Little evidence for fire-adapted plant traits in Mediterranean climate regions

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As climate change increases vegetation combustibility, humans are impacted by wildfires through loss of lives and property, leading to an increased emphasis on prescribed burning practices to reduce hazards. A key and pervading concept accepted by most environmental managers is that combustible ecosystems have traditionally burnt because plants are fire adapted. In this opinion article, we explore the concept of plant traits adapted to fire in Mediterranean climates. In the light of major threats to biodiversity conservation, we recommend caution in deliberately increasing fire frequencies if ecosystem degradation and plant extinctions are to be averted as a result of the practice.

Fire-resistant plant traits

Mediterranean climates and their unique ecosystems are only found on 5% of the land surface of the Earth, yet they contain 20% of the plant species of the world, with high levels of endemism [1–4]. Their effective management and long-term protection of their rich biodiversity is a priority that is being made increasingly difficult by human population pressures and the as-yet not fully understood impacts of global climate change [5–10]. Recent years have seen an escalation in the number and intensity of wildfires in the western USA, Mediterranean basin, Chile, South Africa and southeast Australia that have been linked statistically to an increasing human population [11–14].

The escalated threat posed to human life and property by unplanned fires that have increased in both intensity and frequency, has resulted in wide-ranging policy changes, including the use of prescribed burning [15] that is meant to prevent or ameliorate the impact of such fires [16,17]. However, preventing an increase in fire frequencies can be crucial for maintaining soil integrity, water supplies, water quality and biodiversity, and suitable management practices are therefore difficult to predict [18–24]. Another common perception that underpins current management practices is that plants in Mediterranean ecosystems have been exposed to recurrent fire over long periods of time [25,26] and thus a series of adaptations (Box 1) has evolved that protect them from fire and even, in some cases, make them dependent on fire for reproduction [2,27–29]. In particular, this is thought to be the case with the Australian flora, because much of Australia is fire prone and recurrent fire has been a feature of the environment dating back at least to the Pliocene 2.5–5.5 million years ago (MYA) [27,30–33] and probably to the mid-Miocene 10–15 MYA [32]. The unique flora of Australia has long been thought to have developed numerous morphological and physiological adaptations to fire that are also common in plants from other Mediterranean ecosystems, including resprouting, serotiny, physical dormancy, post-fire flowering and smoke-induced germination [34,35]. Early studies on the importance of soil phosphorus levels in Australia [36] and more recent publications emphasise the need to interpret the evolution of the Australian flora in terms of its apparent adaptation to fire and nutrient-poor soils that are characteristic of much of the landmass [37–39]. The role of fire in engendering adaptive traits in Mediterranean plants, however, has never been tested critically and William J. Bond and Jon E. Keeley [40] note that 'There are few studies of the evolution of fire-adaptive traits, and many plant traits have been uncritically labelled as "fire adaptations" without any rigorous analysis either as to the functional importance of the trait, or its phylogenetic origin'. Stephen D. Hopper [41] similarly challenged the evidence for fire-adaptive plant traits, suggesting instead that Stephen Jay Gould and Elisabeth S. Vrba's [42] concept of exaptation (Box 1) is more apt in many cases, and urging further research given the policy implications of the adaptationist view [43]. Exapted traits can be as effective as adapted traits in enhancing fitness in fire-prone environments, but ever-increasing fire frequencies might overwhelm the potential fire protection afforded by traits that have evolved in response to other, quite different, environmental factors.

Our aim here is to examine critically the proposition that plants occupying Mediterranean ecosystems are adapted to fire as a result of long periods of natural selection in fire-prone environments. We examine evidence from species and ecosystems with and without fire using the rationale shown in Figure 1. We preview the probable long-term impacts of climate change on Mediterranean ecosystems that are predicted to provoke an increase in both fire incidence and intensity, and question the added impact of current fire-management practices on maintaining the unique plant diversity that characterises these Mediterranean biomes.

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Are the traits restricted to plants occupying fire-prone environments?

Resprouting

Resprouting is a common plant response to injury from a variety of insults, including drought, frost, heat wave, waterlogging, herbivory, storm damage, lightning strikes and excessive salt levels. Resprouting is thus not a specific evolutionary response to fire [44]. Many species sprout in the absence of fire [45] and epicormic budding can be as vigorous in *Eucalyptus* spp. following a violent wind storm as after fire [46] (Figure 2a). Resprouting can occur from different sources and tissues, however, and sunken accessory buds that are covered by thick bark survive intense fires and might have been favoured by differential selection under such regimes [47,48]. Resprouting is widespread in plants occupying both fire-prone Mediterranean and less fire-prone environments, the latter including deserts, rainforests, alpine heathlands and fringing riparian vegetation [49]. It has been suggested [50] that, among Mediterranean basin species, the level of post-fire moisture availability was crucial in the extent of resprouting so that drought, rather than fire, was a more important selective agent. Resprouters in general have lower rates of seed production

than do seeders [51] and resprouting can enhance fitness in fire-prone environments; however, its widespread occurrence in non fire-prone ecosystems suggests that it is an exaptation, rather than an adaptation, to fire.

Serotiny (or bradyspory)

Many plants retain seeds for long periods of time in the canopy, releasing them following fire [34]. There are ~40 genera worldwide with some 1200 species that store seeds in woody fruits or cones for periods varying from one to 30 years [52,53]. Serotiny is particularly prominent in the Mediterranean-climate ecosystems of southern Australia, South Africa and the coniferous forests of California, North Africa and the Middle East [54]. Although serotiny among woody species is common in fire-prone regions, most are facultatively pyricent and factors other than fire, including branch death and prolonged exposure to sunlight and rain, will also lead to seed release [55]. Serotiny is most common in the Mediterranean-type vegetation of southwest Australia and the Cape of South Africa [56]. If serotiny were a fire adaptation, one would expect these areas to be the most fire prone among Mediterranean ecosystems. Fire frequencies in the Australian kwongan (a type of heathland) and South African fynbos (fine bush) are typically in the range of 10–20 years [57,58], compared with 20–50 years in California chaparral (sclerophyll shrubland) and Mediterranean basin maquis (dry scrubland) [59,60]; fire is rare in Chilean matarral (xeric shrublands), where there are no serotinous plants [61]. This is consistent with the adaptation hypothesis (Box 1), but other environmental factors could equally have favoured the evolution of serotiny. Foremost among these is a low nutrient supply [62], and seed retention can be favoured in regions with poor soils, where the crop of a single year is unlikely to be sufficient to ensure self replacement. Areas with a reliable growing season would also favour seed retention as recruitment is likely to be favourable following any stochastic catastrophe, such as fire, and both southwest Australia and the South African Cape have the most reliable winter rains of all the Mediterranean-climate regions [63]. High levels of predation on seeds by insects can also lead to seed retention. Masting in plants has been interpreted as a strategy to produce copious amounts of seed at one time so that, no matter how intense the predation from insects, some seeds will survive and germinate [64]. The same can be said of serotiny, where post-fire release of seed is akin to a masting event.

Carbon retention is a typical plant response to a lack of phosphorus [36] and both fire and the occurrence of low-nutrient soils in some Mediterranean-type ecosystems [65] could explain the prevalence of woody fruits and cones in their floras. There are several species-rich plant families with woody fruits both in Australia (Proteaceae, Myrtaceae and Cupressaceae) and in South Africa (Proteaceae and Cupressaceae) and these might have provided the starting point for the evolution of serotiny under conditions of low-nutrient supply combined with limited opportunities for recruitment. An Oligocene fossil cone of *Banksia archaeocarpa* (Figure 2b), with a structure identical in surface morphology to present-day *Banksia* cones, suggests that predation from birds, insects and mammals also favoured
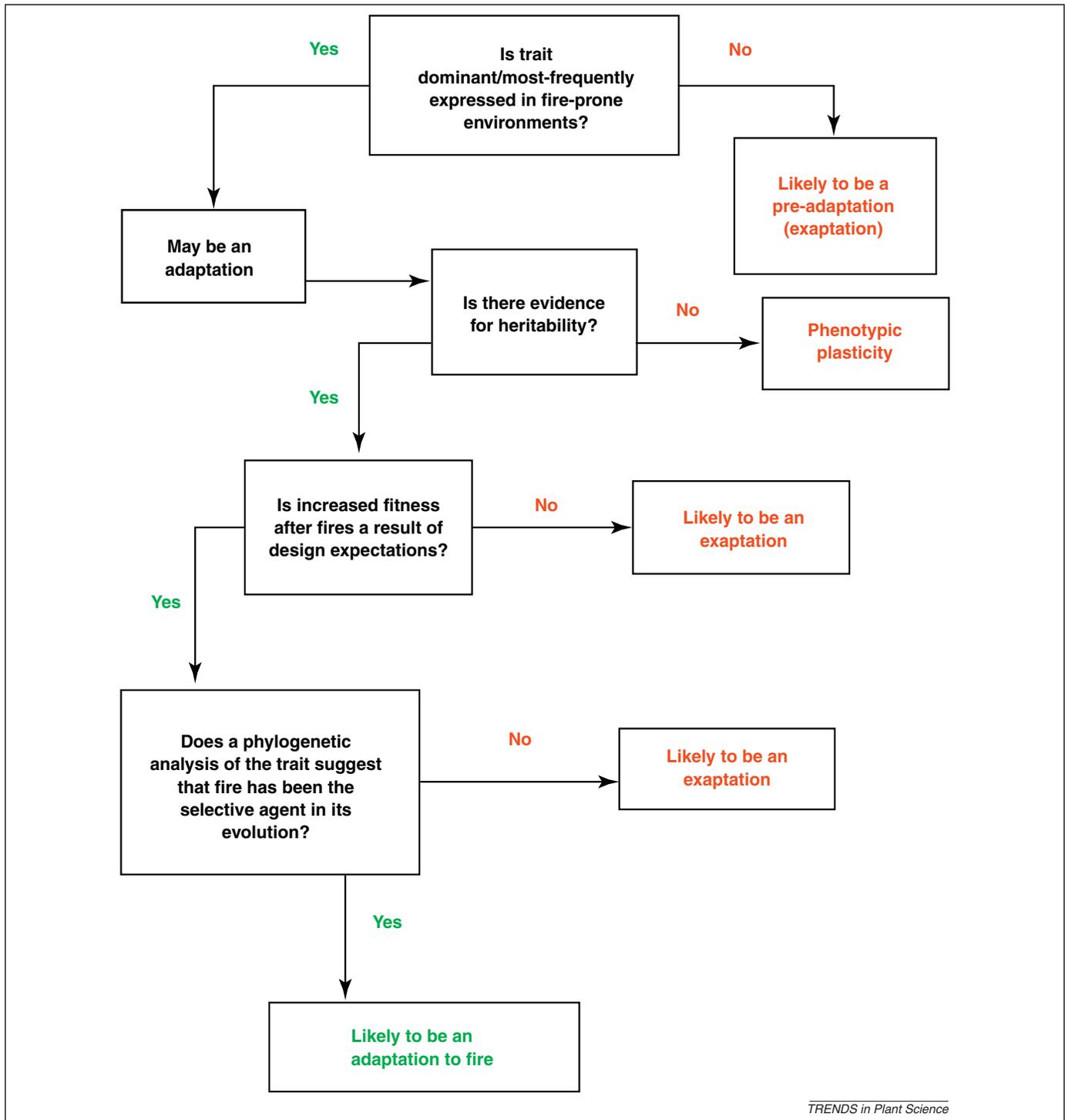
Figure 1. Schematic flow chart illustrating the interrogative procedure used to classify putative fire-adaptation traits in Mediterranean ecosystem plants. 'Exaptations' are defined in [42] as 'features that now enhance fitness but were not built by natural selection for their current role'.

the evolution of woody fruits. It is not possible to separate fire and nutrient status as factors in the evolution of serotiny [28,54] but, as with resprouting, the available evidence suggests that fire has not been the sole selective factor responsible for its evolution.

Physical dormancy
Physical dormancy (PY) ('hard-seededness') is another trait suggested as a response to fire that shows phylogenetic clustering in Mediterranean plant communities [66].

The defining trait of species with PY is having a water-impermeable seed coat that is maintained in this condition owing to the presence of tightly packed palisade layers impregnated with water-repellent substances [67]. Seeds, or indehiscent fruits, with this trait have so far been described in at least 16 plant families [68], with more likely to be discovered [69].

The treatment(s) required for switching a seed from water impermeable to water permeable are generally species specific and vary from acid scarification, hot water, dry

Figure 2. Exaptations or adaptations in fire-prone environments? **(a)** An example of epicormic sprouting in the Bald Island marlock, *Eucalyptus conferruminata*, following a violent wind storm rather than fire. **(b)** A fossil *Banksia archaeocarpa* cone showing apparently woody follicles from a 40-million-year-old Oligocene deposit in the Kennedy Range, 90 km east of Carnarvon in Western Australia. **(c)** Flowering in the grasstree, *Kingia australis*, a few months after fire. **(d)** Seedling recruitment of *Banksia* woodland species in the second year from non-treated re-spread topsoil following sand mining. Reproduced, with permission, from Ken McNamara and [41] (c) and Deanna Rokich (d).

heat, ethanol exposure, cold stratification followed by alternating (spring) temperatures, mechanical scarification, percussion and alternating wetting– drying cycles [70]. Heat has often been viewed as a triggering mechanism, which led to the perception of an evolutionary relationship between germination of PY species and fire [71–73]. Nevertheless, when viewed across all PY taxa, there appears to be little evidence to support this contention. The diversity of plant groups with PY species and the habitats that they occupy, including aquatic, temperate deciduous forests, tropical evergreen rainforests, deserts, Mediterranean scrublands, tropical savannahs and alpine, argue against fire as the principal selective factor for PY [70]. The many and varied specific cues that stimulate dormancy loss under natural conditions also argue against fire *per se* as the driving selective factor in the evolution of the trait.

Most species also respond more effectively to moist heat rather than to the dry heat that is characteristic of a wildfire. In addition, the soil temperatures that have been shown to break PY can be as low as 40 °C [70]. Most species show marked dormancy loss when exposed to temperatures between 40 and 70 °C; that is, temperatures that can readily be reached during extreme summer heat waves in Mediterranean ecosystems [74,75].

Physical dormancy is a phylogenetically widespread trait, occurring in 15–20% of extant flowering plant orders [68]. For many ecosystems in which PY species have been observed, fire is not a prominent factor and several of these ecosystems would be considered to comprise fire-sensitive species. All nine plant orders in which PY occurs, manifest the trait during the Eocene–Oligocene (55–38 MYA), during phases of climatic drying and cooling, and PY might

have evolved from the key trait of persistence within the soil seed bank during times of unfavourable conditions [68]. Viewed in this context, the mass recruitment commonly observed in several PY species following a wildfire can be seen as a clear case of exaptation rather than adaptation to fire.

Post-fire flowering

Post-fire flowering is noticeable in some plants occupying Mediterranean ecosystems (Figure 2c). 'Pyrogenic' flowering was identified in nine species from a total of 429 in south-western Australian shrublands and in seven out of 83 species from a small part of this region with obligate fire-stimulated flowering [76]. These encompassed a range of clonal geophytes, orchids and asparagoid monocots, including Iridaceae, and eudicot sundews (*Drosera*) [77], with the phenomenon probably involving a response to ethylene [37]. Annuals with deeply dormant seed banks have also been identified as 'fire endemics' in California ecosystems [78] in that they germinate, flower prolifically and then retreat to the soil seed bank within one or two years after fire [75]. However, despite a richer annual flora, no such 'fire endemics' have been reported from the Mediterranean basin. Flowering is not an adaptation to fire if it can be shown that equivalent flowering (and recruitment) can be induced by other forms of disturbance that will have occurred widely and frequently in the pre-fire past. Obligate fire-stimulated flowering implies that other forms of damage do not occur or have no effect and so can be considered an adaptation to fire (assuming that the criteria of design, heritability, natural selection and advanced phylogeny are met, although most of these aspects remain unexplored). There have been few studies, however, of socalled obligate post-fire flowering species. The phylogeny of fire-stimulated flowering is also largely unknown in detail, although parallel evolution in several independent lineages has been demonstrated in at least one species complex [79].

Smoke-induced germination

At first glance, the discovery that smoke, rather than heat or ash, is the primary agent responsible for stimulating germination following fire, would seem to provide strong evidence that many species (estimated to be at least 2500 [80]) are not only adapted to fire in the environment, but also have an obligate requirement for smoke that could only come from fire. However, evidence now points to a different scenario. Smoke is the primary agent responsible for cueing germination in a phylogenetically and geographically-diverse range of species from both fire-prone and non-fire-prone environments [80,81]. Many smoke-responsive species, including lettuce, celery, corn, tomato and red rice, are not known from fire-prone communities [80]. Succulent Karoo species in the Aizoaceae (Mesembryanthemaceae) exhibit enhanced seed germination in response to the application of smoke, yet the habitat is unable to carry fire because of the high water content of the dominant succulent shrubs [82].

The production of ethylene gas, which can stimulate germination, is initially elevated in post-disturbed soils and it is possible that the agent in smoke responsible for cueing germination from the soil seed bank is also a by-product of elevated microbial oxidation of soil organic matter. Physical disturbance of soils in fire-prone ecosystems in Western Australia can result in astonishing germination responses akin in most respects to the composition of the post-fire flora (Figure 2d). Fire breaks, road cuttings and most forms of physical disturbance of soils and gap creation in natural vegetation will result in prolific germination responses from the soil seed bank [80]. The responsible chemical in smoke, karrikinolide [80], belongs to a class of compounds known as butenolides [81,83,84]. It is postulated that these can be by-products of microbial activity in soil in the same way that other naturally produced germination agents, such as nitrate, are products of microbial activity in soils [85,86]. Although non-fire release of karrikinolide in soil has yet to be detected, the strong correlation between physical disturbance and smoke-stimulated germination suggests that karrikinolide can also be a product of elevated organic matter decay by microorganisms [80]. The phylogenetic spread of species responding to karrikinolide is so wide, encompassing major clades from the eudicots to monocots, that this trait probably was an early development in the evolution of angiosperms, supporting the concept that organic matter decay rather than fire was the primary force in the development of smoke-mediated germination. As fire frequency increased from the mid-Cenozoic to the present, species with an existing germination response to karrikinolide would have been pre-disposed (exapted) to survive the transition to a post-fire contemporary scenario in which seeds respond to gap creation and physical disturbances of the soil, or to smoke resulting from fire.

Flammability

Flammability has been suggested as a trait that was selected in fire-dependent communities, in that such communities might burn more readily than non-fire-dependent communities because natural selection has favoured attributes that make them more flammable [87]. Flammability varies among plant parts, species and communities, reflecting differences in moisture content, carbon compounds (e.g. cellulose, lignin and terpenoids), volatile compounds, leaf thickness, surface area:volume ratio, particle density and the retention of dead branches [88,89]. Boreal forests, eucalypt woodlands, sclerophyll shrublands, grasslands and savannahs could all be classed as flammable ecosystems, with fire potentially promoted by the physical and chemical attributes of their component species [40].

It has also been argued that many characteristics associated with flammability are probably the indirect result of selection for other traits that are important to fitness, including herbivore deterrence, water-use efficiency and nutrient retention in moisture- and nutrient-limited systems [90]. Others have also criticised the idea on the grounds that flammability is an emergent property of communities rather than of individuals [91]. A simulation model was used to test whether a flammable ('torch') mutant could invade an ancestral, less-flammable ('damp') population and it was found that flammability was favoured only if fire killed the neighbouring plants, and there was an additional fitness advantage associated with

the flammable plant type [92]. Other simulation models suggest that the evolution of flammability in one or more species within a fire-prone community would drive selection of traits in those, and other (non-flammable), species that increased their capacity to cope with fire [89,93]. These models suggest that flammability acts as a 'niche-constructing' trait that modifies the local environment to the benefit of flammable plants [40,94]. There is no experimental evidence, however, to support the notion that flammability has evolved in fire-prone communities and the case is based entirely on theoretical models. It is thus debatable whether flammability represents an adaptation to fire or whether it is simply a trait (or suite of traits) indirectly linked to other functional attributes and trade-offs that optimise plant species fitness in fire-prone environments. High levels of flammability also increase rates of nutrient cycling in environments where the speed of decomposition can otherwise be potentially limiting [95]. Some traits associated with flammability are also found in systems where fire is uncommon: for example, divaricate shrubs are common in the New Zealand flora, and are speculated to have evolved in response to browser pressure (by *Moa*, now extinct flightless birds) and or climatic factors (e.g. cold-induced photoinhibition) [96].

Conclusions

Our review of the literature suggests that traits commonly accepted as 'fire adaptations' of Mediterranean-climate plants have more complex origins and that environmental factors other than frequent fire have promoted their evolution [97]. Traits such as resprouting, serotiny, physical dormancy, facultative post-fire flowering and smoke-induced germination can all enhance survivorship and fitness under certain fire regimes, but these should be considered as exaptations rather than adaptations (Table 1). This selective advantage is readily negated, however, in plant communities in which fires occur with a frequency higher than the time taken to flower and set seed for the slowest-maturing species in that community. The impact of fires on communities is also a function of their intensity and the season in which they occur, both of which can override any inherent advantages flowing from morphological and physiological exaptations. Climate change, with increasing temperatures and declining rainfall predicted in Mediterranean biomes in the coming decades, is likely to exacerbate the current loss of biodiversity in these regions and will present a major challenge for environmental managers also charged with protecting human life and property [98]. We question the widespread assumption that Mediterranean-ecosystem

Table 1. Adaptation–exaptation matrix for putative-adaptation traits of plants in fire-prone Mediterranean environments

Test	Trait					
	Resprouting	Serotiny	Physical dormancy	Post-fire flowering	Smoke-induced germination	Flammability
Design engineering	Dormant buds stimulated to sprout once foliage removed	Heat-resistant resin-sealed cones or fruits; resin melts at 40 °C	Water-impervious seed or fruit coat that becomes water permeable (usually at the water gap only) in response to specific environmental cues	Resprouters or geophytes with shoot apex sensitive to heat or smoke	Respond to the butenolide chemical, karrikinolide, in smoke	Retention of scleromorphic leaves and bark and presence of flammable oils and resins
Heritability	Confirmed in eucalypts: widespread phenotypic plasticity	Confirmed in some genera of Proteaceae; phenotypic plasticity widespread	Highly probable but untested; cultivated species remain hard seeded	Probable but untested; no variation within species known	Confirmed in many groups; cultivated species retain smoke reactivity	Confirmed in many groups; phenotypic plasticity in some traits; cultivated species retain trait
Natural selection	Increases fitness after any damage to canopy	Selective advantage in nutrient-limited environments	Selective advantage in response to highly seasonal environments or where episodic seedling recruitment favoured	Increases fitness after fire only if seedlings survive	Selective advantage after fire and where episodic seedling recruitment favoured	Selective advantage in nutrient-limited or herbivore-prone environments
Phylogeny	Multiple origins, some apparently pre-dating Neogene fires, confirmed by molecular phylogenetic analyses	Multiple origins in conifers to flowering plants; probably post-dates onset of Tertiary drying and might be an evolutionary response to low soil fertility	Multiple origins: occurs in 16 different families (from nine orders) – one monocot, and 15 eudicot; likely to have evolved during the Eocene– Miocene (55–38 MYA) but pre-dates widespread fire	Multiple origins in cycads to angiosperms; pyrogenic flowering might have evolved from post-drought growth-flush	Multiple origins among flowering plants and probably pre-dates onset of Tertiary drying	Multiple origins in cycads to angiosperms; sclerophylly pre-dates onset of Tertiary drying; terpenes, oils and resins deter herbivores
Restricted to fire-prone environments?	No	No	No	No	No	No
Conclusion	Exaptation	Exaptation	Exaptation	Possible adaptation if obligate; exaptation when facultative	Exaptation	Exaptation

species are adapted to fire and suggest that caution is required in the use of frequent prescribed burning if ecosystem degradation and plant extinctions are to be averted as a result of the practice.

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