Fire as an evolutionary pressure shaping plant traits

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Traits, such as resprouting, serotiny and germination by heat and smoke, are adaptive in fire-prone environments. However, plants are not adapted to fire *per se* but to fire regimes. Species can be threatened when humans alter the regime, often by increasing or decreasing fire frequency. Fire-adaptive traits are potentially the result of different evolutionary pathways. Distinguishing between traits that are adaptations originating in response to fire or exaptations originating in response to other factors might not always be possible. However, fire has been a factor throughout the history of land-plant evolution and is not strictly a Neogene phenomenon. Mesozoic fossils show evidence of fire-adaptive traits and, in some lineages, these might have persisted to the present as fire adaptations.

Adaptation to fire

In a recent publication [1], S. Don Bradshaw *et al.* raised concerns about the widespread application of prescription burning in hotspots of biodiversity, and we share those concerns that too frequent prescription burning can negatively affect biodiversity and ecosystem processes. However, their paper used this issue inappropriately as a springboard for speculating on the evolution of plant traits, confusing issues of adaptive traits and adaptations, and missing the fact that different fire regimes can select for very different plant traits. No species is 'fire adapted' but rather is adapted to a particular fire regime, which, among other things, includes fire frequency, fire intensity and patterns of fuel consumption [2]. Species that exhibit traits that are adaptive under a particular fire regime can be threatened when that regime changes. For example, many of the species-rich Mediterranean-type climate (MTC) shrublands are resilient to periodic high-intensity crown fires at intervals of several decades or more. However, when the fire frequency increases, species can be rapidly lost [3,4]. Bradshaw *et al.* [1] incorrectly equate adaptation to fire as adaptation to frequent fires and are not justified in inferring that frequent prescription burning is an 'adaptationist view'. Here, we discuss those traits with ap-

parent adaptive value in fire-prone environments and the extent to which we can demonstrate that they are adaptations to fire. We also address the question of what fire-adaptive traits and fire adaptations can tell us about fire management.

Adaptive traits

Adaptive traits are those that provide a fitness advantage in a given environment. There are many plant traits that are of adaptive value in the face of recurrent fire and these vary markedly with fire regime. For example, North American conifers (Coniferophyta) subject to frequent lightning-ignited fires have thick bark, which functions to protect the living tissues from heat damage during surface fires; they also self-prune lower dead branches, which ensures a gap in fuels between the dead surface litter and live canopy. Thick bark and self-pruning are adaptive in this surface fire regime. At higher latitudes as productivity declines, lodgepole and jackpine forests lack the potential for growth sufficient to keep the canopy away from surface fuels, leading to a crown fire regime; traits change to thin bark, retention of lower dead branches, and serotinous cones that synchronously release seeds following such stand-replacing fires [5,6]. High-intensity crown fires are not stand replacing in Australian eucalypt forests as most of the trees, big and small, resprout epicormically along the length of the bole, replacing the tree canopy within a year of such fires. In MTC shrublands subject to crown fires, many species restrict seedling recruitment to the immediate post-fire years, arising from previously dormant soil-stored seed banks or synchronous seed release from serotinous fruits [2]. These traits are adaptive in fire-prone environments and are key to providing resilience to specific fire regimes.

Adaptive traits as adaptations to fire

A key evolutionary question about fire-adaptive traits is whether they represent fire adaptations, defined as traits that originated in response to fire. Fire-adaptive traits that originated in response to some other environmental factor, and then were appropriated for their value in fire-prone landscapes, are 'exaptations' [7]. Distinguishing between

Box 1. Adaptations and exaptations

An adaptive trait enhances fitness in a defined habitat and adaptation is the process of acquiring adaptive value by the natural selection of new variants [28,29]. Exaptation defines an adaptive trait with a particular contemporary function, but one that was previously shaped by natural selection for another function [7,25]. However, exaptations can become adaptations when natural selection acts and reshapes the trait.

We distinguish five scenarios of change in a trait state (Figure I). An adaptive trait might not change through time regardless of the selective environment (scenarios 1 and 2 in Figure 1). Such traits cannot be described as adaptations to the current selective environment as there is no evidence that natural selection shaped this trait. Other adaptive traits that were shaped by natural selection under a previous evolutionary pressure, but not under the current (fire-prone) environment (scenario 3) would be adaptations to previous evolutionary pressures and exaptations to the current environment.

Fire adaptations are those adaptive traits in which natural selection is acting under the current fire-prone environment to shape the trait, and it is independent of how long this pressure has been present (scenarios 4 and 5). In some cases (scenario 4b) selective pressures can cause traits to revert to a former state and, when conditions change, fire might replace the former selective pressure.

It is crucial to note that our interpretation of adaptations and exaptations depends on current understanding of the entire evolutionary scenario. If the knowledge base only extends back to the second half of the time period in Figure I, it is not possible to distinguish between different scenarios. This problem is inherent in retracing the history of most traits.

Plants can have traits of adaptive value under specific fire regimes, but their origin can follow different evolutionary scenarios. For instance, one might find that resprouting is highly adaptive in some tropical forest trees that are suddenly cast into a fire-prone environ-

ment owing to anthropogenic impacts, but this adaptive trait might not have arisen in response to fire (scenarios 1, 2 or 3). By contrast, it is plausible that some fern lineages have had a long association with fire and resprouting might follow scenario 5 [2]. MTC shrub lineages resprouting from lignotubers might best be interpreted in terms of scenario 4a, an old origin of resprouting in response to diverse factors but reshaped later by fire.
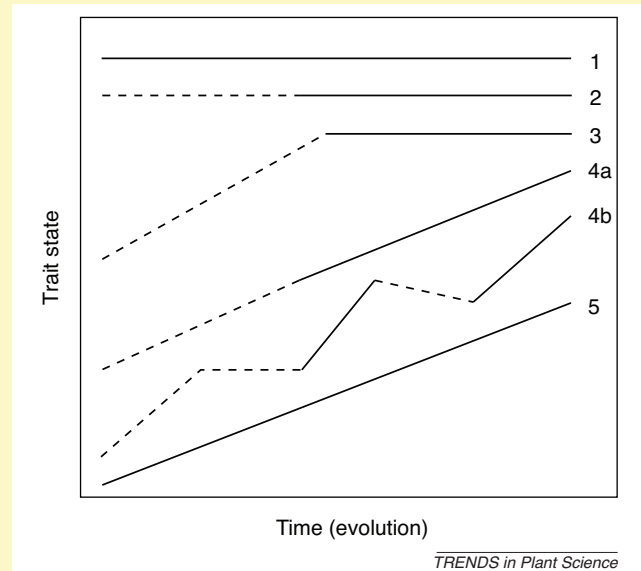

Figure I. Evolutionary scenarios of change in a trait state (continuous lines can be interpreted as representing a period in which fire acted as an evolutionary pressure and dashed lines a period with a different selective environment).

adaptations and exaptations is a high bar that is difficult to demonstrate as there is not a simple dichotomy between paths leading to adaptations and exaptations (Box 1).

There are several flaws in Bradshaw *et al.*'s analysis [1] of fire adaptations. One is the misconception that fire is a recent Neogene [23 million years ago (Ma) to the present] phenomenon; however, fire has been part of Earth system since the Silurian origin of land plants 443 Ma [8]. It was globally important through much of the Mesozoic (251–66 Ma) [9–11] and, by the Late Cretaceous (100–66 Ma), some taxa were already specialized for fire-prone environments [12,13]. In the highly diverse Australian *Eucalyptus,* epicormic resprouting regenerates forests rapidly after high-intensity crown fires and phylogenetic studies support an early Tertiary origin (62 Ma) [14].

Resprouting

Another misconception in [1] is the belief that vegetative resprouting cannot be an adaptation to fire because it is found in non-fire-prone habitats. There are many forms of resprouting and it is expected that different resprouting types might have appeared in different lineages in response to different evolutionary pressures. No one has ever argued that all instances of resprouting are adaptations to fire; however, it is still an open question as to whether post-fire resprouting originated in response to fire in some lineages [2]. For example, resprouting is coupled with a lignotuber in various lineages (Figure 1), and the tight coupling of this ontogenetic trait with fire-prone environments [15] suggests that it is a fire adaptation.

Serotiny

Serotiny as an adaptation to fire has also been questioned by [1] because it 'probably post-dates onset of Tertiary drying and might be an evolutionary response to low soil fertility'. However, phylogenetic studies in the Australian genus *Banksia* conclude that fire-adaptive traits, and serotiny in particular, originated much earlier and they place their origins in the Paleocene (60 Ma) [16].Bradshaw *et al.'s* [1] linking of serotiny to infertile soils follows Stephen D. Hopper's [17] contention that low fertility soils, such as those widespread in Western Australia and South Africa, are derived from ancient Cretaceous substrates. Hopper argues that this ancient association with infertile soils is the primary factor driving the evolution of plant traits in these shrublands. However, plants persist in a multivariate environment stressed by not only soil fertility, but also climate and potentially fire, not to mention biotic interactions. Indeed, low fertility soils select for traits such as small sclerophyll leaves and provide well-drained substrates, both of which increase the likelihood of fires. In our view, evolution on these substrates is driven by a combination of geology, climate and fire [2]. Singling out one of these factors as the only determinate of trait evolution handicaps our ability to understand plant evolution.

Serotiny is tied to crown fire regimes and, in the absence of fire, there is relatively little successful recruitment, making it clearly of adaptive value in these systems. However, demonstrating that serotiny is an adaptation that evolved in response to fire, is another matter. Bradshaw *et al.* [1] conclude that because serotiny is concentrated in the two

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Figure 1. Resprouting after fire from a lignotuber in the California chaparral shrub *Adenostoma fasciculatum*. It is one of a wide diversity of resprouting modes in the plant kingdom. These basal burls are an ontogenetic trait that forms early in development and, in this respect, differ from swollen basal burls initiated in response to cutting or burning observed in many woody plants.

southern hemisphere MTC regions characterized by low soil fertility, it arose in response to soil infertility. However, they conflate two separate issues: the reproductive strategy of a single post-fire pulse of seedling recruitment and aerial versus soil seed storage.

Sorting out the adaptive value of serotiny requires consideration of ultimate versus proximal causation. Four of the five MTC regions have species that restrict seedling recruitment to a post-fire pulse; the reason for this is that fires are a predictable ecosystem process and the removal of the dense shrub canopy by fires provides superior resources for the recruitment of some species. The proximal mechanism of how species do this varies with the region; in two of the MTC regions, dormant seeds are

stored in the soil and serotiny is rare, whereas in two other regions, many dominant shrubs store seeds in serotinous fruits in the shrub canopy. We argue that low soil fertility in South African fynbos and Western Australian heathlands has selected against soil storage in favor of aerial storage because high-nutrient seeds are subject to more intense predation when exposed on the soil surface (Figure 2). Higher fertility soils in northern hemisphere MTC shrublands of California and the Mediterranean Basin allow shrub taxa to capitalize on the advantages of soil-stored seed banks, which includes a capacity for accumulating larger seed banks and a greater resilience to unpredictably long fire-free intervals. The one MTC region not included here is central Chile and the shrublands there
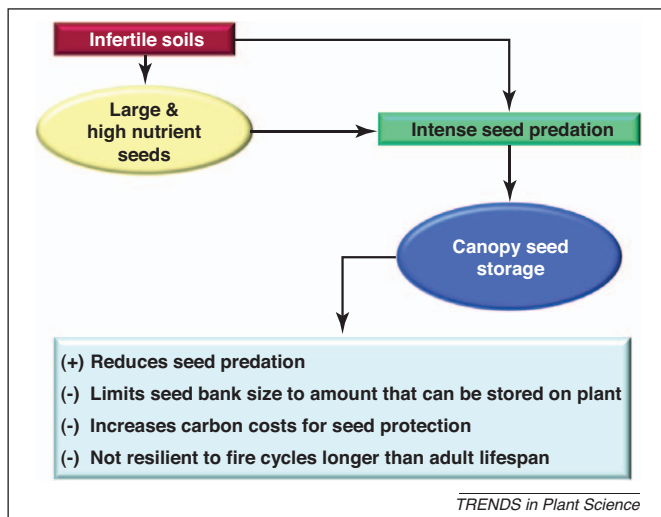
Figure 2. Model of factors selecting for serotiny and costs and benefits of serotiny. Low soil fertility is hypothesized to select for larger seeds with higher nutrient stores to enhance seedling survival. Predation pressure is heightened owing to the lower nutrient stores in most plant tissues in the community and this selects for canopy seed storage. Modified, with permission, from [2].

lack both, a post-fire pulse of seedlings and serotiny, which is interpreted as a result of the diminution of natural fires since the late Miocene, owing to the rise of the Andes that block summer lightning storms [2].

Daniel I. Axelrod [18] also expressed skepticism about the role of fire in the evolution of serotiny in northern hemisphere pines, in part because he understood fire to be an anthropogenic factor and unknown throughout land plant evolution. He proposed that drought was a more probable factor selecting for serotiny. We argue that if drought were a stronger driving force than fire, it would be more likely to select for a bet-hedging strategy in which seed dispersal was spread out over multiple years, rather than all seeds being dumped immediately after fire, when there is a significant probability that it could be a dry year.

Bradshaw *et al.* [1] suggest rainfall predictability is a more probable selective force behind the evolution of serotiny than is fire. They contend that winter rainfall is less predictable in the two northern hemisphere MTC regions and, thus, soil seed storage, which could spread germination over multiple years, would be preferable to serotiny. However, northern hemisphere MTC shrublands with soil stored seed banks do not exhibit seed carryover after fire and, just like their southern hemisphere serotinous cousins, they too have a single pulse of seedling recruitment after fire. Another weakness of this theory is the likelihood that subtle differences in rainfall predictability between the northern and southern hemisphere MTCs have fluctuated greatly since the Tertiary origin of serotiny [2].

Heat-shock triggered germination
We agree with Bradshaw *et al.* [1] that the physical dormancy of seeds has had multiple origins; however, because of this, Bradshaw *et al.* cannot use the presence of physical dormancy in non-fire-prone landscapes as evidence that it is always an exaptation in fire-prone environments. The possibility remains that, in some plant lineages, physical dormancy originated in response to fire and, in other lineages, it was appropriated by species suddenly cast into

a fire-prone setting. Ultimately, however, sorting out adaptation from exaptation might be extremely challenging in some lineages (Box 1). For example, the Fabaceae are well known for being 'hard seeded', meaning that they produce outer integuments of densely packed palisade cells and waxy cuticles that make the seed impermeable to water until scarified by heat or other abrasive agent. However, not all Fabaceae seeds are water impermeable. In California grasslands, there are species of *Lupinus, Astragalus* and *Trifolium* that germinate every spring without any apparent physical scarification, but many of these same species also occur in adjacent chaparral and have deeply dormant seeds that seldom germinate until exposed to heat shock from a fire. Although hard seededness in the Fabaceae is widespread, it appears to wax and wane with local conditions and selection for or against physical dormancy depends on local conditions (scenario 4b in Figure I, Box 1). When derived from grassland ecotypes, deeply dormant chaparral seeds clearly reflect selection for dormancy, despite the fact that the integument structures are a feature of parallel evolution in the Fabaceae. We hypothesize that, although the seed coat structures *per se* might have originated in response to any number of factors, their precise organization into a heat-shock-dependent seed is an adaptation to fire in some situations.

Germination triggered by combustion chemicals
Smoke-induced germination is a trait that, on the surface, would seem to be a clear adaptation to fire, but it is more complicated than appears at first glance. In most MTC ecosystems, there are species with dormant seed banks that only germinate in the first growing season after fire, and can be shown experimentally to only germinate in response to smoke or charred wood extracts. In these cases, smoke-stimulated germination is clearly an adaptive trait. Whether the origin of this adaptive trait represents an adaptation evolved in response to fire remains an open question.

The relatively recent discovery of a butanolide compound (karrikinolide) in smoke that will trigger germination of a vast array of species, many that lack any ecological connection with fire, has raised questions about the selective role of fire in MTC ecosystems [1]. In an apparent quest for the 'unifying theory' of seed germination, several investigators [19,20] have focused intensively on this compound and ignored reports of other compounds in smoke that trigger the germination of MTC species with fire-dependent seedling recruitment [21] and other negative evidence for butanolide being a universal signal [22]. All of the work to date on karrikinolides in germination involves lab studies and essentially nothing is known about its ecological role in fire-prone environments. That this compound triggers germination at levels of parts per trillion [19] raises important ecological questions. If it is the universal germination trigger, then how do MTC soil-stored seed banks remain dormant for decades in the face of such extraordinary sensitivity?

Bradshaw *et al.* [1] do provide a refreshing new theory about the Mesozoic origin of smoke-stimulated germination initially in response to organic matter decay. However, this theory is subject to all of the same criticisms that they

level against fire adaptations. The only potential evidence they present is the observation that karrikinolide-stimulated germination is widespread throughout all major clades of angiosperms and, thus, is a feature of basic seed metabolism that possibly originated during the early evolution of angiosperms. In their view, only organic matter decay and not fire has been present since early angiosperm evolution, but this is not supported by the vast literature on Paleozoic and Mesozoic fires [8–13].

However, assuming for argument's sake that karrikinolides evolved in response to some other environmental factor and are the only compounds in smoke that play a role in germination of species with strict post-fire recruitment, the fact that karrikinolides might have played a role in the evolution of seed metabolism of all angiosperms does not preclude an adaptive role for species that currently use it to cue germination to post-fire conditions. Given that most species seem to be sensitive to karrikinolides, yet only a small subset of MTC species have the capacity to remain dormant and then cue germination to the immediate post-fire environment, it seems feasible that these MTC species might have evolved some level of gene regulation controlling the functioning of karrikinolides in germination. This would constitute a fire adaptation.

Flammability as a fire adaptation
Evolution of flammability implies selection for traits that increase the frequency or intensity of fires. The idea is largely dismissed by Bradshaw *et al.* [1] because of their contention that it is based only on theoretical models. However, studies of trait origins are not readily amenable to experimentation and evolutionary comparative methods are among out best available tools. We believe it is a viable hypothesis that species restricting reproduction to a single post-fire pulse of recruitment might be under selective pressure to affect fire activity in ways that enhance their reproductive success [23]. In crown fire ecosystems, traits that could enhance flammability include small leaves, volatile compounds and retention of dead leaves and branches, to name just a few. There are empirical data showing that trait distribution in some genera and communities is consistent with this hypothesis [6,24,25]. Also consistent with this hypothesis is the observation that, within fire-prone communities, species with post-fire seedling recruitment have the most flammable canopies [2,24]. This could be selected owing either to greater inhibition of neighbors [23] or to enhanced seedbank survival by limiting deposition of dead fuels on the soil surface [26]. We acknowledge that there is limited evidence that characteristics contributing to enhanced flammability actually enhance fitness (i.e. are adaptive) in fire-prone environments, let alone that they represent an adaptation evolved in response to fire. However, evidence is likewise lacking that, in species from crown fire regimes, traits such as retention of dead branches serve another function, which evolved in response to a non-fire-related pressure.

Conclusion
Bradshaw *et al.* [1] raise some legitimate questions about traits that are interpreted to be adaptive in fire-prone environments. However, pointing out gaps in the ability

to trace the origin of many traits to a fire origin is not equivalent to demonstrating these traits arose in response to other environmental factors. Contrary to their assertion, Bradshaw *et al.* have not demonstrated that any fire-adaptive trait has a 'more complex origin' or that any single trait arose in response to some other factor. In several cases, they have rejected a possible adaptive role for traits by defining them in very broad terms so that, across the plant kingdom, the traits appear in many different selective environments. More importantly, trait evolution is shaped by many forces that act throughout the history of the trait, and it is naive to think that each trait should be related to a single evolutionary pressure.

One of the unfortunate aspects of their paper [1] is that it uses evolutionary arguments to draw conclusions about appropriate fire management decisions. The assertion is made that plants with traits interpreted as exaptations perform worse in the face of recurrent fire than do those that represent adaptations originating in response to fire. However, the concept of adaptation versus exaptations only refers to the origin of the trait (Box 1), not to the current role. Thus, there is no reason to believe that plants with exapted fire traits perform worse than do plants with fire adaptations and the authors do not provide any support for such a view. Resource managers and other conservationists are interested in how plants perform under current fire regimes and mostly regard the evolutionary origin of traits as irrelevant to management decisions. It is possible for managers to predict the behavior and dynamics of plants under different alternative fire regimes on the basis of their functional traits [27], without regard to their origins.

References
1 Bradshaw, S. *et al.* (2011) Little evidence for fire-adapted plant traits in Mediterranean climate regions. *Trends Plant Sci.* 16, 69–76
2 Keeley, J.E. *et al.* (2012) *Fire in Mediterranean Climate Ecosystems: Ecology, Evolution and Management*, Cambridge University Press
3 Bradstock, R.A. (2008) Effects of large fires on biodiversity in southeastern Australia: disaster or template for diversity? *Int. J. Wildland Fire* 17, 809–822
4 Keeley, J.E. *et al.* (2009) *Ecological Foundations for Fire Management in North American Forest and Shrubland Ecosystems*, USDA Forest Service, Pacific Northwest Research Station
5 Keeley, J.E. and Zedler, P.H. (1998) Evolution of life histories in *Pinus*. In *Ecology and Biogeography of Pinus* (Richardson, D.M., ed.), pp. 219–250, Cambridge University Press
6 Schwilk, D.W. and Ackerly, D.D. (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94, 326–336
7 Gould, S.J. and Vrba, E.S. (1982) Exaptation – a missing term in the science of form. *Paleobiology* 8, 4–15
8 Pausas, J.G. and Keeley, J.E. (2009) A burning story: the role of fire in the history of life. *Bioscience* 59, 593–601
9 Scott, A.C. (2000) Pre-Quaternary history of fire. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 164, 297–345
10 Bond, W.J. and Scott, A.C. (2010) Fire and the spread of flowering plants in the Cretaceous. *New Phytol.* 188, 1137–1150
11 Falcon-Lang, H.J. (2000) Fire ecology in the Carboniferous tropical zone. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 164, 355–371
12 Watson, J. and Alvin, K.L. (1996) An English Wealden floral list, with comments on possible environmental indicators. *Cretaceous Res.* 17, 5–26

13 Collinson, M.E. *et al.* (1999) Charcoal-rich plant debris accumulations in the Lower Cretaceous of the Isle of Wight. *Engl. Acta Palaeobot.* (Suppl. 2), 93–105

14 Crisp, M.D. *et al.* (2011) Flammable biomes dominated by eucalypts originated at the Cretaceous–Palaeogene boundary. *Nat. Commun.* 2, 1–8

15 Canadell, J. and Zedler, P.H. (1995) Underground structures of woody plants in mediterranean ecosystems of Australia, California and Chile. In *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia* (Arroyo, M.T.K. *et al.*, eds), pp. 177–210, Springer

16 He, T. *et al.* (2011) *Banksia* born to burn. *New Phytol.* 191, 184–196

17 Hopper, S.D. (2009) OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant Soil* 322, 49–86

18 Axelrod, D.I. (1980) History of the maritime closed-cone pines Alta and Baja California. *Uni. Calif. Publ. Geo. Sci.* 120, 1–143

19 Flematti, G.R. *et al.* (2004) A compound from smoke that promotes seed germination. *Science* 305, 977

20 Van Staden, J. *et al.* (2004) Isolation of the major germination cue from plant-derived smoke. *S. Afr. J. Bot.* 70, 654–659

21 Keeley, J.E. and Fotheringham, C.J. (1997) Trace gas emissions and smoke-induced seed germination. *Science* 276, 1248–1250

22 Downes, K.S. *et al.* (2010) The fire ephemeral *Tersonia cyathiflora* (Gyrostemonaceae) germinates in response to smoke but not the butenolide 3-methyl-2H-furol[2,3-c]pyran-2-one. *Ann. Bot.* 106, 381–384

23 Bond, W.J. and Midgley, J.J. (1995) Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* 73, 79–85

24 Saura-Mas, S. *et al.* (2010) Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. *Int. J. Wildland Fire* 19, 783–794

25 Cowan, P. and Ackerly, D. (2010) Post-fire regeneration strategies and flammability traits of California chaparral shrubs. *Int. J. Wildland Fire* 19, 984–989

26 Gagnon, P.R. *et al.* (2010) Does pyrogenicity protect burning plants? *Ecology* 91, 3481–3486

27 Noble, I.R. and Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43, 5–21

28 Dobzhansky, T. (1968) On some fundamental concepts of Darwinian biology. *Evol. Biol.* 2, 1–34

29 Endler, J.A. (1986) *Natural Selection in the Wild*, Princeton University Press

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