Review

Evolutionary fire ecology: lessons learned from pines

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Macroevolutionary studies of the genus *Pinus* provide the oldest current evidence of fire as an evolutionary pressure on plants and date back to *ca*. 125 million years ago (Ma). Microevolutionary studies show that fire traits are variable within and among populations, especially among those subject to different fire regimes. In addition, there is increasing evidence of an inherited genetic basis to variability in fire traits. Added together, pines provide compelling evidence that fire can exert an evolutionary pressure on plants and, thus, shape biodiversity. In addition, evolutionary fire ecology is providing insights to improve the management of pine forests under changing conditions. The lessons learned from pines may guide research on the evolutionary ecology of other taxa.

Pines and fire-driven evolution

Fire is an ancient and recurrent disturbance factor on our planet and has been present since the origin of terrestrial plants [1,2]. However, demonstrating whether fire has acted as an evolutionary force is not easy [3]. In this context, the emerging discipline of evolutionary fire ecology (Figure 1) aims to understand the role of wildfires in shaping biodiversity [2,4]. The negative socioeconomic impact of many wildfires has hindered our understanding of fire ecology, and only now are we starting to build a body of information supporting the evolutionary role of fire. Gaining insight into this topic is not only important from an evolutionary point of view, but also affects how we view and manage our ecosystems [5].

Here, I review what we have learned about evolutionary fire ecology by studying the iconic genus *Pinus*. I suggest that the study of pines has increased our understanding of the role of fire as an evolutionary pressure on plant taxa. Although other taxa have contributed to this knowledge (e.g., [4,6]), *Pinus* is probably the genus that has contributed the most and provides the state-of-the-art on fire ecology and evolution. Given their abundance, geographical extent, diversity, and dominance in many ecosystems, what we have learned from pines may be relevant for a substantial part of our planet; in addition, it may guide further research in other taxa. Below, I review the main traits that enhance fitness in pines living under different fire regimes, and then discuss the advances in fire ecology at both the micro- and macroevolutionary scales. In addition, I highlight some management applications of the lessons learned. Throughout this review, I also point out some current research gaps that need to be filled to fully understand the role of fire in shaping biodiversity.

Fire traits in pines

By fire traits, I mean plant traits that enhance fitness (i.e., that have an adaptive value) under recurrent fires; pines have a plethora of these traits [7]. Some traits enhance fitness in crown-fire ecosystems (see Glossary), whereas others increase fitness in ecosystems with understory fires. For instance, a thick basal bark and self-pruning lower branches are adaptive for living in ecosystems with understory fires (Table 1), because the thick bark protects the cambium and buds from the heat of the fire [8], and the absence of branches in the lower part of the bole prevents the fire from reaching the canopy and gaining in intensity. These traits enable trees to survive recurrent understory fires. In addition, needles that produce a highly flammable litter (thin long needles and,

Glossary

Crown fires: fires in woody-dominated vegetation that affect most of the crown of the dominant plants.

Grass-stage: delayed trunk elongation, whereby internode elongation is suppressed for the first 5–10 y of development, with the resulting juveniles persisting in a bunchgrass growth form. During this stage, needles are decumbent, accumulate as a mantle over the apex, and insulate the apical bud against fire heat.

Fire regime: the characteristic of wildfire activity that prevails in a given area; it is typically determined by its frequency, intensity, seasonality, and type of fuels consumed. Two common and contrasted fire regimes are surface-fire regimes and crown-fire regimes.

Monopyric life cycle: species that perform all their life cycle within a fire cycle. In plants, examples are annual and biennial species, and are post-fire obligate seeders (including the fire-embracers pine syndrome).

Polypyric life cycle: species that perform all their life cycle through multiple fire cycles. In plants, examples are those with fire survival strategies such as resprouting species or trees with thick bark (e.g., the fire-tolerator pine syndrome).

Self-pruning (= branch shedding): ability to shed lower branches and, thus, generate a fuel discontinuity between the understory and the canopy. The opposite is branch retention.

Serotiny: retention of matured seed in closed cones (e.g., pine cones) for more than a year in such a way that seed dispersal is delayed. The heat of the fire acts as a cue to open the cones; thus, seeds are dispersed post fire, when conditions for establishment are favorable (resources, such as light, moisture, and nutrients, are maximal and competition with adults is minimal).

Understory fires: surface fire in forest ecosystems; that is, fires that spread through the herbaceous and litter layer (surface fuels) of forests, without affecting the tree crowns. Forests subject to understory fires typically have a vertical discontinuity of fuels (e.g., lack of lower branches in the bole) in such a way that tree crowns are not affected by the fire.

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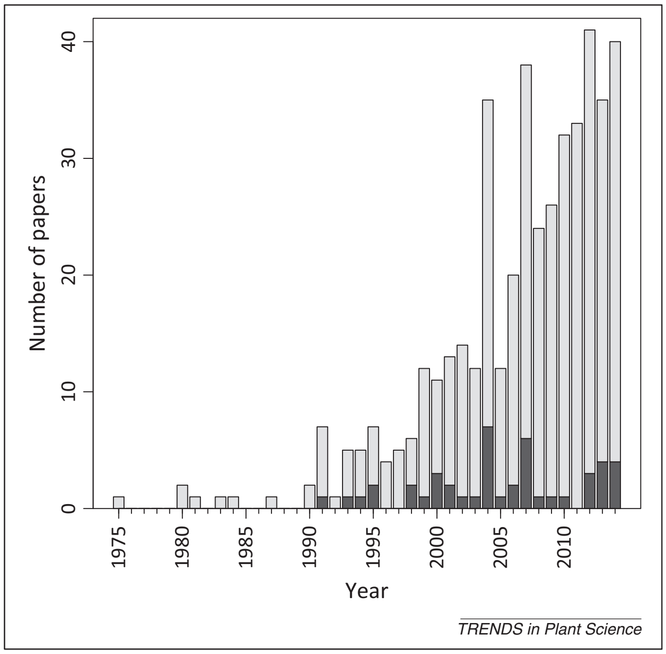

TRENDS in Plant Science

Figure 1. Estimated number of papers published from 1975 to 2013 that took an evolutionary approach to fire ecology. Based on the number of papers in the Web of Science that match the following search ''evolutionary AND (fire* OR wildfire*)'' in the title or abstract (excluding papers in nonenvironmental research areas). The darker shading represents the number of papers that include pines (*Pinus* OR pine*). For the period between 1900 and 1974, the value was 0 (not plotted).

thus, litter with low compaction) are also considered advantageous in understory fire ecosystems [9]; this is because such litter increases the probability of fires that prevent both the build-up of understory fuel (which could generate high intensity fires) and the accumulation of a thick litter layer (which could limit seed germination). By contrast, serotiny is adaptive in ecosystems with frequent crown fires (Table 1), because these fires open gaps where the seeds in the canopy seed bank can germinate profusely. Early reproduction is also advantageous in this fire regime because it enables plants to leave offspring even with relatively short fire intervals [10]. Having the capacity to resprout during the early stages of the plant (e.g., having a 'grass stage') is adaptive in environments with frequent understory fires, because saplings do not have enough bark to protect them from the heat of fires; by contrast, resprouting from stem (epicormic) buds enables the quick regeneration of vegetative and reproductive structures in crown-fire ecosystems (Table 1). All these traits are costly for the plant; for example, serotiny requires resources for maintaining a large amount of seeds alive in the canopy [11,12]. In addition, there are also opportunity costs, such as the loss of seed viability with time [13,14] and increased predispersal predation [15]. Early reproduction, resprouting, and thick bark also incur energy costs to the plant. Thus, all these traits only appear when fires are frequent enough that the benefits (increased reproduction or survival) compensate for the costs.

Overall, the observed correlations among traits, both positive and negative [7,16], define at least three clear syndromes in pines (Table 1): (i) fire-tolerators survive frequent understory fires; (ii) fire-embracers suffer crown fires (the retention of lower branches or the shorter stature favors the fire reaching the canopy) but have mechanisms for quick post-fire recovery of the population (note that fire-embracers is the name used for pines that are post-fire obligate seeders); and (iii) fire-avoiders live in environments that rarely burn. Most pine species can be assigned to one of these syndromes, although, in some species, the variability among populations subject to different fire regimes may reflect different syndromes (e.g., *Pinus pinaster* [17] and *Pinus rigida* [18]; see also 'Microevolutionary approaches' below). In addition, these syndromes also imply different population dynamics (Table 2). For instance, fire-embracers perform all their life cycle within a single fire cycle (monopyric species [10]) and tend to have short, nonoverlaping generations with synchronous recruitment, as opposed to the other syndromes. These different population dynamics may have consequences on the genetic and phenotypic structure and evolutionary potential of the population (e.g., [19]), although this has been little explored in the literature. For instance, we should expect higher among-population genetic differentiation in fire-embracers than in the other pine syndromes as observed when comparing other monopyric and polypyric species [20]. This is because populations of fire-embracers are wiped out after each fire and recruit new individuals from the canopy seed banks. Given that not all trees regenerate profusely after fire (it depends on their serotiny level and the post-fire conditions), allelic diversity of the regenerated population is likely to be a subset of the original population. In addition, the dynamics generated by recurrent crown fires reduces generation time and increases the possibility of acquiring genetic novelties (Table 2 [10,21]).

All of the traits mentioned above (Table 1) are considered adaptive in fire-prone ecosystems because they enhance

Table 1. Main fire traits that define the three fire syndromes in pines[a]

Fire trait[b]	Syndrome		
	Fire tolerator	Fire embracer (post-fire seeder)	Fire avoider
Serotiny	No	Yes	No
Early reproduction	No	Yes	No
Thick basal bark	Yes	No	No
Resprouting	No/Juveniles	No/Epicormic	No
Seedling grass stage	(Yes)	No	No
Self-pruning	Yes (low tree flammability)	No (branch retention; high tree flammability)	~
Litter flammability	High (long, thin needles)	Low	Low
Examples	*Pinus ponderosa, Pinus nigra*	*Pinus attenuata, Pinus halepensis*	*Pinus albicaulis, Pinus cembra*

[a] Based on [7,16,24,26]. For each syndrome, the examples include an American and a European species.

[b] See Glossary for trait descriptions.

Table 2. Dominant characteristics of the fire and population dynamics for each of the three main pine syndromes[a]

Characteristic	Syndrome		
	Fire tolerator	Fire embracer	Fire avoider
Fire type	Understory fires (localized crowning)	Crown fires	Infrequent fires
Fire intensity	Low	High	No, variable
Post-fire population status	Unaffected	Recruiting	Local extinction
Persistence level	Individuals	Populations	None (metapopulation)
Generations	Long, overlapping	Short, nonoverlaping	Long, overlapping
Life cycle [10]	Polypyric	Monopyric	Fire independent
Reproduction cycle	Iteroparous	Semelparous	Iteroparous
Recruitment	Small gaps, fire dependent	Large gaps, synchronous, fire dependent	Small gaps, fire independent

[a] Based on [7,10,16,26].

fitness under recurrent fires. However, to what extent they are a direct response to fire (i.e., fire adaptations) requires further analysis [3]. Both macro- and microevolutionary studies have tried to determine whether this constellation of traits is the product of a close history of pines with fire [22]. Macroevolution reflects the origin and long-term evolution of traits, whereas microevolutionary studies provide information on the short-term evolutionary dynamics in relation to the most recent fire regimes.

Macroevolutionary approaches

Macroevolutionary studies aim to understand the evolutionary history of a given clade and require a robust inference of phylogenetic relations. The origin of the genus *Pinus* has been dated to the Mesozoic, perhaps during the Jurassic or early Cretaceous [23]. By assembling a phylogenetic tree and compiling fire traits for 38 *Pinus* species, a study in 2001 provided the first macroevolutionary evidence linking pines and fire [24]. The authors showed that there were two well-defined basal clades, coinciding with the two subgenera (*Pinus* and *Strobus*), with very different fire traits, that split during the early history of the genus; however, their phylogeny was not dated so it was not possible to trace the origin of the fire traits. In any case, their findings were suggestive because most species of the *Pinus* lineage live in fire-prone ecosystems, while most *Strobus* species live under low-productive environments unaffected by fires (although there are exceptions). This study also confirmed the trait correlations observed previously ([7], Table 1), but in an evolutionary framework (i.e., correlated evolution among traits). A few years later, the split between the two large *Pinus* subgenera was dated to the Cretaceous, based on a few pine species from different lineages [25], but no link with fire was established.

More recently, a step forward was made based on a comprehensive macroevolutionary study of fire traits that included most pine species worldwide (101 species) [26]. By using a dated phylogeny, this study corroborated many of the evolutionary correlated patterns among traits, but more importantly, the authors found that some traits, such as a thick bark and serotiny, first appeared in *Pinus* as early as 126 and 89 Ma, respectively, during the mid-Cretaceous (Mesozoic). This timeframe coincides with a period with a relatively high atmospheric oxygen concentration and high temperatures, conditions that were prone to high fire activity. Consequently these dates correspond to the earliest known evidence of fire acting as an evolutionary pressure on plants. There is an older history of fires on Earth, as evidenced by charcoal indicative of fires (i.e., since the Silurian) [1,2]; however, the existence of fires does not prove that they were acting as an evolutionary pressure. In any case, given that fire is an efficient cause of mortality, and the abundant evidence of fires and conditions prone to fire (e.g., seasonal dry conditions and high atmospheric concentration of oxygen) throughout the Paleozoic and Mesozoic [1,2,27,28], it is likely that fire impacted plant evolution earlier than during the Cretaceous. Perhaps studying the evolution of traits in older taxa could date the evolutionary role of fire earlier. For instance, the widespread presence of resprouting ability in ferns, extinct gymnosperms, and many extant 'old' gymnosperms [10,29] is suggestive and indicative of ancient and widespread disturbances, including fires. In addition, there is evidence from fossils from the early Carboniferous and the Triassic showing relatively thick and protective bark-like structures in arborescent pteridosperms and protoconifers [30–32]. In addition, the Carboniferous was a period with a high atmospheric oxygen concentration and, thus, the moister threshold for inhibiting fires would be higher than it is currently (i.e., fires would burn more easily than nowadays). Although further research on plant evolution and fire in this temporal window is needed, these observations suggest that fire contributed to shape plant traits for post-fire survival much earlier than the Cretaceous period [2,10].

Microevolutionary approaches

The microevolutionary approach looks for trait divergences and local adaptation in populations (within species) living in different selective environments. In the context of fire ecology, this is important because not only is it possible to evaluate the role of fire in generating variability and diversity, but it can also provide insights into responses to changes in current fire regime. Serotiny is the pine trait that has been best studied in this regard. The level of serotiny (e.g., the proportion of closed cones) is a variable trait within and among populations in many pine species [17,19,33–35], and there is evidence that serotiny increases with the frequency of crown fires [18,19,36,37], providing a clear example of trait divergence (Figure 2). In fact, the strength of the fire–serotiny relation varies among species and conditions (reviewed in [19]). Bark thickness is also an important trait for survival in ecosystems with understory fires (Table 1, [8]) and there is also an indication of trait divergence, with thicker bark on populations living under

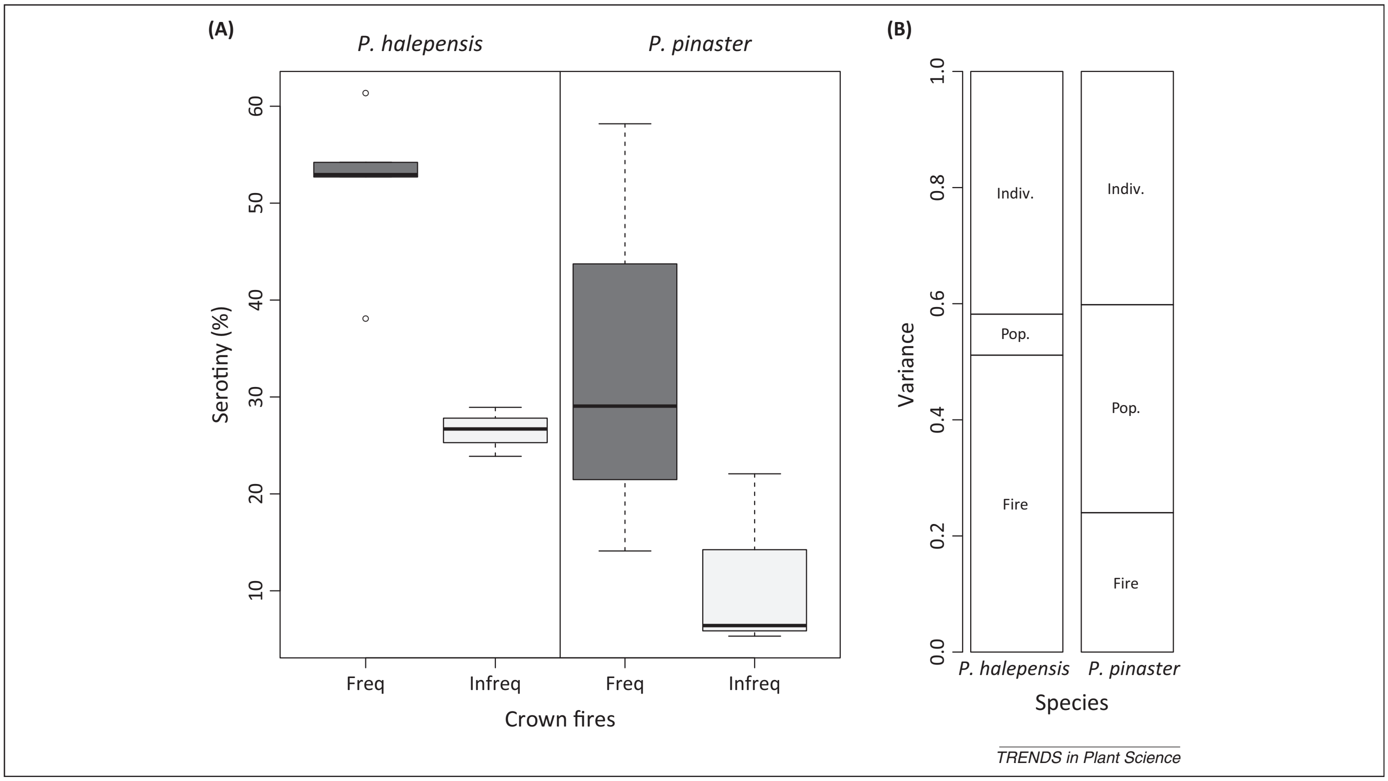

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Figure 2. Example of trait divergence among populations living under different fire regime. **(A)** Serotiny (as % of closed cones) in populations living under frequent crown fires ('Freq', dark boxes) and in populations where crown fires are rare ('Infreq', light boxes) for two pine species, *Pinus halepensis* (Allepo pine) and *Pinus pinaster* (maritime pine). Differences between fire regimes are significant (mixed-model, *P. halepensis*: $P = 0.001$; *P. pinaster*: 0.03). **(B)** Scaled variance component estimates (among fire regimes, populations, and individuals) for the two species. Based on data from [19].

frequent understory fires compared with populations that rarely burn [38].

Plants also interact with many other species; these mutualistic and antagonistic interactions are important evolutionary forces that sometimes may, in turn, interact with fire, generating geographical selection mosaics. Perhaps the best-known selection mosaic in pines is based on the conflicting selection pressure from fire and predispersal seed predation in serotinous cones. Crown fires select for serotiny, whereas seed predators (e.g., crossbills, squirrels, or cone borer moths) select against storing seeds in the canopy and, thus, the presence and abundance of some of these predators in a crown-fire ecosystem may reduce the serotiny level [15]. In addition, different seed predators may select for different cone characteristics [39]. That is, although most of the variability of serotiny among populations may be related to the fire regime, part of the variability can also be explained by the spatial and temporal variability of these predispersal seed predators. It is likely that there are other plant–animal–fire interactions that need to be studied in detail.

To demonstrate that a trait is shaped by natural selection driven by fire, it is not enough to show that the trait is variable and enhances fitness in a given fire regime; evidence is also necessary that the trait is inheritable. Early work using progeny tests and quantitative genetic analysis concluded that cone serotiny is probably a genetic adaptation to fire with one-locus, two-allele control [40–42]. More recently, progeny tests have also been used to show that the variation in several traits (including stature, serotiny, and precocity) among *P. rigida* populations subjected to different fire regimes had a genetic basis [18]. By calculating variance components, it is possible to estimate the fraction of the variance of a trait within a population that is due to genetic factors, and this can be performed by considering the relatedness between individuals in a model explaining the phenotypic variability (e.g., incorporating a pedigree in an 'animal model' [43]). By doing this, recent work used a progeny test to provide the first narrow-sense heritability (h^2) estimate for a fire trait, and suggested that serotiny has a heritability of 0.20 in *Pinus halepensis* [44], which is a relatively high value. The authors also showed that the variability in serotiny (quantitative genetic differentiation, Q_{ST}) was larger than the variability expected from neutral molecular markers (F_{ST}), suggesting that adaptive differentiation is underway. Tree-breeding studies have also used progeny tests to estimate the heritability of many pine traits, including bark thickness (e.g., h^2 ca. 0.15-0.24 in *P. halepensis* [45]).

The traditional estimation of heritability using phenotypic data from progeny tests is a valid approach, but may lack some ecological realism. This is because the survival of individuals in a common garden experiment is different from survival in natural populations and, thus, the distribution of traits and heritability estimates may differ from what is occurring in the field [46,47]. The difficulty of estimating a pedigree in natural plant populations limits the estimation of the realized heritability and, thus, the potential for evolutionary change in the wild. However, recent advances in molecular techniques, especially the use of genome-wide scans, has opened the possibility of overcoming this problem even in nonmodel plants. It is now possible to study the phenotypic variability in a natural population and to use molecular markers in high density to define relatedness among wild individuals [48] to obtain a realistic heritability estimate; this remains to be done for fire traits.

Current genomic advances are contributing to understanding the genetic architecture of plant adaptive traits, including pine traits (e.g., [49]). For fire traits, a recent study used 98 000 SNPs in 98 *Pinus contorta* individuals and found that approximately 50% of the variability in serotiny was explained by 11 SNPs [50]. A similar study showed that 17 SNPs from candidate genes in *P. pinaster* explain *ca*. 30% of the variability in serotiny (509 trees) [51]. These genetic association studies suggest that serotiny has a genetic basis, but that its inheritance is more complex than the assumption of one gene with two alleles suggested previously. This polygenic basis for serotiny is also consistent with the existence of large variability in the level of serotiny in many natural populations (Figure 2). However, there is still a lack of understanding of the role of adaptive plasticity in explaining trait variability. Given that fire regimes can vary in space and time, some times abruptly [52], variability may be adaptive and, therefore, the selection for plasticity in fire traits such as serotiny should be considered [53]. Similar genomic advances for fire traits other than serotiny remain to be done, but all the evidence points to an inheritable genetic basis for the variability of fire traits. The increasing availability of new genomic resources for pines (e.g., [54,55]) provides promising tools for more detailed analyses of the genetic basis of adaptations (considering both the mean and the variance), that is, the genetic changes that determine performance in different ecological niches such as those generated by different fire regimes.

Applying the lessons

Evolutionary biology is providing new insights to promote sustainable management [56], and evolutionary fire ecology is not an exception. What we have learned about the ecology and evolution of pines provides information that can be used to improve the management of pine woodlands. For instance, current understanding of pine syndromes is providing evidence for targeting fire regimes in ecosystem restoration processes or when managing fire regimes under climate change conditions [5]. The zero-fire policy is not ecologically sustainable in pine forests dominated by fire-embracers or fire-tolerators. Misunderstanding fire syndromes can generate, and has generated, abrupt fire regime changes with important biodiversity consequences [52,57,58].

Afforestation and restoration projects are typically performed using local seed sources from good-quality stands to maximize plant establishment and growth. These local stands are selected on the basis of bioclimatic and geographic conditions and on high seed production. However, there is growing evidence that these seed sources are not always the best, especially under changing conditions or in highly fragmented landscapes [59,60]. Evolutionary fire ecology suggests that afforestation of pines in ecosystems susceptible to fire would be more sustainable if performed using seeds of populations that have the appropriate traits to persist under the expected fire regimes. For instance, given that serotiny is heritable [44], the post-fire generation of a fire-embracer pine would be more serotinous than a mature population in a good-quality site and, thus, this seed source would be more suited for restoring an area prone to crown fires. By selecting seeds from young post-fire populations, we are also selecting for individuals with early maturation, which is also adaptive in ecosystems with crown fires. In addition, current evolutionary thinking would suggest using seeds from more than one source to avoid relying on the possible reduced genetic diversity from a single post-fire population and, thus, would ensure high evolutionary potential in the restored system.

Overall, there is a new emerging paradigm in forestry that considers the lessons learned in fire ecology to maximize not only survival and productivity, but also the evolutionary processes. To what extent this new paradigm may allow us to managing forests to cope with the current climate and fire regime changes is unknown, but certainly sets the direction for more sustainable forestry in a changing world.

Concluding remarks

Many plant species have traits that enable them to survive and reproduce under different fire regimes [3,10], and pines are among the most evident, given that different pine species show a range of traits and fire syndromes for living in different fire regimes. Pines show the oldest current evidence of fire as an evolutionary force, which dates back to more than 100 Ma [26], although it is likely to be older [2,27]. Fire even currently acts as an evolutionary force driving trait divergence and local adaptations in populations living under different fire regimes, and pine serotiny is an outstanding example of this trait divergence within species (Figure 2; [19,44]). Overall, pines probably provide the most convincing evidence of species shaped by fire, as suggested by both macro- and microevolutionary studies. That is, the fact that fire acts as a selection agent driving plant evolution is now well established, especially thanks to the research undertaken in pine species.

As we enter the new genomic era, there is an increasing opportunity for a more in-depth analysis of the genetic basis of adaptations for any species, including nonmodel species. For instance, the increasing availability of candidate genes and the possibility of sequencing targeted genomic regions enable the detection of outlier loci or the association between traits and markers to be more informative than previously [61,62]. This opens the possibility to detect genes or genomic regions linked to fire traits and to study their variation in contrasted fire regimes or after strong fire regime shifts. Given the high correlation among fire traits (Table 1), disentangling the genetic association with a specific trait may be difficult, and creative approaches will be needed. Because of the large intrapopulation variability of some of these traits (Figure 2), one possibility would be to study individuals with rare trait combinations. The genomic information can also help us to accurately estimate heritability in field conditions, which in turn would enable us to predict the intensity of selection and the evolutionary potential. In fact, many fire regimes are currently changing as a result of different global change drivers. These ecosystem changes may be abrupt, and sometimes catastrophic [52,63,64]. They cause increased tree mortality and, thus, an increase in the evolutionary pressure on plants. To what extent this may speed evolution, just as antibiotics and herbicides speed up the evolution of pathogens and weeds, respectively, remains to be studied in detail. We expect pines from different syndromes to respond differently to changes, with fire-embracer pines to be more likely to evolve than other syndromes due to their dynamic characteristics (Table 2); however, local extinctions due to short fire intervals are also possible (immature risk [10]). New genomic tools may provide clues for disentangling the possible outcomes.

Given the old and recurrent presence of fires in the history of plants, it is expected that fire has acted as an evolutionary pressure in many other lineages different from pines. Evidence for this is accumulating, especially from macroevolutionary studies [4,6,65,66]; and there is a need to go back in time to understand the evolutionary role of fire before the Cretaceous. Few microevolutionary studies currently demonstrate the role of fire as an evolutionary pressure in nonpine species [67–69] and this gap needs to be filled urgently so that we can fully understand the role of fire in shaping biodiversity.

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