that often there is sufficient genetic diversity within a single clade for different congenerics to occupy all five

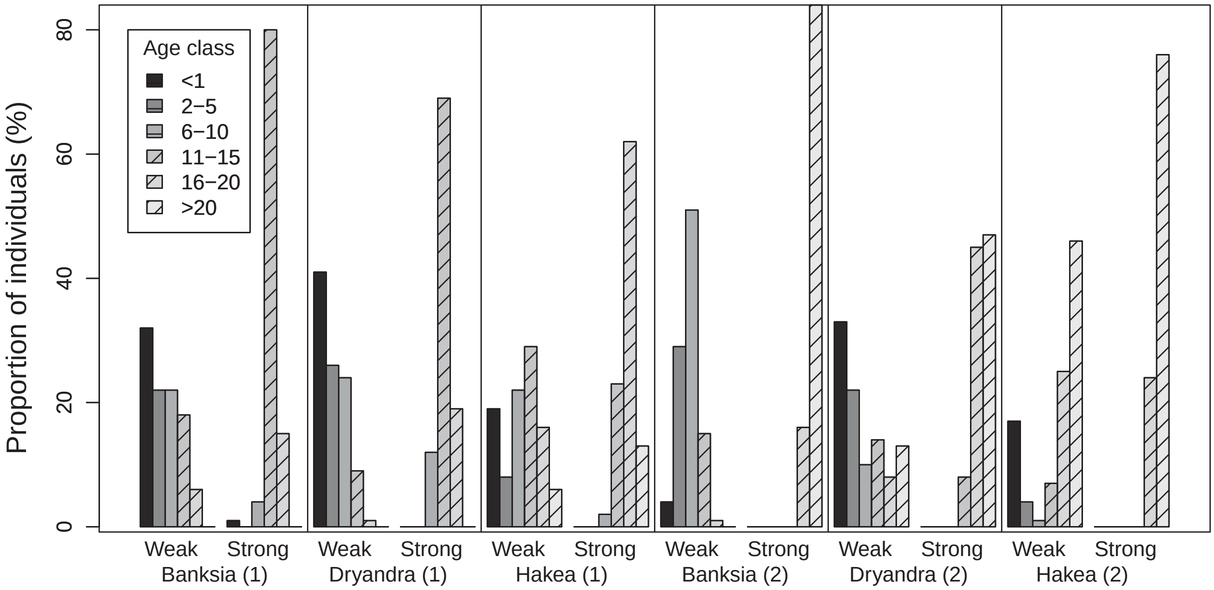

Figure 9. Distribution of age classes among 12 species of woody shrubs in the Proteaceae (2 *Banksia*, 2 *Dryandra*, 2 *Hakea* species pairs) in scrub-heath vegetation of SW Australia. Within each genus, pair 1 is separated from pair 2 by 700 km and one of the pair is weakly serotinous (recruits spread over many years) and the other is strongly serotinous (recruits restricted to the year or so after fire). If a fire occurred at this time and assuming interfire plants <10-years-old make little contribution to seed availability (non-hatched bars), then 36% of weakly serotinous, prefire plants on average would contribute seeds to the next generation while 97% of strongly serotinous plants would. Drawn from data in Hanley and Lamont (2001).

fire-frequency classes recognized here, given sufficient time to adapt. When fire frequency is ranked from nil to high, the level of serotiny increases to a maximum at a low-moderate frequency and then diminishes. Different species, often within the same genus, will only be adapted to a few, often just one, of these fire-regime/environmental combinations, depending on their life-history traits (maturity age and plant longevity, Figure 5). Either the species respond genetically to all of these agents of selection or they are excluded. Note how nil/weak serotiny can exist in contrasting habitat/fire classes, but that strong serotiny is more environmentally constrained.

C. Intracladal variation in serotiny

We have noted how serotiny may vary greatly within (Table 3, Figure 8) and between (Table 4, Figure 9) species occupying different fire-related habitats. We now consider how levels of serotiny are distributed within clades in relation to fire type and whole-plant fire response (killed or survives). Is selection for serotiny always tied to fire type (no fire, surface, or crown fire) or coupled with the type of fire response? If serotiny is a fire-related phenomenon, then, if the habitat is non-fireprone or only subject to surface fires (trees whose reproductive structures cannot be reached by fire), then serotiny should be absent; and this is what we find when we look at five key clades with serotinous species (Table 5). [That insufficient flame height is not the full explanation is indicated by many subshrub geoxyles in grasslands whose crowns are burnt every time there is a fire.] This is consistent with chronogram analyses that show the presence of fire is a pre- or co-requisite for the evolution of serotiny (Lamont and He, 2017; Lamont *et al.*, 2019b). Serotiny will be confined to crown-fire habitats but not necessarily all species within a clade as (a) some have adequate annual production for self-replacement upon death should a fire occur, or (b) the probability of a fire occurring between maturity age and longevity of the species is too small to guarantee seed release by fire in that time (Enright *et al.*, 1998a; Keeley and Zedler, 1998; Figure 5). Again, this is what we find (Table 5).

Because resprouters, and other fire-resilient species, do not rely on seeds for persistence in the postfire stand, one might predict that serotiny is a relaxed condition in these species: this is not what we find. In the long-term, fitness and genetic diversity of resprouters is just as dependent on seeds as nonsprouters and their levels of serotiny may be similar (Enright *et al.*, 1998b). This might be exacerbated by their typically low annual seed set compared with nonsprouters (Lamont and Wiens, 2003; Pausas *et al.*, 2004). Thus, selection favors serotiny among resprouters as much as among nonsprouters under crown-fire regimes. Only resprouters survive under surface-fire regimes and serotiny is absent here as there is no advantage in storage when fire is so frequent (Table 4).

Table 4. Levels of serotiny associated with habitat-vegetation type, fire regime, relative interfire/postfire recruitment conditions and plant life span, with specific examples to show the wide variation that may occur even in the same genus.

Habitat–vegetation type	Fire frequency (relative to plant life span)	Fire type	Interfire (I) recruitment conditions*	Postfire recruitment conditions	Plant life span	Serotiny	Examples
Rainforest, rock outcrop, desert, deciduous forest, wetlands, alpine	■ Nil	Not apply	Variable	Not apply	Variable	■ Nil	*Hakea clavata*, *Banksia integrifolia*, *Protea glabra*, *Pinus edulis*, *Larix decidua*
Wet/boreal/mixed forest, wetland margins, subalpine	■■ Low	Crown	Good	Good (> i)	Long	■■ Weak	*Hakea lasiantha*, *Banksia littoralis*, *Protea rubropilosa*, *Pinus serotina*, *Larix gmelinii*
Dry forest, woodland, scrub, heath	■■■ Low–moderate	Crown	Poor	Good	Variable	■■■ Strong	*Hakea cucullata*, *Banksia serrata*, *Protea neriifolia*, *Pinus contorta*
Woodland, scrub, heath, savanna	■■■■ Moderate	Crown–surface	Good	Good (> i)	Limited (not dominants)	■■ Weak	*Hakea trifurcata*, *Banksia prionotes*, *Protea scabra*, *Pinus halepensis*
Savanna, (sub)tropical grassland with subshrub geoxyles	■■■■■ High	Surface	Variable	Variable	Long	■ Nil	*Hakea lorea*, *Banksia dentata*, *Protea caffra*, *Pinus cubensis*, *Larix occidentalis*

The squares indicate in a semiquantitative way how the levels of serotiny rise and fall with increasing fire frequency. *As perceived by the species (see Figure 9).
Supporting references: Heinselman (1981), Rebelo (2001), He *et al.* (2011; 2012), Lamont, El-Ahmir, *et al.* (2017), Lamont *et al.* (2019b).

Table 5. Number of serotinous species/total number of species in relation to fire response and fire regime, for five clades: *Pinus* (Pinaceae; He *et al.*, 2012), *Banksia* (Proteaceae; He *et al.*, 2011), Callitroideae (Cupressaceae; Ladd *et al.*, 2013; Crisp *et al.*, 2019), *Protea* (Proteaceae; Lamont *et al.*, 2013, 2017a), and *Hakea* (Lamont, El-Ahmir *et al.*, 2017; Figure 10).

		Fire regime		
Clade	Fire response	No fire	Surface fire	Crown fire
Pinus (113 Ma)	Fire-killed	0/165	0/0	17/17
	Fire-survivor	0/0	0/11	11/11
Banksia (62 Ma)	Fire-killed	0/0	0/0	43/45
	Fire-survivor	0/0	0/1	33/39
Callitroideae (58, 48 Ma)	Fire-killed	0/14	0/0	17/17
	Fire-survivor	0/0	0/3	2/2
Protea (28 Ma)	Fire-killed	0/0	0/0	51/51
	Fire-survivor	0/0	0/23	20/22
Hakea (20 Ma)	Fire-killed	0/0	0/2	41/44
	Fire-survivor	0/1*	0/2	31/33
Overall	Fire-killed	0/179	0/2	169/175
	Fire-survivor	0/1*	0/40	97/107

Clades are listed in increasing time since their origin of serotiny (in brackets).
*Lignotuberous.

VII. Temporal aspects

A. Evolution of serotiny and nonserotiny among genera

We now consider the evolutionary history of serotiny and nonserotiny among three well-studied clades: *Hakea* (Australia), *Pinus* (Northern Hemisphere), and *Protea* (Africa). The onset of serotiny in *Hakea* is associated with the departure of the ancestral parent from the rainforest into fire-prone sclerophyll woodland, 18–20 Ma (Figure 10). Diversification of moderately serotinous species escalated in the mid-late Miocene, possibly associated with the advent of a Mediterranean climate in SW Australia (Lamont and He, 2017) with its intense, moderately frequent, summer-autumn fires. The appearance of much woodier and more strongly serotinous fruits 5 million years (My) after the origin of the clade can be attributed to selective pressure from the increasingly abundant granivorous black cockatoos (*Calyptorhynchus*) (White *et al.*, 2011) in the face of the increasing advantages of serotiny for seedling recruitment as the climate became drier and more seasonal (Lamont, He, *et al.*, 2016). Weak serotiny originated at much the same time but diversified more slowly at first then escalated from 7 Ma with smaller fruits that tended to stay green, mimicking the leaves and branchlets and remained embedded among the spiny leaves. This, in turn, was an adaptive consequence of the large fruits arising from exposed, bird-pollinated flowers, such that mimicry and crypsis, available to insect-pollinated flowers concealed within foliage, were not options

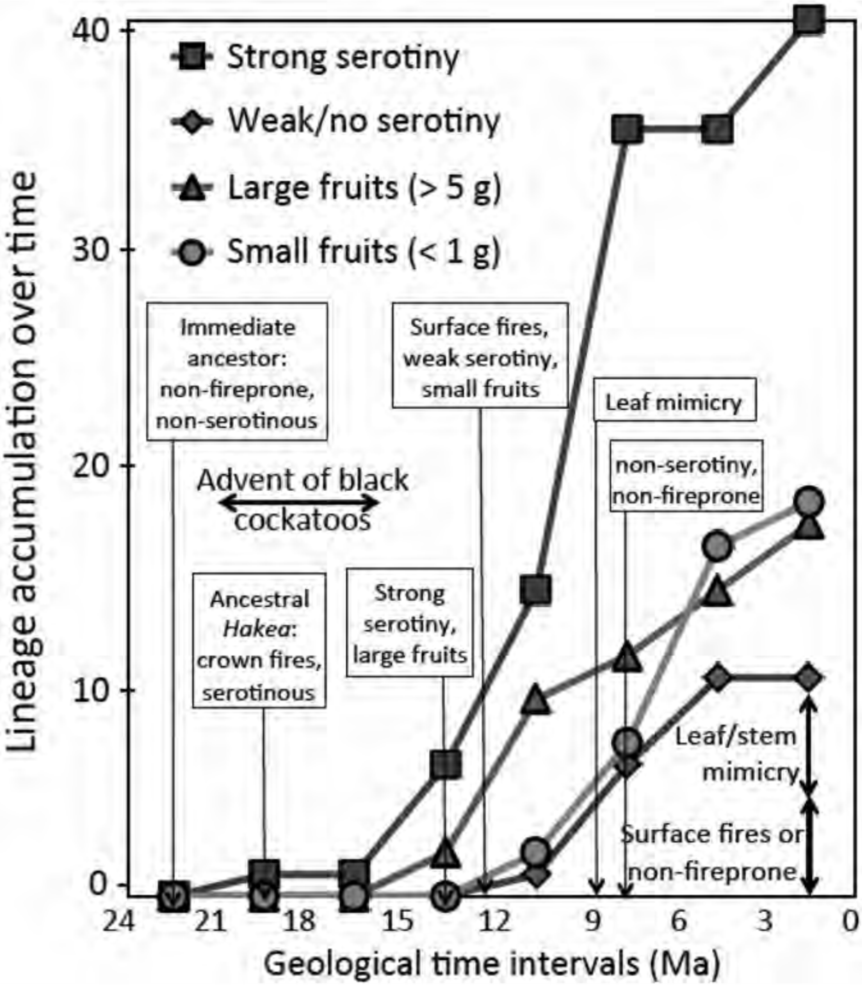

Figure 10. Evolutionary history of serotiny and nonserotiny in the world's most sclerophyllous genus, *Hakea* (Proteaceae), in Australia based on ancestral trait assignment and molecular clock techniques (the subclade that possesses only strong serotiny has been omitted from this analysis). Arrows refer to the earliest evidence for the presence of certain traits or fire regimes. Note the few species with intermediate-sized serotinous fruits (1-5 g) are not plotted separately but are included in the total numbers under strong serotiny. Figure collated from Lamont, Hanley, *et al.* (2016), Lamont, He, *et al.* (2016), and Lamont, El-Ahmir, *et al.* (2017).

(Hanley *et al.*, 2009). Some lineages were successful at interfire recruitment (Hanley and Lamont, 2001) while others by now had spread into sparse vegetation (arid or saline) or summer-rainfall savannas (Lamont, He, *et al.*, 2016) where flames were unlikely to reach the crown, both promoting weak/nonserotiny. The only species to complete the evolutionary cycle by occupying nonfireprone rock outcrops and becoming nonserotinous is *Hakea clavata* that arose about 6.5 Ma.

Serotiny arose in *Pinus* ~113 Ma from nonserotinous congeneric ancestors subject to surface fires over the previous 25 My, and coincided with the advent of crown fires that could now reach the cones and stimulate seed release (Figure 11). Diversification of the serotinous lineage (subgenus *Pinus*) did not occur until 50–45 Ma or else speciation was balanced by extinction up until then. As diversification of nonfireprone, nonserotinous lineages escalated from the mid-Paleogene and into the Neogene-Quaternary, peaking over the last 5 My, so too did the fireprone, serotinous lineages but at a lower rate. Six species lost serotiny on entering fire-free habitats over the last 25 My. While a nonserotinous lineage (subgenus *Strobus*) developed wingless seeds 50–45 Ma (Figure 11), diversification only began 30–25 Ma, increasing linearly at a low rate until the present associated with dispersal by granivorous birds (corvids) and squirrels. Since winged seeds are part of the serotinous syndrome (He, Belcher, *et al.*, 2016), a return to serotiny remains possible for most of the currently nonfireprone pines should the fire regime change, but this becomes less likely for those species with wingless nutlets as these are now entrenched in their genome.

Protea was serotinous from the time of its separation from nonserotinous relatives 28 Ma in the SW Cape of South Africa, and diversification escalated

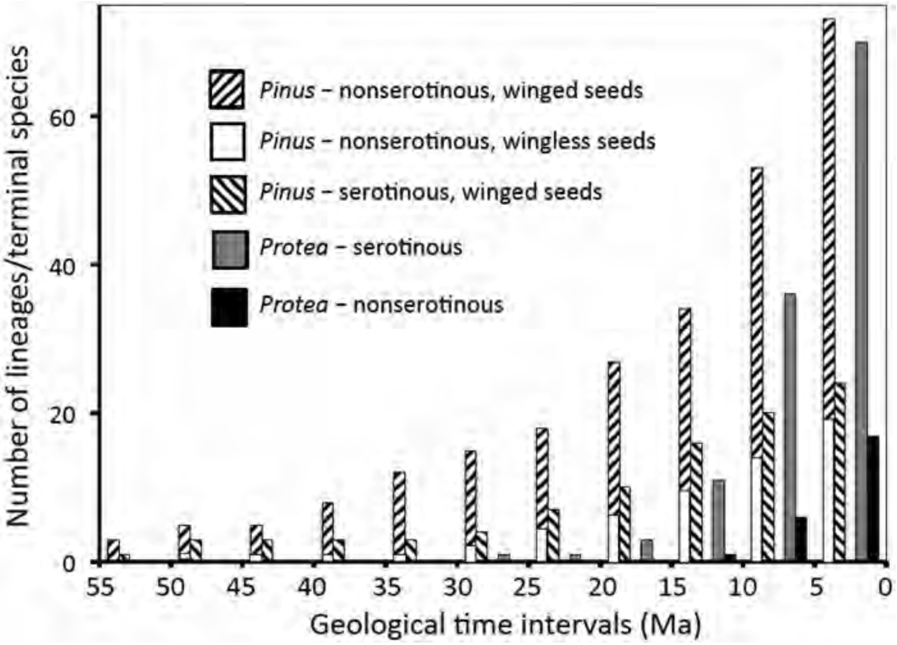

Figure 11. Net total diversification of serotiny over geological time for *Pinus* and *Protea*, including the conversion of winged to wingless seeds among nonserotinous lineages in *Pinus* and loss of serotiny among resprouters in *Protea*. Data obtained from chronograms presented in He *et al.* (2012), Lamont *et al.* (2013), Lamont, He, *et al.* (2017), and Lamont *et al.* (2019b).

there from 20 to 15 Ma (Figure 11) possibly coinciding with the advent of a predominantly winter-rainfall climate and summer-autumn fires at moderate intervals (Lamont and He, 2017). As the clade migrated north and east to the summer-rainfall zone in the 15–10 My period, one lineage adopted both resprouting in response to fire and loss of serotiny and could now enter this zone where it diversified strongly. Resprouting is required to survive the frequent (often annual) winter-spring fires and serotiny is redundant or even maladaptive if it involves a fitness cost. Thus, serotiny has gone in opposite directions in the same genus as determined by the contrasting fire regimes in different regions. A general picture emerges among these three clades of (a) nonserotinous ancestors in nonfireprone habitats (or surface fires in the case of pines), (b) initiation and proliferation of serotiny with the introduction of crown fires, and (c) loss of serotiny with migration to (almost) fire-free habitats or greatly expanded summer-rainfall grasslands/savannas with frequent fire but diversifying at a much lower rate than the serotinous lineages.

B. Evolution of serotiny and nonserotiny among families

Moving from the genus to family-scale shows how serotinous and nonserotinous genera can arise independently numerous times within the same parent clade (Figure 12). Each of the 10 serotinous lineages in Proteaceae commences in a fireprone environment but not all fireprone environments lead to serotiny. Geospory is diagnostic for 17 lineages that requires heat or smoke to break dormancy. Why one fire-response type is selected for rather than the other is unclear, but it must involve possible differences in the selective fire regime and postfire recruitment conditions as well as phylogenetic constraints. One lineage (*Faurea*) lacks any storage and occurs in savanna (highly fireprone) or rainforest (nonfireprone). In addition, the serotinous structures are matched (same ontogeny) at the fruit level within each subfamily (homologous) but the fruit types are quite different between subfamilies (analogous – homoplasious). Thus, the Proteoideae has indehiscent achenes while the Grevilleoideae has dehiscent follicles.

Further, the infructescence types are nonhomologous within each subfamily. For example, *Protea* has a capitulum plus an involucre of bracts that wrap around the entire head of fruits, while in *Aulax* and *Petrophile* each fruit has its own scale attached to a rachis (multiple rachises in the case of *Aulax*). Among the five fireprone, Grevilleoid lineages, *Banksia-Dryandra* alone has a compound fruit with persistent bracteoles. In addition, its follicles rarely open on severance of the cone from its vascular supply but the serotinous structures of all other lineages release their seeds when their vascular supply ceases. Further, the

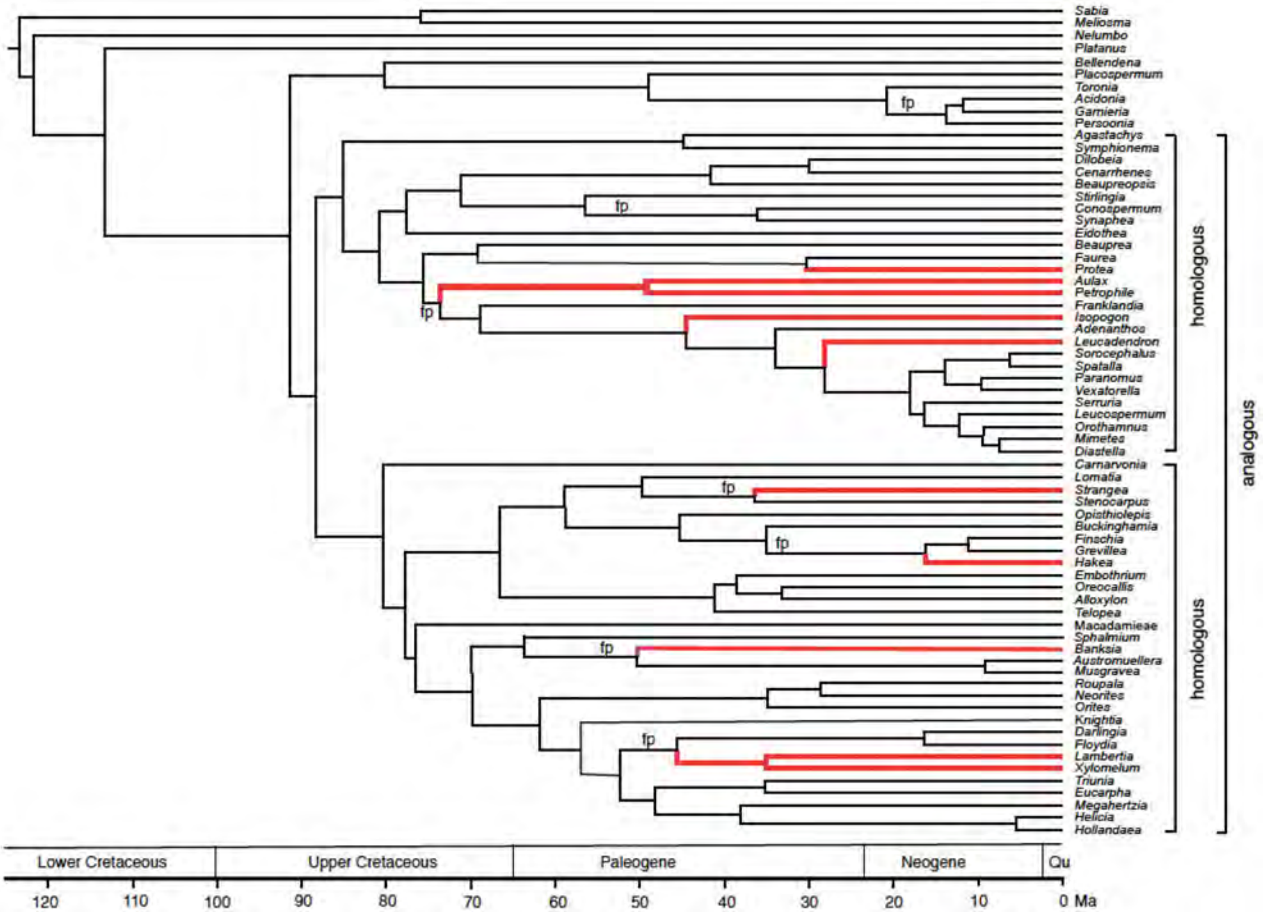

Figure 12. Chronogram for the family Proteaceae showing the geological history of serotinous lineages (in red) vs nonserotinous lineages. Note how each of the 10 serotinous lineages commences in a fireprone (fp) environment but not all fp environments lead to serotiny. Homology exists at the fruit level within subfamilies but not between them (analogy, homoplasy). Adapted from Lamont and He (2017) and supplementary material in Lamont and He (2012).

various serotinous structures originated at quite different times (Lamont and He, 2012). Thus, the serotinous cones of *Aulax*/*Petrophile* arose at least 75 Ma while those of *Leucadendron* appeared 50 Ma, assuming that the cones were serotinous then based on ancestral trait assignment techniques (Lamont *et al.*, 2019a). *Banksia* was serotinous from its beginnings >60 Ma while the serotinous follicles of *Hakea* can be dated to 20 Ma (although the node is set where it separated from *Grevillea*, and the complex is at least 35 Ma so it may be older). The issue of the origin of particular serotinous structures, therefore, cannot be separated from the reasons for the origin of particular lineages in geological time that is steeped in their fire history (Lamont *et al.*, 2019a).

At an even broader global scale, serotiny has arisen independently among 12 families throughout the phylogeny for seed-bearing plants (Figure 13). This covers a time span of almost 150 My, coincident with the history of fireprone floras over that period, with serotiny arising well before, or coincidentally with, the onset of susceptibility to fire (Lamont and He, 2017). Beginning with two conifer families (Taxodiaceae is embedded in Cupressaceae in this phylogeny), this proceeds to the monocots (two families – Lyginiaceae is embedded in Restionaceae in this phylogeny). This is followed by two ‘old’ Eudicot families, Proteaceae and Myrtaceae, then a moderately old family, Casuarinaceae, and finally the modern Eudicot families, Ericaceae, Bruniaceae, and Asteraceae. Each of the ten families begins with nonserotiny and serotiny arrives later, sometimes early (Anarthriaceae, Bruniaceae) and sometimes only recently (Ericaceae). Note that hundreds of other clades are fireprone apart from the serotinous ones but they have quite different adaptations for fire survival.

C. Overall evolutionary history of serotiny

Collating the 31 records available for the ancestral condition of serotiny shows that it has arisen in every 10-My interval over the last 110 My (Figure 14).

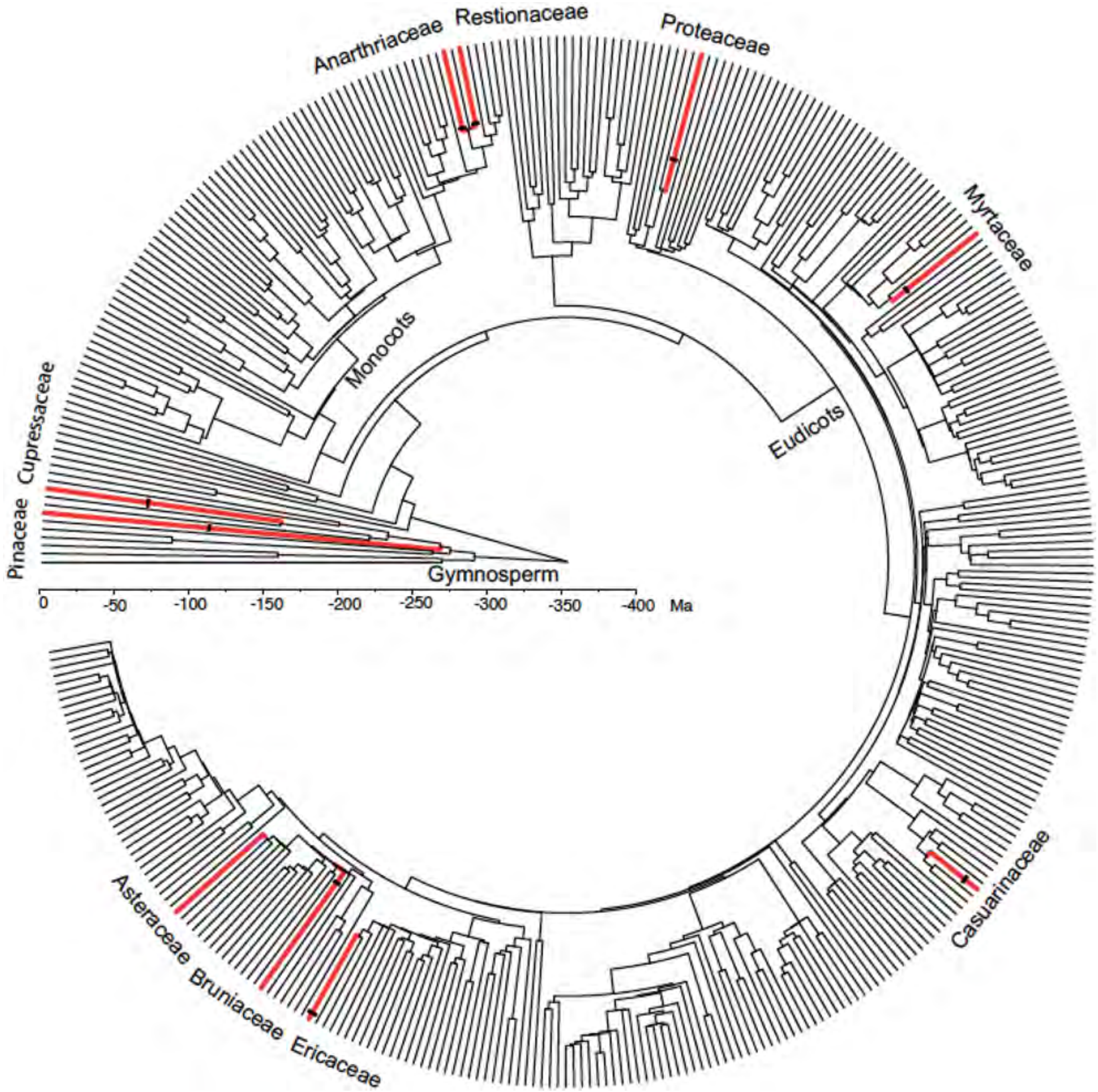

Figure 13. Dated phylogeny for the world's seed-plant clades to which have been added lineages possessing serotinous species at the rank of family – in red. The approximate time that the lineage first displayed serotiny is indicated by a cross-bar. Note that in all cases the lineage would have been fireprone before, or at least coincident with, the onset of serotiny (Lamont and He 2017). *Sequioadendron* is embedded in Cupressaceae at about 20 Ma though it could be up to 45 Ma (Lowe, 2013). Backbone of the phylogeny adapted from Zanne *et al.* (2014).

Three peaks may be identified: a small peak toward the close of the Cretaceous corresponding to the origin of many extant families and their early radiation, and two larger peaks in the Cenozoic: the Paleocene–mid-Eocene and Oligocene–Early Miocene. The drop in trait diversification and proliferation rates in the 80–70 and 40–30 Ma periods corresponds to local depressions in charcoal deposition, temperature, and atmospheric O_2 (Lamont *et al.*, 2019a). Of particular note is the sharp drop of 4 °C at 34 Ma corresponding to the completion of the Antarctic circumpolar current at that time (as Australia finally broke away) that correlates with the dip in O_2 levels and no doubt decreasing incidence of fire as a selective force. The peaks at 60-40 and 30-0 Ma cannot easily be attributed to an increase in charcoal deposits but they do correspond to the Early Eocene Thermal Optimum (55–45 Ma) and Mid-Miocene Thermal Optimum (17–14 Ma) with their expected positive effect on fire activity and the evolution of fire-adapted

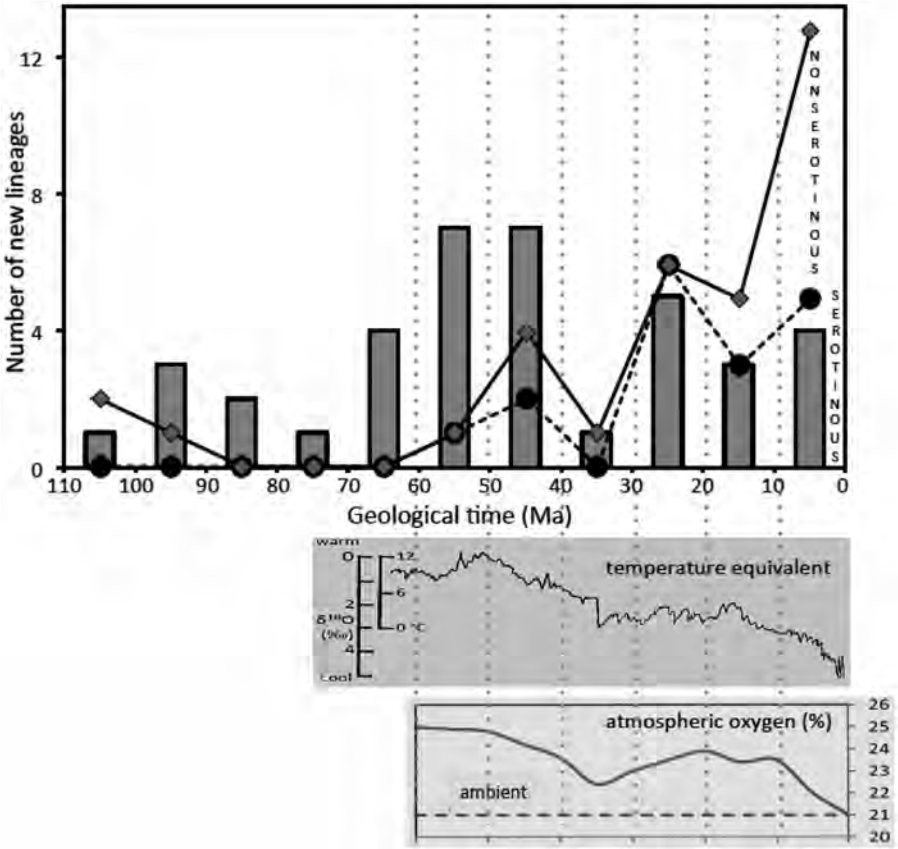

Figure 14. Number of new lineages (bars) possessing serotinous cones/fruits (recorded using Bayesian probability trait reconstruction techniques) arising at 10-million-year intervals since 110 Ma (mid-Cretaceous). Collated from data for 31 clades in the families Casuarinaceae, Cupressaceae, Myrtaceae, Pinaceae and Restionaceae in the Supplementary Material, Lamont and He (2017). Included are $\delta^{18}O$ values (as a surrogate for temperature, redrawn from Zachos *et al.*, 2008) and estimated atmospheric O_2 values (from Bergman *et al.*, 2004). Adapted from Lamont *et al.* (2019a). Added are equivalent new data for the subfamily Callitroideae, Cupressaceae showing total new lineages (diamonds) and those with serotiny (filled circles) collated from supplementary data in Crisp *et al.* (2019). The difference between these two values is the number of nonserotinous lineages.

traits. Clearly, seasonality began to take control of the fire patterns as O_2 levels started to fall from 30 Ma. Conversely, because evolution of serotiny/pyriscence requires fireprone conditions, these patterns of speciation can be used to imply the prevailing levels of fire activity as experienced by these clades through time, independent of charcoal data that will always be an inadequate and biased record of the occurrence of fire beyond wetlands where fossils are best preserved (He *et al.*, 2012).

It is noteworthy that a recent independent analysis of the subfamily Callitroideae, Cupressaceae, produced much the same pattern with geological time (Crisp *et al.*, 2019; Figure 14). The exception was the marked diversification of nonserotinous taxa over the last 10 My that can be attributed to both diversification of nonfireprone species and entry into savanna-type habitats. Novel fire-adapted traits may appear in response to the imposition of an initial fire regime (the outcome of primary directional selection) and be replaced later by a change in the fire regime (secondary directional selection) or be retained in the daughter lineage while nonfire-related traits arise in response to other agents of selection (stabilization) (Lamont *et al.*, 2019a). Overall, the initiation/(loss) of serotiny coincided with the simultaneous origin of the genera or clade and advent of fire-proneness in 31% of cases, millions of years later due to a change in the fire regime in 29% of cases, and serotiny was retained (stabilized) as continuing to be adaptive in 32% of cases. The evolution of serotiny from nonfireprone ancestors is associated with the historical occurrence of fire, and its occasional absence in serotinous clades has been the result of more recent changes in the fire regime. The loss of serotiny completes the evolutionary cycle but under quite different environments than originally – there are few records so far of lineages returning to the everwet forests of their ancestors. Leptospermoid Myrtaceae may provide one exception, where trees with vestigial (blind) epicormic buds may be present in nonfireprone rainforest (Clarke *et al.*, 2013) and these are also nonserotinous.

Over geological time, the only way to gauge the incidence and net rate of trait change is via speciation. The four well-studied clades already considered here (Figures 10, 11, and 14) are now collated (Table S3) to show enormous variation in the rates over the Cenozoic with a tendency for both serotiny and nonserotiny to peak over the last 5 My in three clades, but over the last 15–5 My in *Hakea*. The three clades whose ancestral state is serotiny have tended to favor serotiny over evolutionary time, and vice versa, consistent with their preferred habitats.

Callitroideae is fascinating for the fluctuating dominance of serotiny and nonserotiny over evolutionary time: the immediate ancestors of Cupressaceae were probably nonserotinous immediately followed by serotiny in Callitroideae then nonserotiny with a general decline in the speciation rate coinciding with the world drops in temperature and O_2 (and a likely decrease in the incidence of fire) peaking at 34 Ma (Figure 14). This was followed by a marked increase in serotinous species in the Oligocene-Miocene, followed by greater nonserotinous speciation over the last 10 My. The greatest net rate for the evolution of serotiny over the last 5 My is 14 species/My among temperate shrubland proteas followed by 5 species/My among pines. At the same time, pines yielded 18 nonserotinous species/My and savanna grassland proteas 3.5 species/My but the reasons differ: pines migrated strongly into fire-free habitats, for example, alpine (as did Callitroids), or frequently (understory) burnt savanna woodlands/forests, while proteas migrated into frequently burnt, savanna shrubby grasslands only (Table 4). *Hakea* is of particular interest for speciation of the serotinous lineage far outstrips that of the nonserotinous in the Upper Miocene (contributing to this as the only time in which serotiny exceeds nonserotiny overall for the four clades) with a few species moving into nonfireprone habitats and summer-rainfall savannas in the late Miocene.

VIII. Conservation issues

Understanding how anthropogenic climate change influences plant reproductive ecology is fundamental to understanding how climate variation affects plant communities (Parmesan and Hanley, 2015). As we have shown, the expression of serotiny depends on the interplay of fire-regime and a number of post-fire environmental conditions that dictate germination and seedling recruitment success. Despite an expectation that fire frequency and intensity will increase in Mediterranean-climate regions (at least until decreasing rainfall has a significant effect on reducing fuel loads), the magnitude of shifts in the fire regime remains uncertain (Pausas, 2004; Pachauri and Meyer, 2014). The level of serotiny was higher among two Mediterranean pine species (*P. pinaster* and *P. halepensis*) in populations from areas affected by more frequent fires over the last 30 years (Hernández-Serrano *et al.*, 2013; Vincenzi and Piotti, 2014). Added to this, declining and more unpredictable interfire precipitation regimes in Mediterranean-climate regions, especially during the key winter seedling recruitment period (Pachauri and Meyer, 2014), will add further stress on fire-following plants with the serotinous habit in particular at serious risk of local extinction (Lamont *et al.*, 2007; Enright *et al.*, 2014) and possible selection for earlier reproductive maturity and increased serotiny (Vincenzi and Piotti, 2014). On the other hand, invasion by serotinous pines, with their greater seed stores, is now occurring in regions where endemic levels of serotiny are negligible (Raffaele *et al.*, 2016).

Habitat fragmentation may also affect fire regimes, with any impact on fire frequencies depending on proximity to human activity (e.g., arson) and local land-use type (Keeley *et al.*, 1999; Syphard *et al.*, 2007; Regan *et al.*, 2010). Moreover, despite a considerable amount of work on the separate effects of altered fire frequencies and fragmentation on plant populations, few, if any, studies have considered the two factors in combination (Regan *et al.*, 2010). Habitat fragmentation also affects serotinous species in other ways. Many of the serotinous Proteaceae characteristic of SW Australia and the Cape of South Africa, for instance, are bird pollinated and effective cross-pollination (in the case of *Banksia hookeriana*) often involves the movement of bird pollinators over considerable distances (Krauss *et al.*, 2009). Although by no means unique to serotinous species, disruption of plant mating systems in fragmented landscapes represents a further problem for the many bird-pollinated species that also tend to be strongly serotinous (Lamont, Klinkhamer, *et al.*, 1993). When faced with shifts in land-use, weakly serotinous or nonserotinous species may take advantage of increased disturbance. Hanley and Lamont (2001) not only showed how weakly serotinous Western Australian Proteaceae exhibited much greater interfire recruitment than their strongly serotinous conspecifics, but at least two weakly serotinous species (*Dryandra sessilis* and *Hakea trifurcata*) are common invasives in disturbed areas near roadways and tracks through reserves (M. E. Hanley, personal observations). Thus, it seems likely that increased anthropogenic creation of bare areas will favor non- or weakly serotinous species over strongly serotinous species.

Serotinous species in South Africa and Australia are highly favored in the wildflower trade (Rebelo and Holmes, 1988; Lamont *et al.*, 2007; van Deventer *et al.*, 2016). Harvesting is usually undertaken from wild populations but plantation sources are increasing (Blokker *et al.*, 2015). Thus, 34% of produce exported among 170 species in Western Australia are from serotinous species (Anonymous, 2018), even though they only contribute 14% of the total flora. Of the 41 species harvested in the wildflower trade in the Agulhas Plain, 76% are serotinous (van Deventer *et al.*, 2016), even though serotinous species only account for 2% of the Cape flora. The conservation status of many of these species is considered threatened or vulnerable. Bloom harvesting greatly reduces the subsequent size of the canopy-stored seed bank, especially when levels of harvesting rise above 30% (Lamont *et al.*, 2001; Treurnicht, 2017). This is especially so for the fire-killed nonsprouters, which account for 80% of the harvested species (van Deventer *et al.*, 2016), as this group is entirely dependent on seedlings for postfire recovery. This exacerbates the likelihood of local extinction among serotinous nonsprouters that are already the most vulnerable to decreasing rainfall and increasing fire frequency/intensity associated with climate change (Enright *et al.*, 2014). High levels of harvesting can also substantially increase plant mortality, for example, mortality in commercially exploited *Brunia albiflora* populations ranged 8–33% compared with only 1–3% natural mortality (Rebelo and Holmes, 1988). Many serotinous species are also highly susceptible to the root-rot fungus, *Phytophthora cinnamomi* (Lamont *et al.*, 2007).

IX. Research challenges

Much has been learned about the processes controlling the biology of serotiny since the publication of a major review on its ecological significance 30 years ago (Lamont *et al.*, 1991). Lamont and Enright (2000) listed worthwhile research topics that remained, some of which have been achieved and others that have not. Enright *et al.*, (2007) stands alone as an overt comparison of the relative taxonomic and spatial distribution of geospory and serotiny in an entire fireprone system, concluding that 95% of species exhibited some sort of storage. That serotiny might enhance genetic diversity equivalent to that of the multiple generations represented by soil storage has been examined only once and shown to occur surprisingly fast in a postfire population of *Banksia hookeriana* (Barrett *et al.*, 2005). It was noted then that demographic models would be greatly improved if there was a sounder knowledge of plant longevity – this has received little overt monitoring since but it continues to be important and there have been attempts at estimating longevity among long-lived species (Merwin *et al.*, 2012, Martín-Sanz *et al.*, 2016). The early indications that the germination of some serotinous seeds could benefit from heat pulses or survive extraordinarily high temperatures, both akin to the responses of geosporous species, has been confirmed (Hanley and Lamont, 2001; Tangney *et al.*, 2019). This suggests that selection for insulation from fire heat may not be the prime or only function of protective structures.

Once it is recognized that seed serotiny is only part of a vital reproductive syndrome for hundreds of species, it opens the way to examine how selective forces shape a wide array of traits, not just those that control the rate of cone/fruit opening. We list 23 that appear relevant here (Table 1): the operating mechanism of only one is beginning to be understood in any detail (Huss *et al.*, 2018, 2019) and the genetic basis of any one of them is only understood at a crude correlative level. Having identified what traits are involved in the serotiny/nonserotiny syndromes this opens the way for intensive study of their genetic basis and what genes control their expression. With increasing interest in the heritability of serotiny (Parchman *et al.*, 2012, Budde *et al.*, 2014, Vincenzi and Piotti, 2014; Castellanos *et al.*, 2015; Feduck *et al.*, 2015), it is essential that the index reflects the extent to which viable seeds remain stored on the plant over time and is not confounded by plant age, fecundity or growing conditions. The most stable index in this regard is the slope measure of serotiny but our literature survey shows that it has only been adopted as the standard measure in Australia. Indices of serotiny are most meaningful when calculated on a viable seed basis but this is almost never done. A critical look at what exactly the indices of serotiny currently available measure, and how they can be improved, is now available (Lamont, 2020).

A particular challenge is identifying the morphological, environmental and/or genetic basis for why some seeds are released early and others late (in the absence of fire) within the same population, plant, or cone (Salvatore *et al.*, 2010). Huss *et al.*, (2018) have done an excellent job in elucidating the anatomical (although not yet chemical) basis of the differences in the level of serotiny along a climatic gradient. Fruits or cones exposed to direct sunlight appear to open early (soliscence, Lamont, 1991) that has yet to be formally documented, but this only occurs under special circumstances. These local effects, along with other causes of interfire seed release such as 'hot' winds (Nathan *et al.*, 1999), are only adaptive if they lead to successful recruitment of fecund adults before the next fire, but this has yet to be demonstrated (Daskalakou and Thanos, 1996). We have assumed that the seeds released in the absence of fire have minimal genetic support for serotiny in our models (Figures 4 and 6). What is the actual gene store for serotiny (S) among individuals in a population at increasing times since fire? One puzzle is, if they are (epi)genetically distinct, how weakly/nonserotinous and serotinous seeds are recognized by the mother plant such that the former is released early and the latter later or never? Are there within-plant/cone spatial, temporal, morphological, or physiological aspects that control the early or late release of seeds? This may well involve epigenetic inheritance (Lind and Spagopoulou, 2018); maternal control has received insightful recent study in some species (Li *et al.*, 2017), but has yet to be tackled in the context of serotiny (Hudson *et al.*, 2015).

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