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Opinion

Can plants keep up with fire regime changes through evolution?

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Patterns of fire are rapidly changing across the globe and causing mismatches between plants and their environment. These mismatches have ecological and evolutionary consequences, but the latter are often overlooked. A critical question is whether plant populations can evolve quickly enough to keep up with changing fire regimes. Fire-related traits, such as canopy seed storage with fire-stimulated seed release, vary within species and can enhance fitness and be heritable – the preconditions for adaptive evolution. Here, we develop a framework that recognizes mismatches between traits and fire based on variation within and among conspecific populations and that opens new ways of forecasting environmental changes and conserving plants. Advances in genomics enable evolutionary potential to be estimated even in wild, long-lived plants.

Highlights

Mismatch between plant traits and their environment will reduce survival and reproduction but also increase selection pressure for adaptation.

While mismatch is often studied in the context of climate change, fire-related mismatches merit specific attention, given fire's global nature, rapid shifts, and far-reaching impacts on plants and biodiversity.

Variation in fire-related traits – such as resprouting, serotiny, and bark thickness – is widespread within plant species, from grasses and herbs to shrubs and trees. This intraspecific variation provides fuel for evolutionary adaptation.

Recasting fire-driven evolution as ongoing offers new ways of forecasting contemporary environmental changes, reducing mismatches and conserving plants.

Plants and rapid environmental changes

An important way that fire contributes to global plant diversity is by producing selection pressures on populations [1,2]. Plants have evolved traits, such as fire-released seed dormancy [3,4], resprouting [5,6], **serotiny** (see Glossary) [5,7], and thick bark [8,9], that provide **phenotypes** matched to prevailing **fire regimes** (Figure 1). However, phenotypes that enhance fitness under one fire regime may not enhance survival and reproduction under another [10,11]. Human activity is modifying when, where, and how fires burn [12,13] – directly altering fire impact on plants and indirectly changing the environmental conditions they rely on – and this is putting an estimated 28% of threatened gymnosperms, 19% of threatened legumes, and 18% of threatened monocots at greater risk of extinction [14].

Plant populations can counter modified patterns of fires and associated environmental changes in three main, nonexclusive ways. First, plants can disperse to areas with suitable fire patterns and environmental conditions [15]. Second, they can respond through **phenotypic plasticity** and **epigenetic changes** [16]. Third, plants can adapt by changing their genetic makeup through evolution [17]. Of these, genetically based evolutionary responses are the most likely means for plants to adapt *in situ* to environmental conditions beyond those under which they evolved [18]. While there are observations of rapid evolution in plants under contemporary climatic changes [19], the capacity for plants to adapt to difficult-to-predict changes in fire regimes merits specific attention.

Here we develop the concept of 'trait–fire mismatch,' a type of phenotype–environment mismatch that brings together ecological and evolutionary fire science and supports forecasts of fire-driven environmental changes. We first identify **fire-related traits**, their variation within species, and heritable basis. We then describe how mismatches between traits and emerging fire regimes can reduce plant fitness and lead to selection. Fire science will benefit further from evolutionary insights. Fire-related adaptation in turn reveals how evolutionary changes can occur in response to disturbance.

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Evidence of fire-driven evolution across species

Studies of interspecific variation (variation between species) provide one line of evidence that fire-driven selection acts on plant traits [1,20]. Tree species in fire-frequent savannas have bark that is three times thicker than in fire-infrequent forests, because thick bark insulates vascular tissues from lethal temperatures during fires, preventing topkill or plant mortality [9]. In the genus *Pinus*, comparative research shows that serotiny, involving storage and postfire release of seeds, is more common of species in ecosystems with frequent crown fires; this adaptation enables germination and recruitment when resources are available [21].

Dated molecular phylogenies provide information on how fire has driven the development of traits across species and higher taxonomic levels, including fire-stimulated resprouting, flowering, seed release, and germination [5]. For example, fire likely preceded the evolution of woody cones with fire-stimulated seed release (i.e., serotiny) in the genera *Banksia* (Australia) and *Protea* (Africa) [22]. While variation at the species level and higher taxonomic levels provides insights into fire-driven adaptation, it is intraspecific variation (variation within species) that primarily determines the potential for contemporary adaptive evolution [23].

Variation in fire-related traits within species

Variation in fire-related traits is widespread within and among conspecific populations, spanning life forms including grasses, herbs, shrubs, and trees (Figure 2).

Several studies have identified intraspecific variation in fire-related traits that influence plant survival. Coastal populations of Monterey pine (*Pinus radiata*) in North America have thicker bark in areas with a long history of Indigenous burning and thinner bark on islands where planned fire has been absent or rare [24]. Mediterranean gorse (*Ulex parviflorus*) exhibits higher flammability in fire-prone areas, which, despite reducing mature plant survival, may produce heat shock that breaks seed dormancy and enhances offspring recruitment [25]. Candlestick banksia (*Banksia attenuata*) in southwestern Australia resprout from underground lignotubers in environments with frequent crown fires, while epicormic resprouting occurs in areas with infrequent crown fires – interpreted as a form of plasticity that enhances survival [26].

Fire-related reproductive traits also vary within species. Seeds from fire-exposed populations of tassel heath (*Erica coccinea*) in South African fynbos and common heather (*Calluna vulgaris*) in Norwegian heathlands exhibit strong smoke-induced germination, whereas those from fire-free populations respond more strongly to seasonal temperature cues [27] or lack this response [28]. Jack pine (*Pinus banksiana*) in Canadian forests display high levels of serotiny in areas with frequent wildfires, while populations in less fire-prone areas adopt a bet-hedging strategy, with variation in serotiny supporting recruitment both postfire and during fire-free intervals [7]. In the Mediterranean basin, Aleppo pine (*Pinus halepensis*) reaches age of first reproduction more quickly in populations subject to shorter fire intervals [29].

Intraspecific variation in recolonization traits is less studied than other traits that help plants respond to changing fire regimes [15]. However, within-species variation in traits related to seed dispersal and shifts in dispersal ability occur under other forms of global environmental change [30]. This suggests that fire could also shape recolonization traits, offering a promising area for further research.

Intraspecific variation in phenotypic traits arises from mechanisms acting within and between generations [31], including genetic changes, plastic responses within generations, and cross-generational plasticity including epigenetic effects. These mechanisms differ in how quickly and effectively they drive adaptation [23], making it important to understand the contribution of

Glossary

Epigenetic changes: modifications in gene activity that do not alter the DNA sequence itself. These changes, influenced by environmental factors, can occur in individuals within and between generations.
Fire regime: the temporal and spatial dimensions of recurrent fires and their characteristics.
Fire-related traits: phenotypes that enhance the fitness of organisms subject to recurrent fires.
Genotype: the genetic composition of an organism, including nuclear and extranuclear components.
Heritability: a measure that explains how much variation in a phenotypic trait within a population is due to genetic differences among individuals. Ranges from 0 (all variation due to environmental effects) to 1 (all variation due to genetic differences).
Phenotype: the observable characteristics of an organism, including morphological, physiological, and behavioral characteristics, which can interact with the environment.
Phenotypic plasticity: the ability of genotypes to express different phenotypes, depending on environmental conditions.
Serotiny: the retention of mature seeds in a canopy seedbank, with seed release triggered by environmental cues such as fire.

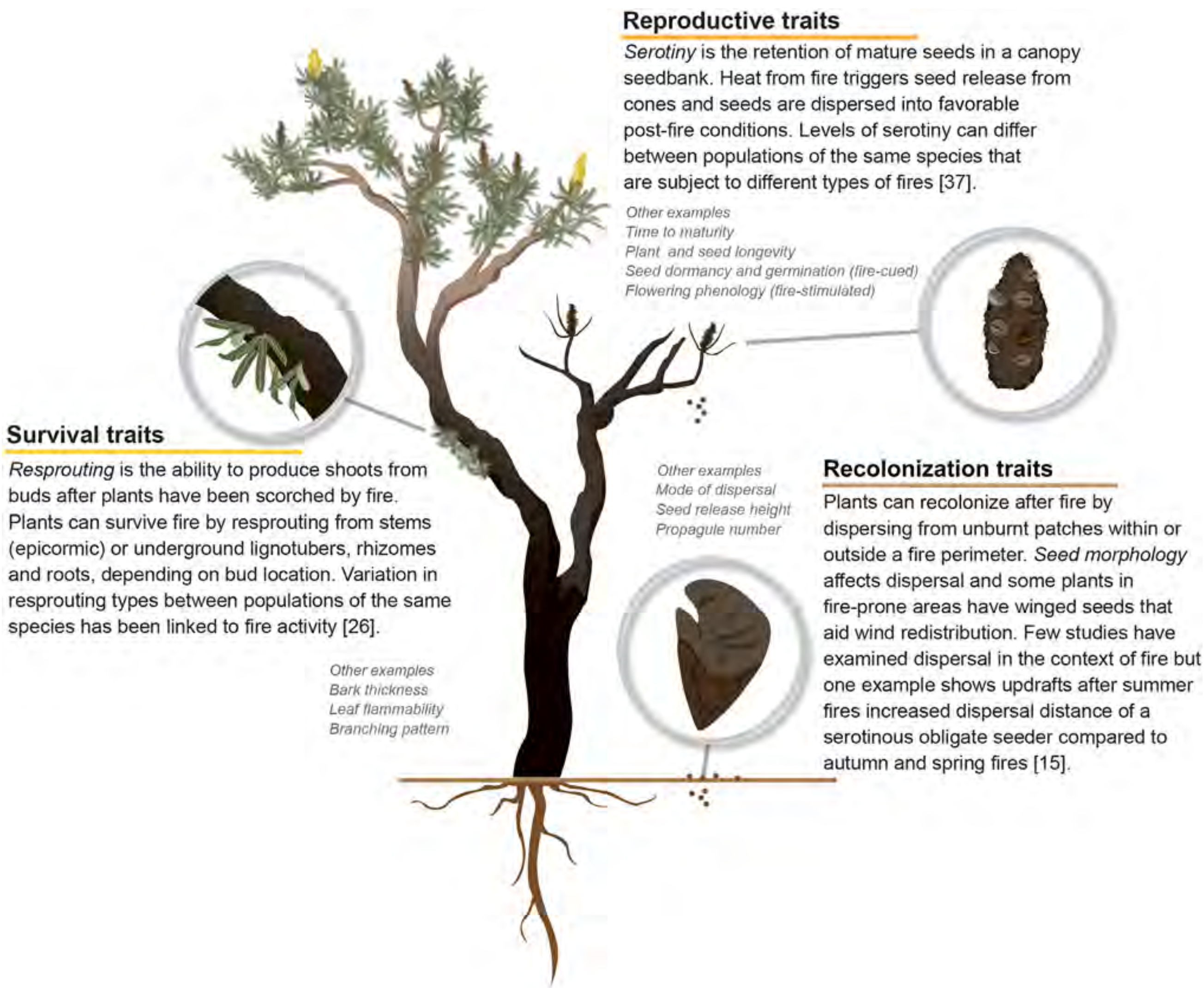

Figure 1. Plant traits through the lens of fire science. Fire-related traits are those traits that enhance the fitness of plants subject to recurrent fires. We distinguish between three groups of traits that shape plant fitness in fire-prone environments – those related to fire survival, postfire reproduction, or recolonization after fire – while shaping conditions under which evolutionary processes operate. Some traits contribute to more than one of survival, reproduction, and recolonization. The graphic is a stylized *Banksia* with the trunk and some stems burnt.

heritable genetic differences, environmental conditions, and cross-generational plasticity to predict plant adaptations to changing fire activity.

Genetic variation in fire-related traits

Several approaches are helping to estimate the genetic component of fire-related intraspecific variation in controlled environments and wild populations and to distinguish the effects of fire from other influences on trait variation.

Common gardens, where plants from different provenances are grown under the same conditions, are one method [32]. Pitch pine (*Pinus rigida*) plantings from across eastern North America, grown in uniform conditions, showed that plasticity in litter flammability varied by source

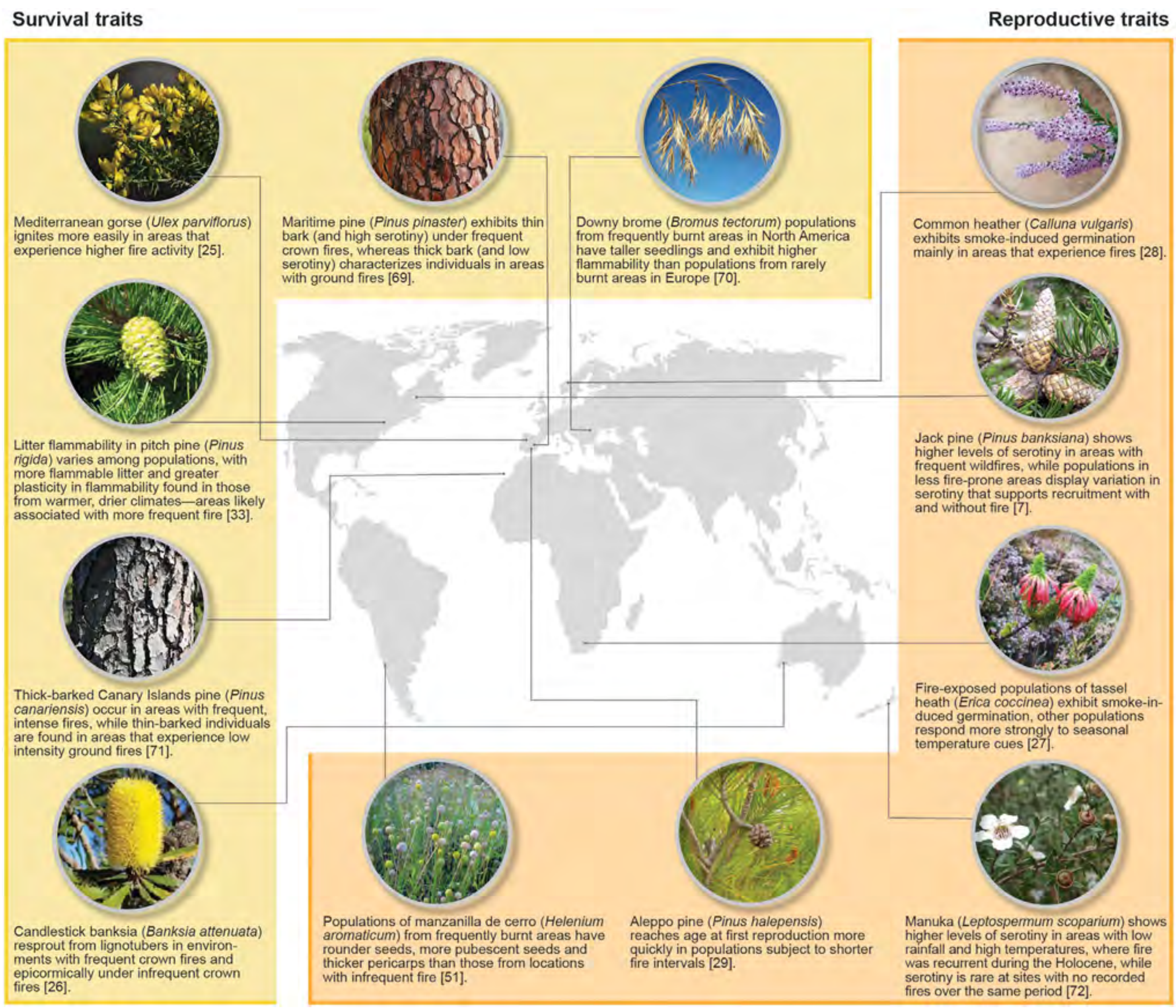

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Figure 2. Illustrative cases of intraspecific variation in fire-related traits across different plant forms. Each example illustrates how within-species variation in traits aligns with different fire regimes. Some cases highlight adaptive variation, where heritable traits likely underpin fitness differences, and others may reflect phenotypic plasticity, which can also confer survival or reproductive advantages under different fire patterns. (See [7,25–29,33,51,69–72].) Photo credits from Wikimedia Commons: Mediterranean gorse – Tylwyth Eldar, CC BY-SA 4.0; Pitch pine – bobistraveling on Flickr, CC BY 2.0; Canary Islands pine – Krzysztof Ziarnek, Kenraiz, CC BY-SA 4.0; Candlestick banksia – Anagoria, CC BY-SA 3.0; Manzanilla de cerro – Tubifex, Public domain; Aleppo pine – Balles2601, CC BY-SA 4.0; Manuka – Krzysztof Ziarnek, Kenraiz, CC BY-SA 4.0; Tassel heath – Mahendran Moodley, CC BY-SA 4.0; Jack pine – Doug McGrady, CC BY 2.0; Common heather – Josep Gesti, CC BY-SA 4.0; Downy brome – lefnaer, CC BY-SA 4.0; Maritime pine – Les Meloures, CC BY-SA 3.0.

locations, indicating heritable differences in a plastic trait [33]. Similarly, a common garden experiment on *P. halepensis* in Spain showed heritable differentiation in seed storage, with higher levels of serotiny in populations from areas with higher fire activity [34].

Experimental manipulation (phenotypic selection) can help pinpoint the role of fire and the heritable basis of variation in fire-related traits. Experimental fires revealed that awn length in the clonal grass *Hyparrhenia diplandra* from a Côte d'Ivoire savanna influenced seed burial and survival, with heritable differences present among the clones across a generation suggesting an evolutionary response to fire intensity [35]. By contrast, another experiment did not detect heritable differences between grasses exposed to different fire patterns; instead, intraspecific variation in growth and flowering was likely due to developmental plasticity following burning [16].

Advances in genomics enable studies of evolutionary changes in wild and long-lived plants and help identify whether genetic changes are involved in selection. Sequencing technologies provide molecular markers such as single nucleotide polymorphisms (SNPs) that can be used to estimate relatedness among individuals and genetic contributions to phenotypic variation [36]. This approach has been used to quantify **heritability** of serotiny in two Mediterranean pine species, with field heritability estimates of approximately 10%, indicating some genetic variance in this trait that could lead to a selection response [37]. Further evidence of the genetic component of intraspecific variation comes from quantitative trait locus (QTL) markers and genome scans. A genome scan indicated that a significant proportion of phenotypic variation in flammability of *U. parviflorus* was explained by specific loci [38], while in blue gum (*Eucalyptus globulus*), QTL analysis provided evidence for genetic control of fire-related epicormic resprouting [39].

Genetic markers associated with traits or showing extreme differentiation among populations may point to candidate genomic regions and processes underlying adaptive shifts. A survey of approximately 10 000 SNPs in *B. attenuata* populations sampled across fire, precipitation, and temperature gradients identified SNPs in four candidate genes potentially linked to fire interval and climate [40]. In *P. halepensis*, 251 SNPs in the coding regions of targeted candidate genes for fire adaptation provided evidence for genetic differentiation in three of these SNPs between stands with high or low frequency of crown fires [41].

In summary, there is growing evidence that fire-related traits vary within species, enhance plant fitness, and are heritable – the preconditions for adaptive evolution. We now explore the ability of plants to adapt to contemporary environmental changes through these traits.

Mismatches between phenotypic traits and emerging fire regimes

Insights into plant vulnerability to changing fire regimes have come largely from studies of population dynamics, offering valuable insights into demographic responses [42]. An influential approach considers time to reproductive maturity and lifespan, highlighting immaturity risk, when fire intervals are too short for plants to mature and accumulate seeds, and senescence risk, when intervals exceed the lifespan of seeds and plants [43]. Other ecological approaches link seed traits to the risk of altered fire seasonality [44], bark thickness to fire frequency [9], or combinations of fire-related traits to components of fire regimes [45,46]. However, trait-based predictions largely neglect evolutionary changes, incorrectly assuming that phenotypes are always static over time and across environments.

To examine consequences of shifting fire patterns on both plant demography and evolution, we present a framework – 'trait–fire mismatch' – that recognizes variation within and among populations of single species and its critical role in adapting to fire-related environmental changes (Box 1). This framework is based on the concept of phenotype–environment mismatch, which explores misalignment of organisms and human-altered environments [47], and is also informed by research on phenological mismatch, which examines climate-driven asynchrony in consumers and their resources [48]. Trait–fire mismatch arises when a population's trait distribution differs from that best suited for a given fire regime. Large mismatches, which are likely when fire regimes shift, result in two main outcomes: demographic changes and increased selection.

In some cases, trait–fire mismatches will reduce survival and reproduction to the point where a population declines or is extirpated. In others, the selection promoted by mismatches may lead to adaptation that helps to counter fire regime changes – a process called 'evolutionary rescue' [49]. Strong selection alone may not save a plant population if realized heritability is limited or quickly plateaus to near zero, if few individuals are well adapted, and/or if evolution cannot keep pace with rapid changes [47]. For instance, short fire intervals increase precocity in *P. halepensis*, lowering the age of reproduction from 13 to 9 years [29], but to what extent can this be further reduced? Put more broadly, how effective is adaptive evolution in stabilizing or recovering populations under emerging fire regimes? Answering this will require using a variety of methods (Box 2), including those that quantify interactions between population size, adaptive responses, and rates of evolutionary change.

There is widespread evidence that mismatches between plant traits and fire activity contribute to demographic changes and population declines [14]. Notable cases include reduced recruitment of serotinous obligate seeders following short intervals between wildfires in eastern Australia [50] and western North America [11], where repeated fires occur before canopy seedbanks have developed. Few studies have tested whether fire patterns drive rapid plant evolution, but a pioneering example comes from research on the herb manzanilla de cerro *Helenium aromaticum* in the Chilean matorral [51,52]. In this ecosystem, human activity has increased fire frequency since the 19th century and has been linked to evolutionary changes in seed traits: populations in frequently burnt areas have more rounded and pubescent seeds – traits shown to be heritable [51] – and one way these traits may function is by conferring resistance to heat and smoke [52]. This rare example, alongside extensive evidence of intraspecific variation in fire-related traits (Figure 2), highlights the need for further research at the intersection of ecology and evolution to predict plant responses to environmental changes.

Evolutionary responses to fires are complex, and additional patterns and processes should be considered. First, covariation among fire-related (and unrelated) traits and trade-offs between traits associated with different syndromes [53] may constrain evolutionary responses. A range of mathematical and statistical models are available to examine these linkages (Box 2). Second, while directional selection is critical, stabilizing and disruptive selection are also likely to play a role in fire-driven evolution of plants [52] and other biota [54] and can be explored using nonlinear modelling [23]. Third, gene flow and the genetic mechanisms underlying plasticity are often overlooked in fire-related models and should also be considered. Finally, fire interacts with

Box 1. Trait–fire mismatch

'Trait–fire mismatch' occurs when a population's phenotypic trait distribution differs from that best suited for a given fire regime (Figure I). The size of a mismatch is the distance between the peak of the current trait distribution and the optimum (i.e., the distribution where fitness is highest). Large mismatches between phenotypes and fire-prone environments will reduce survival and reproduction but also increase selection pressure for adaptation [47]. Whether plants can successfully adapt to modified fire regimes through key traits can be quantified using mathematical and statistical models (Box 2).

Plant traits are likely shaped by different characteristics of fire regimes. To date, ecological frameworks have focused primarily on single traits or small sets of traits to describe fire-related risks associated with fire regimes. For example, age to maturity has been linked to immaturity risk when fire intervals are too short [11,42,43], and germination timing has been linked to the risk posed by altered fire seasonality [44]. The concept of trait–fire mismatch enables exploration of interactions between traits and fire regimes – including others beyond those shown here, such as those arising from reductions in fire activity – within a single framework (Figure I). By incorporating intraspecific variation, the adaptive potential within species to modify the degree of mismatch can be considered, offering new opportunities for forecasts, management, and conservation that incorporate evolutionary responses.

We consider that specific attention on trait–fire mismatch is merited because of the widespread and variable nature of fire, its broad impacts on plants with implications for the rest of biodiversity, and the rapid pace of changes in fire activity. While much research on phenotype–environment mismatch has focused on adaptation to climate change, and in particular to temperature, fire regimes generate selection pressures different from those associated with climate alone because of their variation in frequency, intensity, seasonality, and size. We also consider that fire-related adaptations, such as fire-released seed dormancy, serotiny, and thick bark, provide insights into how organisms evolve in response to disturbances more generally.

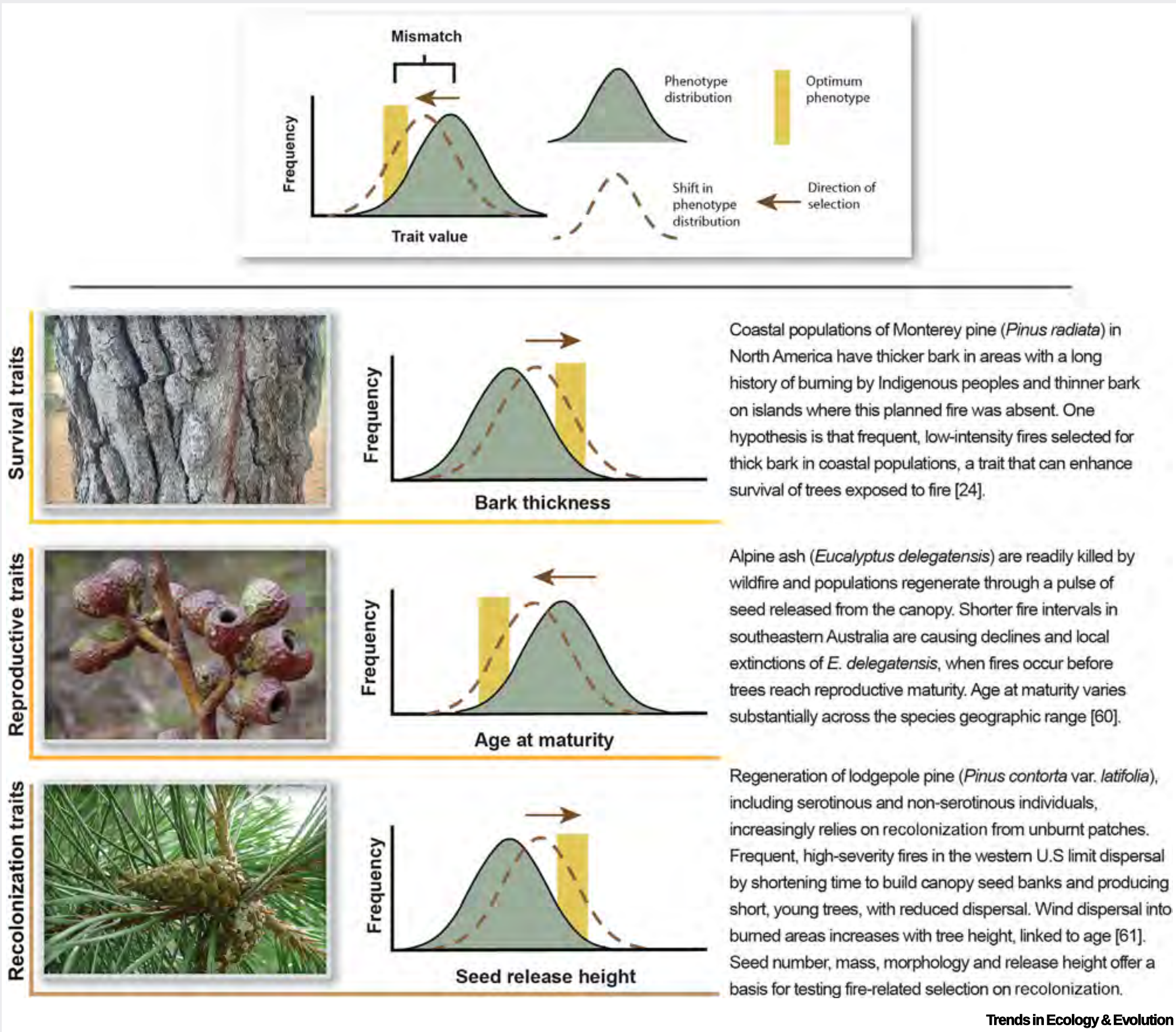

Figure I. Trait–fire mismatching. Illustrative examples of mismatch are shown where anthropogenic shifts in fire patterns have plausibly reduced plant fitness. The first example highlights a mismatch and accompanying shift in phenotype distribution that may have occurred thousands of years ago, and the other two illustrate more recent, human-driven changes in fire regimes and resulting selection pressures. In each case, different fire-related traits are likely under selection from fire regime changes. The evolutionary potential of fire-related traits, represented here by idealized phenotypes that are in transition and hypothesized to be under directional selection, is uncertain even for relatively well-studied species. (See [24,60,61].) Photo credits: Monterey pine – Luke Kelly; Alpine ash: Neil Blair, CC BY-NC-SA 4.0; Lodgepole pine – Retama, CC BY-SA 4.0, via Wikimedia Commons.

multiple biotic and environmental processes that can amplify its direct impacts, create new indirect impacts, and hinder plant recovery. To understand how plants adapt to contemporary fire regimes, it is essential to examine traits also influenced by climate [8,55] using common gardens, manipulative experiments, and field studies of wild plants. This includes traits under selection during climate-driven 'interval squeeze' [42], where shorter fire intervals and drier conditions challenge plants, as well those influenced by processes such as herbivory [6] and seed predation [56].

Box 2. Measuring the pace of adaptation

Quantitative genetic methods can be used to predict how plant traits respond to fire-driven selection.

As a simple starting point, the change in a single fire-related trait per generation (*R*) can be explored using the breeder's equation [62]:

$$R = h^2 S \quad [1]$$

where *R* is the change in the mean trait value in the next generation; h^2 is narrow-sense heritability, the proportion of variation in the trait that has an additive genetic basis; and *S* is the selection differential, calculated as the difference between phenotypes before and after selection or determined using regression of the relationship of fitness and the trait.

Consider a grass population where the mean awn length is 50 mm and heritability is high (h^2 = 0.4). Long-awned seeds may be more likely to survive high-intensity fires by burying deeper and avoiding heat [35]. After high-intensity fire and death of individuals with shorter awn lengths, the mean awn length shifts to 55 mm. Using the breeder's equation, the predicted change in awn length is:

$$R = h^2 S = 0.4 \times (55 - 50 \text{ mm}) = 2 \text{ mm} \quad [2]$$

Thus, a 5-mm increase in the selected population's mean awn length (*S*) results in an expected 2-mm increase in the next generation. If another population experiences the same selection but with lower heritability (h^2 = 0.2), the predicted change would be 1 mm. The response (*R*) is proportional to heritability (h^2).

Extensions of the breeder's equation improve predictions of evolutionary responses to fire-driven selection. These include approaches for quantifying changes in multiple traits [63], making it possible to assess how selection on one trait might influence another, as well as expansions for incorporating demographic factors such as population size, gene flow, physiological constraints, and plasticity [64,65] – all of which can potentially be analyzed in a spatially explicit framework [66]. The pace of evolutionary adaptation – underpinned by response to selection and generation time – can then be compared with empirical or simulated fire data to better understand if plants can keep up with fire regime changes.

Additional genomic approaches can be used to examine how plant traits with monogenic or oligogenic architecture respond to fire-driven selection [67,68]. Candidate loci underlying adaptation can be identified using genome-wide association studies (GWAs), which link genotypes to variation in phenotypic traits, and genotype-environment associations (GEAs), which relate genotypes to environmental variables such as fire and climate measured where samples were collected [67,68].

Managing plants in a changing world

A consideration of trait–fire mismatch can help identify species with limited adaptive capacity and inform effective conservation actions. Understanding how intraspecific variation is distributed geographically and across spatial scales and how it promotes adaptive capacity enables managers to promote strategies that assist fire-driven evolution and enhance levels of adaptive diversity necessary for population persistence.

One strategy to reduce trait–fire mismatch involves actively managing fires to align plant traits with their environment. For example, understanding when plants mature or produce seeds helps identify when and where fire should be applied or suppressed [13]. Knowledge of intraspecific variation in these traits can then guide fire management decisions tailored to specific locations [57]. A range of actions, including prescribed burns and fire suppression efforts, can be used to adjust the timing, location, and type of fires to support plant populations.

A second strategy focuses on managing phenotypes to promote adaptation. Enhancing the size of plant populations and improving connectivity and gene flow can build resilience and adaptive potential in response to shifting fire patterns [58]. In some cases, translocating individuals to reinforce genetic diversity within a species' geographic range could be beneficial [58]. Postfire restoration will be improved by understanding the genetic basis of traits and selecting appropriate source material. This may include using preadapted **genotypes** from conspecific populations suited to emerging fire regimes, such as seeds from high-frequency fire areas favoring greater precocity [29]. More radical approaches, such as moving populations or species to areas matching their historical fire regimes, may be required, given the rapid pace of change. Identifying areas with high evolutionary potential in fire-related traits, such as genetic hotspots or even fire refugia, could help prioritize conservation efforts.

Ultimately, we recommend conserving plants across the full range of their fire-related trait variation [59] and maintaining fire patterns that promote environmental heterogeneity and adequate selection pressure for adaptation.

Concluding remarks

Mismatches between plants and emerging fire patterns can reduce fitness while driving selection and adaptation. Recasting fire-driven evolution as an ongoing process and recognizing variation within species offer new ways of forecasting ecosystem changes and conserving plant diversity. However, recognizing the role of evolution in shaping plant responses to fire should not imply that all species will adapt to rapid changes – evidence to date indicates many will not. The urgent task is to quantify whether plant populations can evolve quickly enough to keep pace with these changes and to ensure that our predictions and conservation strategies do the same (see Outstanding questions). We reason that fire science will benefit from insights provided by evolution and genomics and, in turn, that these fields can be enriched by the fascinating and diverse ways fires shape contemporary plant evolution.

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Declaration of interests

The authors have no interests to declare.

References

1. Keeley, J.E. and Pausas, J.G. (2022) Evolutionary ecology of fire. *Annu. Rev. Ecol. Evol. Syst.* 53, 203–225
2. Pellegrini, A.F.A. *et al.* (2023) Consistent physiological, ecological and evolutionary effects of fire regime on conservative leaf economics strategies in plant communities. *Ecol. Lett.* 26, 597–608
3. Pausas, J.G. and Lamont, B.B. (2022) Fire-released seed dormancy - a global synthesis. *Biol. Rev. Camb. Philos. Soc.* 97, 1612–1639
4. Overton, J. *et al.* (2024) Some like it hot: seed thermal threshold variation in obligate seeding *Acacia pulchella* along a climate gradient. *Sci. Total Environ.* 948, 174929
5. Lamont, B.B. *et al.* (2019) Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biol. Rev. Camb. Philos. Soc.* 94, 903–928
6. Archibald, S. *et al.* (2019) A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytol.* 224, 1490–1503
7. Pelletier, E. *et al.* (2023) Hedging at the rear edge: intraspecific trait variability drives the trajectory of marginal populations in a widespread boreal tree species. *J. Ecol.* 111, 479–494
8. Nolan, R.H. *et al.* (2021) Limits to post-fire vegetation recovery under climate change. *Plant Cell Environ.* 44, 3471–3489
9. Pellegrini, A.F.A. *et al.* (2017) Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecol. Lett.* 20, 307–316
10. Gallagher, R.V. *et al.* (2021) High fire frequency and the impact of the 2019–2020 megafires on Australian plant diversity. *Divers. Distrib.* 27, 1166–1179
11. Turner, M.G. *et al.* (2019) Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proc. Natl. Acad. Sci. U. S. A.* 116, 11319–11328
12. Jones, M.W. *et al.* (2022) Global and regional trends and drivers of fire under climate change. *Rev. Geophys.* 60, e2020RG000726
13. Kelly, L.T. *et al.* (2023) Understanding fire regimes for a better Anthropocene. *Annu. Rev. Environ. Resour.* 48, 207–235
14. Kelly, L.T. *et al.* (2020) Fire and biodiversity in the Anthropocene. *Science* 370, eabb0355
15. Keith, D.A. *et al.* (2020) Dispersal: the eighth fire seasonality effect on plants. *Trends Ecol. Evol.* 35, 305–307
16. Simpson, K.J. *et al.* (2019) Frequent fires prime plant developmental responses to burning. *Proc. R. Soc. B* 286, 20191315
17. Mazer, S.J. *et al.* (2022) What determines the evolutionary trajectories of wild plant species? Approaches to the study of quantitative fitness-related traits. *Am. J. Bot.* 109, 1673–1682
18. Hoffmann, A.A. and Sgrò, C.M. (2011) Climate change and evolutionary adaptation. *Nature* 470, 479–485
19. Vahsen, M.L. *et al.* (2023) Rapid plant trait evolution can alter coastal wetland resilience to sea level rise. *Science* 379, 393–398
20. Dai, D. *et al.* (2025) Leaf dry matter content is phylogenetically conserved and related to environmental conditions, especially wildfire activity. *Ecol. Lett.* 28, e70056
21. Pausas, J.G. (2015) Evolutionary fire ecology: lessons learned from pines. *Trends Plant Sci.* 20, 318–324
22. Lamont, B.B. and He, T. (2017) Fire-proneness as a prerequisite for the evolution of fire-adapted traits. *Trends Plant Sci.* 22, 278–288
23. Hendry, A.P. (2017) *Eco-evolutionary Dynamics*, Princeton University Press
24. Stephens, S.L. and Libby, W.J. (2006) Anthropogenic fire and bark thickness in coastal and island pine populations from Alta and Baja California. *J. Biogeogr.* 33, 648–652
25. Pausas, J.G. *et al.* (2012) Fires enhance flammability in *Ulex parviflorus*. *New Phytol.* 193, 18–23
26. He, T. *et al.* (2019) Environmental drivers and genomic architecture of trait differentiation in fire-adapted *Banksia attenuata* ecotypes. *J. Integr. Plant Biol.* 61, 417–432
27. Leonard, J. *et al.* (2018) Differences in germination response to smoke and temperature cues in 'pyrophyte' and 'pyrofuge' forms of *Erica coccinea* (Ericaceae). *Int. J. Wildland Fire* 27, 562–568
28. Vandvik, V. *et al.* (2014) Management-driven evolution in a domesticated ecosystem. *Biol. Lett.* 10, 20131082
29. Guiote, C. and Pausas, J.G. (2023) Fire favors sexual precocity in a Mediterranean pine. *Oikos*, e09373
30. Johnson, J.S. *et al.* (2019) Rapid changes in seed dispersal traits may modify plant responses to global change. *AoB Plants* 11, plz020
31. Albert, C.H. *et al.* (2011) When and how should intraspecific variability be considered in trait-based plant ecology? *Perspect. Plant Ecol. Evol. Syst.* 13, 217–225

Outstanding questions

What is the extent and nature of intraspecific variation in recolonization traits potentially influenced by fire? Studies of seed number, mass, morphology, and release height, for example, will help reveal the ability of plants to disperse in fire-prone ecosystems, how strongly recolonization traits are shaped by fire-driven selection, and how gene flow influences adaptation.

What is the heritability of fire-related traits that influence plant survival, reproduction, and recolonization? Do some fire-related traits have greater evolutionary potential than others? How does evolutionary potential in fire-related traits vary across taxa, ecosystems, and locations?

What is the relative importance of heritable genetic differences, within-generation plasticity, and cross-generational plasticity, including epigenetic effects, in shaping plant responses to fire regime changes? Answering this will require consideration of plasticity that may be genetically controlled.

How does covariation among fire-related (and other) traits shape evolutionary adaptation under modified fire regimes and associated environmental changes? Which traits are under selection as fire regimes and other factors, such as climate, pathogens, pollinators, and predators, shift?

Trait–fire mismatches are likely widespread. What are the most common forms, and where and when are these mismatches most pronounced? For which species, and under which conditions, will evolutionary rescue occur? What are the limits to fire-driven evolutionary changes?

Is the full range of fire-related trait variation adequately protected for most plant species? How can conservation actions be informed by this variation and adjusted to support it? How effective are translocations, sourcing pre-adapted genotypes, and population relocations in dealing with shifting fire regimes – and what are the risks of action versus inaction?

32. Schwinning, S. *et al.* (2022) What common-garden experiments tell us about climate responses in plants. *J. Ecol.* 110, 986–996
33. Kane, J.M. *et al.* (2022) Evidence of local adaptation in litter flammability of a widespread fire-adaptive pine. *J. Ecol.* 110, 1138–1148
34. Hernández-Serrano, A. *et al.* (2014) Heritability and quantitative genetic divergence of serotiny, a fire-persistence plant trait. *Ann. Bot.* 114, 571–577
35. Garnier, L.K.M. and Dajoz, I. (2001) Evolutionary significance of awn length variation in a clonal grass of fire-prone savannas. *Ecology* 82, 1720–1733
36. Gienapp, P. *et al.* (2017) Genomic quantitative genetics to study evolution in the wild. *Trends Ecol. Evol.* 32, 897–908
37. Castellanos, M.C. *et al.* (2015) Field heritability of a plant adaptation to fire in heterogeneous landscapes. *Mol. Ecol.* 24, 5633–5642
38. Moreira, B. *et al.* (2014) Genetic component of flammability variation in a Mediterranean shrub. *Mol. Ecol.* 23, 1213–1223
39. Hernández, M.A. *et al.* (2022) Genetic variation in fire recovery and other fire-related traits in a global eucalypt species. *Tree Genet. Genomes* 18, 42
40. He, T. *et al.* (2016) Evolutionary potential and adaptation of *Banksia attenuata* (Proteaceae) to climate and fire regime in southwestern Australia, a global biodiversity hotspot. *Sci. Rep.* 6, 26315
41. Budde, K.B. *et al.* (2017) Increased fire frequency promotes stronger spatial genetic structure and natural selection at regional and local scales in *Pinus halepensis* Mill. *Ann. Bot.* 119, 1061–1072
42. Enright, N.J. *et al.* (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Front. Ecol. Environ.* 13, 265–272
43. Zedler, P.H. (1995) Fire frequency in southern California shrublands: biological effects and management options. In *Brushfires in California: Ecology and Resource Management* (Keeley, J.E. and Scott, T., eds), pp. 101–112, International Association of Wildland Fire
44. Miller, R.G. *et al.* (2019) Mechanisms of fire seasonality effects on plant populations. *Trends Ecol. Evol.* 34, 1104–1117
45. Plumanns-Pouton, E. *et al.* (2024) Using plant functional types to predict the influence of fire on species relative abundance. *Biol. Conserv.* 292, 110555
46. Rodman, K.C. *et al.* (2021) A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. *J. Ecol.* 109, 313–326
47. Carroll, S.P. *et al.* (2014) Applying evolutionary biology to address global challenges. *Science* 346, 1245993
48. Visser, M.E. and Gienapp, P. (2019) Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* 3, 879–885
49. Carlson, S.M. *et al.* (2014) Evolutionary rescue in a changing world. *Trends Ecol. Evol.* 29, 521–530
50. Bowman, D.M.J.S. *et al.* (2014) Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Glob. Chang. Biol.* 20, 1008–1015
51. Gómez-González, S. *et al.* (2011) Anthropogenic fire drives the evolution of seed traits. *Proc. Natl. Acad. Sci. U. S. A.* 108, 18743–18747
52. Gómez-González, S. *et al.* (2016) Seed pubescence and shape modulate adaptive responses to fire cues. *PLoS One* 11, e0159655
53. Jaureguiberry, P. and Díaz, S. (2023) A three-dimensional approach to general plant fire syndromes. *Funct. Ecol.* 37, 2143–2158
54. Jones, G.M. *et al.* (2023) Fire-driven animal evolution in the Pyrocene. *Trends Ecol. Evol.* 38, 1072–1084
55. Tonnabel, J. *et al.* (2018) Life-history traits evolved jointly with climatic niche and disturbance regime in the genus Leucadendron (Proteaceae). *Am. Nat.* 191, 220–234
56. Talluto, M.V. and Benkman, C.W. (2014) Conflicting selection from fire and seed predation drives fine-scaled phenotypic variation in a widespread North American conifer. *Proc. Natl. Acad. Sci. U. S. A.* 111, 9543–9548
57. Morgan, J.W. *et al.* (2021) Does intraspecific variation in demography have implications for fire management of an obligate-seeder shrub across its geographic range? *Austral. Ecol.* 46, 315–323
58. Hoffmann, A.A. *et al.* (2021) Genetic mixing for population management: from genetic rescue to provenancing. *Evol. Appl.* 14, 634–652
59. Forester, B.R. *et al.* (2022) Linking evolutionary potential to extinction risk: applications and future directions. *Front. Ecol. Environ.* 20, 507–515
60. Doherty, M.D. *et al.* (2017) Seed viability of early maturing alpine ash (*Eucalyptus delegatensis subsp. delegatensis*) in the Australian Alps, south-eastern Australia, and its implications for management under changing fire regimes. *Aust. J. Bot.* 65, 517
61. Gill, N.S. *et al.* (2021) The propagule doesn't fall far from the tree, especially after short-interval, high-severity fire. *Ecology* 102, e03194
62. Lush, J.L. (1937) *Animal Breeding Plans*, Iowa State College Press
63. Lande, R. and Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution* 37, 1210–1226
64. Urban, M.C. *et al.* (2024) When and how can we predict adaptive responses to climate change? *Evol. Lett.* 8, 172–187
65. Martin, R.A. *et al.* (2023) When will a changing climate outpace adaptive evolution? *Wiley Interdiscip. Rev. Clim. Chang.* 14, e852
66. Bush, A. *et al.* (2016) Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. *Ecol. Lett.* 19, 1468–1478
67. Capblancq, T. *et al.* (2020) Genomic prediction of (mal)adaptation across current and future climatic landscapes. *Annu. Rev. Ecol. Evol. Syst.* 51, 245–269
68. Schmidt, T.L. *et al.* (2024) How can genomics help or hinder wildlife conservation? *Annu. Rev. Anim. Biosci.* 12, 45–68
69. Tapias, R. *et al.* (2004) Life histories of Mediterranean pines. *Plant Ecol.* 171, 53–68
70. Fenesi, A. *et al.* (2016) Enhanced fire-related traits may contribute to the invasiveness of downy brome (*Bromus tectorum*). *Invasive Plant. Sci. Manag.* 9, 182–194
71. Climent, J. *et al.* (2004) Fire adaptations in the Canary Islands pine (*Pinus canariensis*). *Plant Ecol.* 171, 185–196
72. Battersby, P.F. *et al.* (2017) Exploring fire adaptation in a land with little fire: serotiny in *Leptospermum scoparium* (Myrtacea). *J. Biogeogr.* 44, 1306–1318