

Review

Fire-driven animal evolution in the Pyrocene

Gavin M. Jones^{1,*}, Joshua F. Goldberg,¹ Taylor M. Wilcox,² Lauren B. Buckley,³ Catherine L. Parr,^{4,5,6} Ethan B. Linck,⁷ Emily D. Fountain,⁸ and Michael K. Schwartz²

Fire regimes are a major agent of evolution in terrestrial animals. Changing fire regimes and the capacity for rapid evolution in wild animal populations suggests the potential for rapid, fire-driven adaptive animal evolution in the Pyrocene. Fire drives multiple modes of evolutionary change, including stabilizing, directional, disruptive, and fluctuating selection, and can strongly influence gene flow and genetic drift. Ongoing and future research in fire-driven animal evolution will benefit from further development of generalizable hypotheses, studies conducted in highly responsive taxa, and linking fire-adapted phenotypes to their underlying genetic basis. A better understanding of evolutionary responses to fire has the potential to positively influence conservation strategies that embrace evolutionary resilience to fire in the Pyrocene.

Fire and animal evolution

Fire has burned in the Earth system for millions of years [1]. Variation in fire activity – controlled by climate, fuels, and ignitions – has shaped patterns of life [2,3]. Fire exerts selective pressure on organisms to survive fire events [4], generates vegetation patterns that create niches to which species can adapt [5,6], alters accessible habitats [7,8], and drives large-scale mortality and dispersal events [9,10]. Most research studying the evolutionary role of fire has focused on plants, but emerging work is illuminating the role of fire in animal evolution [4,11].

Growing interest in the influence of fire on animal evolution comes as **fire regimes** (see Glossary) across many ecosystems are changing, driven by interactions among human land use and climate change [12]. Across different systems fires are burning more frequently [13], more severely [14], across larger areas [15], and with different seasonality [16], which can lead to ecosystem reorganization and/or collapse [17–19] with consequences for fauna [20,21]. Over 4400 species are vulnerable to extinction because of changing fire regimes, including >1000 species of birds, amphibians, reptiles, and mammals [22]. While these numbers are concerning, they do not consider how **phenotypic plasticity** or evolutionary responses to fire may facilitate persistence.

Will animals undergo adaptive evolution in response to changing fire regimes, or are changes happening too quickly for evolution to keep pace? Emerging evidence and syntheses suggest that animals not only have a greater capacity to rapidly evolve in novel environments than previously thought [23–25], but also that adaptive evolution may be occurring in direct response to fire regimes. Simultaneously, the widespread application of genomic methods has revealed the diverse impact of fire on evolutionary processes at the population level [26–28]. This has implications for biodiversity conservation and opens up a field of research investigating fire as a shaping force of animal evolution in the **Pyrocene** [4,29]. In this review we aim to synthesize the growing evidence for fire as a force in animal evolution, to define frameworks for its continued study, and to discuss the implications for wildlife and conservation under continued global change.

Highlights

Fire-driven animal evolution may occur rapidly in the Pyrocene, with potentially significant implications for biodiversity conservation.

Fire is an important evolutionary force that exerts strong selective pressure on many domains of life on Earth, including animals.

Innovative research has demonstrated genetic evolution by animals in response to fire and fire regimes, and suggests that evolution in wild populations can occur more quickly than was previously thought.

¹USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM 87102, USA

²National Genomics Center for Fish and Wildlife Conservation, USDA Forest Service, Rocky Mountain Research Station, Missoula, MT 59801, USA

³Department of Biology, University of Washington, Seattle, WA 98195, USA

⁴Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Liverpool, L3 5TR, UK

⁵Department of Zoology and Entomology, University of Pretoria, Pretoria 0028, South Africa

⁶School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa

⁷Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

⁸Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA

*Correspondence: gavin.jones@usda.gov (G.M. Jones).

The potential for rapid fire-driven animal evolution

Most literature demonstrating fire as an evolutionary force focuses on plants [11]. Because plants cannot evade fire, they must either evolve or perish. As such, plants experience strong selective pressure to develop morphological and physiological fire survival traits, or to ensure genetic legacies (e.g., seeds) survive fire [30]. Many plants thus have evolved physical traits such as thick bark (to survive fire) and serotiny (i.e., prolonged seed storage in closed cones, often in the canopy) to pass genetic material to the postfire environment. Such physical traits make plants emblematic of how life has evolved in fire-prone environments [3,30,31].

The literature on fire-adapted animal traits is less well developed. Does this lack of evidence suggest that animals are less fire-adapted? Not so. Because of their ability to evade fire, traits that confer fire survival in certain animals (**fire-adapted fauna**) [11] appear to be primarily behavioral, and thus are perhaps less conspicuous. However, morphological or physiological adaptations are also evident in animals, and the evolution of sensory capacity to recognize olfactory, auditory, and visual cues in response to fire is central to behavior-mediated fire evasion [4].

Whereas some adaptations are driven by the need to survive an active fire event, fire-driven animal evolution does not cease once the burning stops. Adaptations to the fire environment can occur along the full temporal axis of postfire vegetation succession, making some species early colonizers and others long-unburnt specialists (**fire-dependent fauna**) [11]. The black-backed woodpecker (*Picoides arcticus*) capitalizes on resource pulses that occur in recently burned forests [32], and eggs of Temminck's courser (*Cursorius temminckii*) are camouflaged to blend into recently burned substrates to reduce nest predation [33]. Higher solar radiation and lower humidity in postfire landscapes favor Iberian lizard individuals with higher preferred body temperatures and lower water stress [34]. Other animals are associated with the structure, composition, or dynamics of the postfire environment [5,35]. Pale field rats (*Rattus tunneyi*) in northwestern Australia depend on long-unburnt patches of vegetation within fire mosaics [36]. Thus, even animals with no clear associations with fire may have experienced strong selective pressure because of the fire regime that shaped vegetation dynamics over evolutionary time.

Because fire regimes are rapidly changing, animals do not have the luxury of time. Do animals have the capacity to rapidly evolve to contend with changing fire regimes over shorter time periods (i.e., tens of years)? Recent evidence suggests the answer might be yes. Bonnet *et al.* [25] studied population dynamics of 19 birds and mammals, finding that additive genetic variance – the prime determinant of rates of adaptive evolution – was substantially higher than was previously thought. Such high genetic variance could lead to rapid genetic evolution, even if such changes are phenotypically cryptic [37,38]. Rapid evolution may be most important where it counteracts environmental change and reduces the ecological impact of the disturbance (e.g., fire) on populations [39,40]. However, the mechanisms driving evolutionary responses to fire remain poorly understood.

Mechanisms for fire-driven animal evolution

Evolution is a change in allele frequencies in populations over time, resulting from selection (directional changes in allele frequencies because of a fitness differential), genetic drift (random sampling bias in alleles due to chance), gene flow (the exchange of alleles among populations), and/or mutation (the generation of new alleles during DNA replication) [41]. Fire regimes may influence all of these mechanisms, with the possible exception of mutation.

Selection

Pausas and Parr [11] identified three classes of traits that might be adaptive for animals living in fire-prone environments: behavioral (e.g., burrowing [42]), morphological (e.g., dark coloration

Glossary

Evolutionary trap: a phenomenon in which evolved cues become unreliable and ultimately maladaptive due to anthropogenic-induced environmental changes.

Fire-adapted fauna: animals that have evolved behavioral, morphological, or physiological traits that help them survive fires.

Fire-dependent fauna: animals that lack specific fire-adapted traits but are strongly associated with fire-prone ecosystems and/or the vegetation associated with postfire landscapes.

Fire naivety: a condition describing animals that are exposed to novel fire environments to which they are not appropriately adapted.

Fire regime: the typical size, severity, configuration, frequency, and related fire characteristics that occur across a landscape over long time periods. Fire regimes often vary across different climatic regimes, vegetation types, and topographies.

Megafire: a fire >10 000 ha in size arising from single or multiple ignitions [95]. Megafires are often also characterized by higher severity, but this is not always the case.

Phenotypic plasticity: the capacity of a genotype to result in a range of phenotypes under different environmental conditions.

Pyrocene: the modern, human-caused era of extreme fire behavior, characterized by greater negative impacts to society and ecosystems than in the past.

[43]), and physiological (e.g., thermophilia [44]) (Box 1). These groups of traits may respond to multiple modes of selection in response to fires and fire regimes (Figure 1). In stable fire environments (i.e., environments that have experienced similar fire regimes over many generations), fire reinforces dominant phenotypes (and genotypes) that help individuals cope with these specific fire regimes through stabilizing selection (Figure 1A). For example, we should expect stabilizing selection to act on effective and heritable fire escape behaviors in stable fire environments. Australian frilled lizards (*Chlamydosaurus kingii*) have evolved an escape behavior in which they

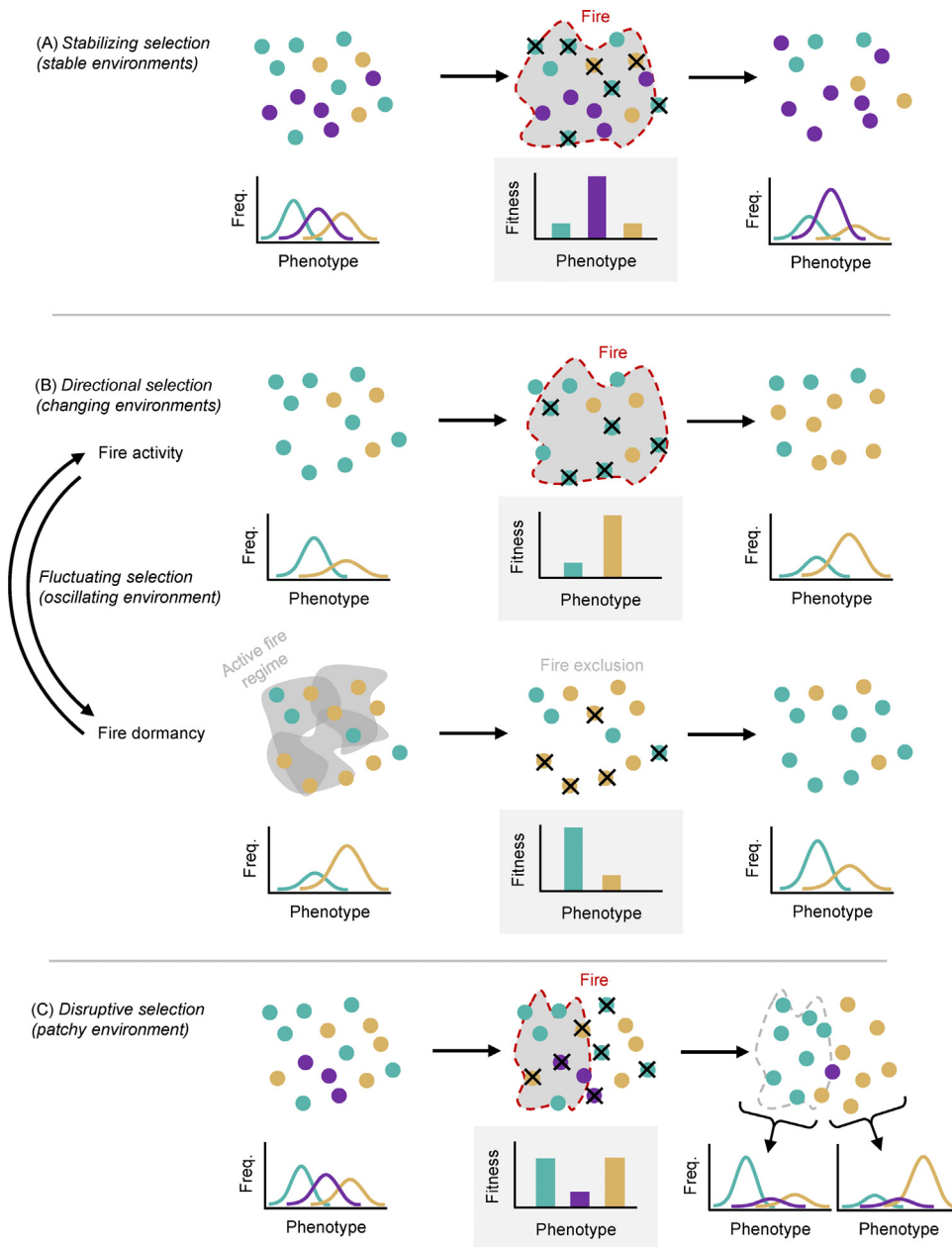
Box 1. Adaptive traits in animals related to characteristics of fire regimes

Natural selection has led to the accumulation of morphological, physiological, and behavioral traits allowing animals to survive fire or thrive in postfire environments. Western fence lizards (*Sceloporus occidentalis*) (Figure 1A) in southern California perch on blackened stalks of burned shrubs (that closely match the color of their scales) for several years postfire, but avoid perching on white stalks [96], an adaptive behavior reinforcing dark morphology in lizards in fire-prone shrublands. *Melanophila acuminata* beetles (Figure 1B) have evolved infrared sensory pits on the underside of their midsection (thorax) that allow them to sense forest fires and help protect individuals engaging in reproductive behaviors while fires are still burning [70]. California spotted owls (*Strix occidentalis occidentalis*) (Figure 1C) preferentially hunt in small (e.g., <1–10 hectare) patches of forests that have recently burned at high severity, where they find high densities of their small mammal prey [97]. *Antechinus* spp., small mouse-like marsupials (Figure 1D), have adapted a behavioral syndrome in which they shelter in place and enter a period of torpor while a fire passes through their habitat [4,98].



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Figure 1. Examples of animals with apparent fire-adapted traits. (A) Western fence lizards (*Sceloporus occidentalis*); (B) *Melanophila acuminata* beetles; (C) California spotted owls (*Strix occidentalis occidentalis*); and (D) *Antechinus* spp., a small mouse-like marsupial.



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Figure 1. Modes of selection in response to fire. (A) In stable environments, stabilizing selection promotes intermediate or average phenotypes. In this example, purple represents an intermediate phenotype, and teal and gold represent phenotypic extremes. When fire affects the population, fitness is higher for the intermediate purple phenotype than for the gold or teal extreme phenotypes, resulting in postfire dominance of the intermediate phenotype. We might expect these types of situations to occur in historically fire-prone landscapes that experienced predictable and short fire-return intervals. (B) In a changing environment, directional selection can shift the balance of phenotypes by favoring those that are beneficial in novel environments. In the first of two examples in this section, the teal phenotype is dominant prefire, but fire favors the gold phenotype that yields higher fitness in response to fire. The result is a shift of dominance from teal to gold. We might expect these situations under changing fire regimes, where previously beneficial phenotypes no longer provide the same benefits that they did under historical fire regimes. The second example in this section shows the same process,

(Figure legend continued at the bottom of the next page.)

use tree perches to shelter from low-severity fire early in the dry season and seek refuge in larger trees and termite mounds during high-severity, late-season fires [45].

Similarly, under stable fire regimes, cycles of fire impacts and recovery can result in fluctuating selection (i.e., periodic reversals in selective pressures [46]) (Figure 1B). Fluctuating selection leads to different phenotypes being favored during different postfire periods. This dynamic has been observed with cryptic coloration in a spur-throated grasshopper *Ronderosia bergii* [47]; darker morphs are more difficult for predators to detect in charred, postfire landscapes than lighter morphs, leading dark morphs to become relatively common after fires. As vegetation recovers, darker morphs become more detectable than lighter morphs and the population becomes dominated by lighter morphs. These cycles of selection maintain phenotypic variation in a population with regular fire cycles.

Altered fire frequencies may also trigger a shift from fluctuating to directional selection. Under directional selection, non-dominant, lower-fitness phenotypes under historical conditions may become advantageous in novel fire environments and become dominant (Figure 1B). For example, changing fire regimes can alter prey vulnerability [48], resulting in selection for less conspicuous phenotypes. Although few studies have quantified directional selection with shifts in fire, analogous shifts in selection for tawny owl (*Strix aluco*) plumage color have occurred as climate warming has reduced snow cover and altered background matching [49]; similar dynamics may occur as fire regimes change.

Fire may set the stage for disruptive selection in 'patchy' environments, favoring phenotypes associated with different resources or postfire characteristics (e.g., burned vs. unburned patches) while suppressing intermediate phenotypes (Figure 1C). In the southeastern USA coastal plain, a dynamic mosaic of burned and unburned patches of forest vegetation produced by frequent lightning fires appears to drive a disruptive selection in coat color melanism in the fox squirrel (*Sciurus niger*). In areas with higher lightning fire incidence, melanism is more common in fox squirrels, possibly because of the cryptic survival advantage of blending with blackened wildfire substrates; by contrast, nonmelanistic coat colors are more common in areas of lower fire incidence [50]. Subsequent work has shown that coat color polymorphism in fox squirrels is associated with fire-driven environmental heterogeneity (i.e., patchiness) [51], further suggesting a process of disruptive selection in fire-prone patchy environments.

Traits that were adaptive under historical fire conditions may become maladaptive under novel conditions, generating **evolutionary traps** [52]. Under low-severity fire regimes, animals may have evolved shelter-in-place behaviors to survive fire events; a similar tactic may produce substantial mortality in the face of large, high-severity **megafires**. The aforementioned behavioral adaption of frilled lizards to seek refuge in tree canopies during early dry-season grass fires may become maladaptive as invasive gamba grass (*Andropogon gayanus*) causes such fires to burn into the canopy, killing lizards [4]. At the same time, mortality can lead to rapid evolution of effective responses to new fire regimes. If the trait(s) related to fire are heritable, vary within the population, and create a fitness differential (i.e., different phenotypes show variance in survival), selection will act upon the distribution of trait values within a population. Trait evolution will proceed rapidly

but with the removal of fire from the landscape (i.e., through fire suppression) and a loss of traits that provide benefits in fire-prone environments. Periodic oscillations in fire activity and dormancy may result in a switching between the two selection syndromes, resulting in fluctuating selection. (C) In patchy environments, disruptive selection can create bifurcated patterns in phenotypic expression, promoting phenotypic 'extremes' that can capitalize on diverse resources. In this example, fire favors the teal and gold phenotypes (perhaps they specialize on different features of the burned landscape), resulting in a decline in the purple phenotype.

when selection events are of sufficient magnitude to kill a substantial proportion of individuals, but not so strong that phenotypic variation is insufficient to result in differential fitness.

Genetic drift

Fire, like other disturbances, can reduce census population size directly (e.g., fire-induced mortality) and indirectly (e.g., lowering habitat carrying capacity) [53,54], leading to a decreased effective population size and increased genetic drift [55]. Extreme instances of this phenomenon, population bottlenecks, are characterized by drastic reductions in the genetic diversity of the surviving population [56]. Strong genetic drift may lead to rapid fixation of neutral and adaptive traits [57], altering regional phenotypes and leading to inbreeding depression, behavioral failures, and an extinction vortex [58] in the absence of immigration. Maladaptive traits can also become fixed in small populations, increasing the genetic load of the population, and lowering population fitness. Small, declining, and/or fragmented populations may be particularly vulnerable to genetic drift as fire regimes change (Figure 2 and Box 2). Interactions between genetic drift and selection can also occur; genetic drift can counteract the effect of selection when effective population sizes are sufficiently small, as selection is inefficient in the face of drift [59]. Large, high-severity megafires seem especially likely to alter the evolutionary trajectory of range- and dispersal-limited species through their influence on genetic drift dynamics because of potentially high mortality rates at the population level [10,60].

Gene flow

In metapopulations, megafires may eliminate source populations, stepping stones, or corridors, thereby decreasing connectivity and gene flow [61,62] and leaving isolated populations more vulnerable to the impacts of genetic drift (Figure 2). Wildfires in the southwestern USA fragmented the coastal sage scrub habitat of cactus wrens (*Campylorhynchus brunneicapillus*), reducing genetic connectivity and diversity [61]. By contrast, fire can sometimes increase gene flow (Figure 2). For example, black-backed woodpeckers evolved to have extensive gene flow from the Rocky Mountains to Quebec, Canada, through the boreal forests, relying on fires to move in a stepping-stone pattern, whereas populations separated by unforested habitat became substantially isolated [63]. Many invertebrates rely on floral communities that emerge rapidly following fire. Wildfire increased the genetic connectivity of Boisduval's blue butterfly (*Plebejus icarioides*) in Yosemite National Park, CA, USA, by promoting regrowth of perennial lupin (*Lupinus* spp.), a larval food resource [64]. Whether fire facilitates or inhibits gene flow likely depends on the scale of the fire relative to animal dispersal capabilities [65], fire frequency, fire impacts on vegetation, and whether the species has existing fire-adapted traits [66].

Directions in fire-driven animal evolution research

Here we identify six priorities in fire-driven animal evolution research: (i) development of testable hypotheses, (ii) identification of promising study taxa, (iii) understanding the role of phenotypic plasticity and (iv) life-history strategies on evolutionary response, (v) connecting phenotypes to their underlying genetic basis, and (vi) exploring the potential for ecoevolutionary feedbacks.

First, we encourage the development of multiple broad, theory-driven hypotheses of animal evolution in response to fire. As an analog, we point to research on how physiological limitations to heat have informed the hypothesis that warming temperatures will shift species ranges upslope and to higher latitudes. This and other hypotheses about species-warming interactions have been tested extensively [67,68], and continuous evaluation of evidence against their predictions has refined our understanding of species responses to climate change. Are there similar, general hypotheses regarding how species might adapt to changing fire regimes? Nimmo *et al.* [4] developed hypotheses about animal adaptation to changes in fire cues using a predator-prey

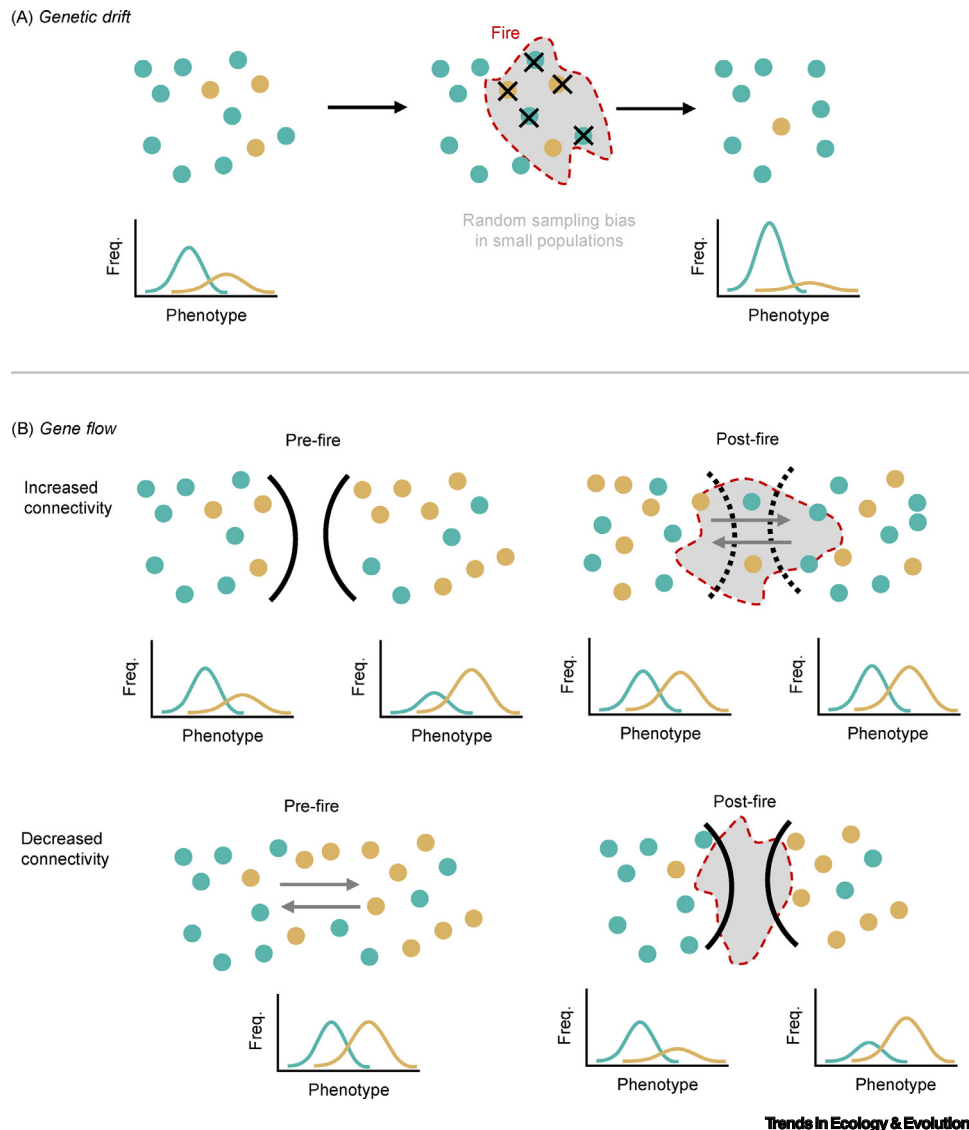


Figure 2. Fire-induced genetic drift and changes to gene flow. (A) Environmental stochasticity can lead to random loss of alleles from small populations, resulting in genetic drift. In this example, the teal phenotype is dominant in the population prefire and a fire wipes out the minority gold phenotype in the population, resulting in a random loss of genetic diversity following fire. (B) Depending on the species under study and the characteristics of the fire, fire can result in either increased or decreased gene flow through its influence on landscape connectivity. In the first of two examples, two populations with different levels of phenotypic dominance are isolated prefire, but fire increases the connectivity between the two populations and results in greater allelic mixing in the postfire landscape. In the second of two examples, a single population with relatively even distribution of phenotypes and high gene flow is split into two isolated groups postfire, resulting in lower gene flow and a skewing of phenotypes in the remaining populations.

framework. We expand on their work to propose several generic hypotheses for fire-driven animal evolution (Figures 1 and 2). Increasingly common megafires may create ‘natural experiments’ in which to evaluate such hypotheses [10].

Second, rapid selection-driven evolutionary change is best studied in species with large population sizes and short generation times. Although rapid evolution can and does occur in wild

Box 2. Genetic drift from fire in the Mallee Emu-wren

A globally endangered passerine, the Mallee Emu-wren (*Stipiturus mallee*) (Figure 1A) is endemic to small, isolated populations in southeastern Australia (Figure 1B). The Mallee Emu-wren is also a habitat specialist, strongly dependent on spinifex grass (*Triodia scariosa*) which provides important cover from predators (Figure 1C). Its short wings and long tail make the Mallee Emu-wren a poor flier, and thus the species is characterized with limited dispersal abilities. The Mallee shrubland ecosystem in which the Mallee Emu-wren lives is highly fire-prone, raising the possibility of fire-driven evolution via genetic drift. Between 2006 and 2009, Brown *et al.* [99] captured 72 Mallee Emu-wrens and sampled the genetic diversity and structure across six study areas in Victoria, Australia, using mitochondrial and nuclear loci.

In some study areas, researchers found evidence of recent population bottlenecks and genetic drift, indicating recent declines in effective population size (i.e., the number of individuals contributing to the breeding population). These genetic features were consistent with population declines that had been documented following a series of fires in the region that occurred just prior to the onset of the study (between 1999 and 2006). These fires resulted in further isolation of small populations of Mallee Emu-wrens, contributing to the observed prevalence of several monomorphic loci resulting from bottlenecks and genetic drift. The authors concluded that the persistence of the species is now precarious, threatened by continuing megafire events and now the potential for inbreeding depression.

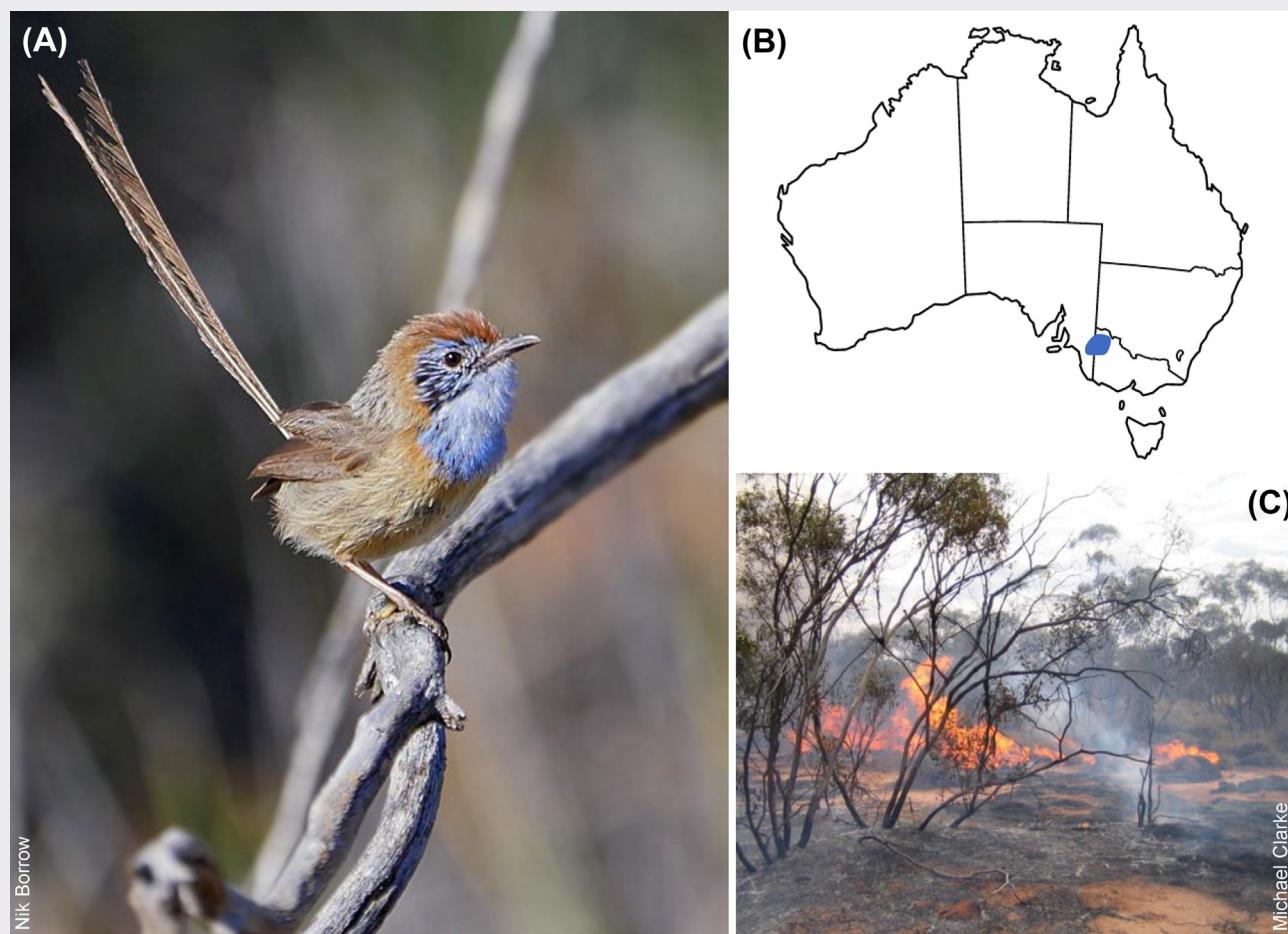


Figure 1. (A) The Mallee Emu-Wren (*Stipiturus mallee*), (B) its range, and (C) a Mallee bushfire.

vertebrate populations [25], insects might provide a more immediately promising group for the study of rapid fire-driven evolution [69]. Insects appear most often to have developed morphological fire adaptations [11]. For example, *Melanophila* beetles have evolved infrared sensory pits that enhance their reproductive success in burning environments, allowing them to navigate safely and oviposit on exposed tree roots [70]. Given the strong evolutionary pressure of fire on plants,

we further expect that insects – often closely dependent on plant communities and floral structures – will coevolve with plants in response to novel fire regimes in some cases. Insects also lend themselves more easily to controlled laboratory experiments involving adaptive responses to fire or fire stimuli.

Third, little is understood regarding the distinction of, and interplay between, genetic adaptation and phenotypic plasticity in animal responses to fire. Given its role in animal response to global change [71,72], phenotypic plasticity will likely influence how animals respond to changing fire regimes. Phenotypic plasticity was responsible for differences in movement speeds in eastern fence lizards (*Sceloporus undulatus*) across landscapes with different burn characteristics, a trait closely linked to fitness in this species [73]. Phenotypic plasticity varies across populations, and is often greater in populations experiencing more variable environments [74,75]. Species inhabiting historically fire-prone environments may exhibit greater levels of phenotypic and behavioral plasticity in their response to fire than those inhabiting environments where fire is historically uncommon. Additionally, the adaptation–plasticity interplay may be complex. Although plasticity may enable persistence by creating time for adaptive changes to accumulate, plasticity can shield genotypes from selection, slowing adaptive responses [76]. Behavioral buffering of selection can slow evolution (i.e., the Bogert effect [77]), and the dynamic is likely to be particularly relevant for fire given the prominence of behavioral buffering in animals. However, plasticity might also facilitate fire-driven evolution by exposing and allowing selection on phenotypic variation (e.g., traits related to escaping fire).

Fourth, evolution of fire-adapted traits may occur within a broader constellation of traits, such as the ‘bold–shy continuum’ [78] or the ‘slow–fast continuum’ [79] of life-history strategies. This view provides a potential framework for understanding how individuals respond differently to fire-associated risk [4]. Bold individuals, or organisms with relatively fast life-history strategies, may wait longer to flee an approaching fire or may explore riskier postfire environments. In both cases, individuals on the fast/bold end of the spectrum accept greater risk in return for a potentially greater reward. If this variation within species is heritable, then these correlated trait syndromes can become the target of selection and explain changes in the distributions of traits within the population.

Fifth, genomic tools should be leveraged to reveal connections between fire-adapted phenotypes and their underlying genetic basis, which remains poorly understood. Adaptive traits vary widely in their underlying genetic architecture, although clues can be gained by examining the strength of their response to selection. Adaptive melanation in the peppered moth (*Biston betularia*) has been linked to a single locus [80], leading to predictable patterns of inheritance and a rapid, well-characterized response to directional selection. By contrast, behavioral traits, even relatively ‘simple’ ones, tend to have a complex, multilocus genetic basis [81], leading to unpredictable evolutionary dynamics [82]. We suggest that the majority of fire-adapted phenotypes in animals will likely be polygenic, and encourage researchers in this area to stay abreast of developments in empirical and theoretical quantitative genetics.

Finally, animals may influence fire regimes via ecoevolutionary feedbacks, where ecological interactions influence evolutionary change, which in turn influences ecological interactions [83]. Animals can act as ecosystem engineers, influencing fire behaviors by altering fuel amount, fuel structure, fuel condition, and wind patterns or ignitions [84]. For example, black kites (*Milvus migrans*) modify ignitions by dropping burning sticks from nearby fires into unburned areas, facilitating their hunting activities [85]. Thus, as fire regimes change, animals may evolve behaviors to capitalize on such changes, which may subsequently influence fire regimes.

Implications for biodiversity in the Pyrocene

How might fire-driven animal evolution in the Pyrocene influence biodiversity conservation? Often, when considering fire–biodiversity interactions, conservation scientists consider proximate fire effects to animal populations and communities. Does fire make populations increase or decrease in size? Does fire result in fewer or more species? Illuminating fire’s role in animal evolution – a process that by definition occurs on the scale of generations and thus extends beyond its influence on contemporary populations – will help conservation practitioners embrace fire as a tool in ecosystem restoration (Box 3) and open evolutionary frameworks for conservation in fire-prone landscapes.

While fire-adapted traits may accumulate in populations with active fire regimes, the same traits may be lost during fire exclusion. Fire exclusion policies and widespread abolition of indigenous burning practices [86,87] has led to a transformation in forest conditions in some systems [88,89]. During fire exclusion, fire-adapted traits might provide little to no fitness benefits (or may even be maladaptive), exposing them to negative selection and reducing their frequency in the population if their maintenance results in fitness costs (Figure 1B). For example, sensory traits

Box 3. Shaping animal evolution through fire management?

A popular hypothesis in the scientific literature is that ‘pyrodiversity begets biodiversity’ [5], or that the presence of a wide variety of postfire landscape characteristics are associated with a greater number of species. Yet another framing of this hypothesis is that over evolutionary time, pyrodiversity might have influenced the rise of animal diversity itself [2]. To our knowledge, this second framing has never been tested, and we suggest it might be a fruitful area of evolutionary research. Looking ahead, however, could the way we manage fire influence evolutionary trajectories of animals?

People have used fire to influence natural resources for their benefit over millennia. Indigenous communities across the globe have long used cultural fire to modify resources (Figure 1A), which has led to enormous benefits for biodiversity [87]. Government-prescribed fire programs seek to reduce accumulated fuels and fire risk to communities and resources (Figure 1B). Whether natural or human-caused, fire will influence the evolution of animal communities through selection, genetic drift, or connectivity (see Figures 1 and 2 in main text). Populations with long histories of exposure to human fire use may have adapted a unique suite of traits to capitalize on cultural fire.

While the timescales of modern fire management are unlikely to result in speciation, changes to fire policies could be evaluated in part by how they influence the genetic diversity and evolutionary potential of wildlife populations. For example, cultural fire use could increase the genetic connectivity of populations of Boisduval’s blue butterfly (*P. icarioides*) in Yosemite National Park (CA, USA) [70], thereby altering the distribution of beneficial alleles among subpopulations and increasing species evolutionary resilience.



Trends in Ecology & Evolution

Figure 1. Human use of fire (A,B) influences patterns of fire, vegetation regeneration, and biodiversity.

of fire vigilance and fire cue perception and assessment in animals could be weakened during long periods of fire exclusion (e.g., that span several generations) when such traits may provide no fitness benefits [90]. Loss of fire-adapted traits has implications when considering restoring fire; introducing fire may be seen as beneficial, but local populations may have lost traits needed for resilience and persistence. Thus, systems experiencing differing levels of fire exclusion might follow different evolutionary trajectories in the Pyrocene because they begin with different degrees of variation in fire-adapted traits.

Populations may enter the Pyrocene with differing capacity to effectively respond to the fitness challenges fire poses. Nimmo *et al.* [4] proposed animal populations will exhibit varying levels of **fire naivety** to novel fire regimes. Level 1 fire naivety occurs in populations seldom exposed to fire over evolutionary time, thus having no behavioral capacity to survive fire. Levels 2 and 3 fire naivety occur when historically effective reactions are now ineffective to promote survival in the face of novel fire behaviors (e.g., megafires). Fire naivety raises a crucial question for conservation in the Pyrocene: can populations rapidly evolve new traits that facilitate persistence during and after fire? Will populations show evolutionarily resilience to ‘mass-selection’ events imposed by megafires [10]?

Evolutionary resilience describes the ability of a species to persist in its current state (i.e., fitness under current conditions) while also maintaining the capacity to adapt in response to novel environments [91]. Animals inhabiting fire-prone landscapes will likely have high average fitness under historical fire regimes (i.e., they will be fire-savvy). However, under novel fire regimes, all populations will express some degree of fire naivety [4], and the degree of naivety might depend on historical variation in fire regimes. The key to evolutionary resilience under novel fire regimes will be whether populations are sufficiently large and genetically diverse to contain adequate variation in fitness-relevant trait values to maintain evolutionary potential [92,93], exhibit sufficient phenotypic and behavioral plasticity to endure extreme fire events [94], or whether they have the capacity to recover quickly after fire (i.e., because of high immigration or population growth rates). If conservation practitioners can obtain information on variation in fire response traits in natural populations, conservation actions could be prioritized to facilitate propagation of fire savviness and influence evolutionary resilience.

Concluding remarks

Changing fire regimes are likely to have a profound influence on the evolutionary trajectory of animal populations, which will likely manifest rapidly over ecological timescales. We must acknowledge that fire is not just a process that influenced evolution long ago, and it is not simply an external force that periodically disrupts contemporary population dynamics. Instead, changing fire regimes are influencing animal evolution in front of our eyes. We see a need to incorporate evolutionary thinking into approaches for conserving populations under changing fire regimes, including detecting symptoms of fire naivety and identification of potential fire-savvy traits that could be leveraged for conservation. Our approaches for research in fire-prone environments must recognize this changing view (see [Outstanding questions](#)). Doing so will allow for improvements to conservation efficacy in the Pyrocene.

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Declaration of interests

No interests are declared.

Outstanding questions

How will the rate of animal evolution in response to changing fire regimes (in terms of both gaining and losing traits that will facilitate persistence) balance with the rate of fire-induced extinction?

How will changing fire regimes alter the quantity and distribution of neutral and adaptive genetic variation? Might the impacts of novel fire regimes interact with other stressors to shape evolutionary responses of populations?

How might the spatial and temporal scales of altered fire regimes interact with the dispersal ability and generation times of species to influence fire-driven animal evolution?

How widespread are fire adaptations in animal communities, including cryptic phenotypes?

How have historical fire regimes shaped the quantity and distribution of genetic variation in animal species, and how will novel fire regimes shape it in the Pyrocene? In what taxa, ecological guilds, and context can we convincingly link fire events to changes in gene flow and effective population size?

Are there certain phenotypes (e.g., on the fire-naïve–fire-savvy spectrum) that are predicted to be beneficial under novel fire conditions that were not advantageous under historical fire regimes? How might this inform conservation and restoration actions?

How can fire management programs be informed by science to help shape evolutionary resilience of animal populations in fire-prone environments?

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