


Towards an understanding of the evolutionary role of fire in animals

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Abstract Wildfires underpin the dynamics and diversity of many ecosystems worldwide, and plants show a plethora of adaptive traits for persisting recurrent fires. Many fire-prone ecosystems also harbor a rich fauna; however, knowledge about adaptive traits to fire in animals remains poorly explored. We review existing literature and suggest that fire is an important evolutionary driver for animal diversity because (1) many animals are present in fire-prone landscapes and may have structural and phenotypic characters that contribute to adaptation to these open landscapes; and (2) in some cases, animals from fire-prone ecosystems may show specific fire adaptations. While there is limited evidence on morphological fire adaptations in animals, there is evidence suggesting that different behaviors might provide a rich source of putative fire adaptations; this is because, in contrast to plants, most animals are mobile, unitary organisms, have reduced survival when directly burnt by fire and can move away from the fire. We call for research on fire adaptations (morphological, behavioral, and physiological) in animals, and emphasize that in the animal kingdom many fire adaptations are likely to be behavioral. While it may be difficult to discern these adaptations from other animal behaviors, making this distinction is fundamental if we want to understand the role of fire in shaping biodiversity. Developing this understanding is critical to how we view and manage our ecosystems in the face of current global and fire regime changes.

Keywords Adaptations · Behavioral traits · Evolutionary fire ecology · Fire-fauna

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Introduction

It is now well known that fire is an intrinsic and natural process in many ecosystems (Pausas and Keeley 2009). Yet while plants have a plethora of adaptive traits that enable them to persist under recurrent fires (Keeley et al. 2011, 2012), understanding of how fauna has responded to fire is much more limited (Parr and Chown 2003). There is a rich fauna occurring in fire-prone ecosystems that has evolved under frequent fires, therefore it is likely that this recurrent and predictable disturbance has influenced the evolution of fauna. However, the evolutionary role of fire on animals remains inadequately explored (Fig. 1), and this gap in knowledge has cascading effects on how we view and manage our ecosystems.

Different fire responses are expected to evolve in animals and plants (in terrestrial ecosystems) due to their intrinsic differences in mobility and modularity. Plants are rooted (i.e., immobile) and modular; they cannot easily escape from fires but can survive with a reduced number of modules. This has allowed the evolution of structural traits for in situ persistence (survival and population persistence; Pausas et al. 2004; Keeley et al. 2011). There are also some plants that rely on seed dispersal (the mobile phase of plants) for postfire recolonization from neighbor populations (exogenous regeneration), although they are not common in most fire-prone ecosystems. Most terrestrial animals are mobile and unitary organisms (colonies that function as a superorganism, such as those of ants and termites, may be a notable exception); survival and persistence is negatively affected if they are burnt, although they have the capacity to move away from the fire. Consequently, behavioral traits to avoid fires are expected to be particularly important in animals in flammable environments. However, if demonstrating that some structural traits in plants are the response to a history of fire is challenging (Keeley et al. 2011), disentangling the

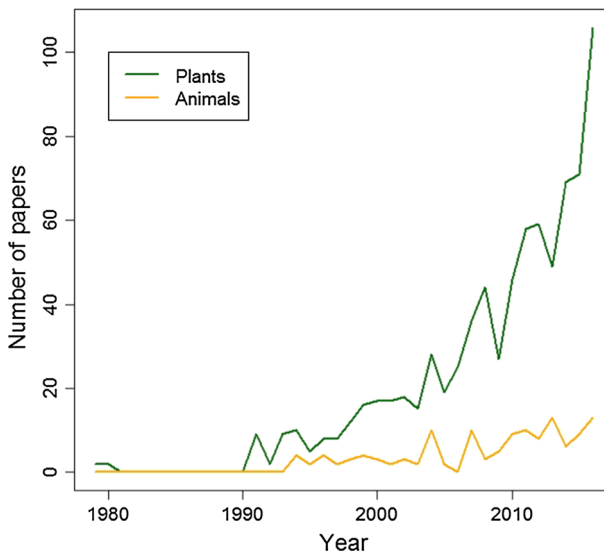


Fig. 1 Number of papers published on the evolutionary fire ecology of plants (green line; upper line) and animals (orange line; lower line) during the recent years. Data based on the number of papers in the Science Citation Index Expanded that matched the following searches: for plants: “fire AND (plants OR vegetation) AND evolution*”; for animals: “fire AND (animals OR fauna OR wildlife) AND evolution* NOT ‘fire ant*’”

role of fire from the role of other enemies (predators) in shaping fire avoiding behavior in animals is even harder; yet this is fundamental if we aim to understand the role of fire in shaping biodiversity.

There are many papers and several reviews (e.g. Whelan 1995; Smith 2000; Swengel 2001; Whelan et al. 2002; New 2014; van Mantgem et al. 2015; Bowman et al. 2016) on the ecological responses of fauna to fire, including postfire successional studies and studies of animal communities under different fire regimes. They depict a reorganization of animal communities in response to fire, with positive and negative responses, depending on the species, fire characteristics, and recovery speed of the system. Our aim is not to summarize these studies but to highlight that fires are an important evolutionary driver for understanding animal biodiversity. To do so we briefly compile evidence suggesting that there are animals well adapted to fire-prone ecosystems, that is, to the habitat generated by recurrent fires; yet although they require fires for survival (**fire-dependent animals**), they do not necessarily show any specific morphological adaptation to fire. There are also a few documented cases of animals with traits that can be considered shaped by fire (**fire-adapted fauna**). However, research on the evolutionary aspects of the fire-fauna relationship is still in its infancy, and many of the putative adaptations have not been rigorously tested. Here we aim to stimulate further research in this potentially fruitful area to fill a gap in understanding biodiversity drivers (Table 1). Developing this understanding is critical in the face of the current rapid global changes, which certainly include fire regime changes (mostly increasing in size and intensity, although it depends on the ecosystem; see Keeley and Syphard 2016; Schoennagel et al. 2017; Chergui et al. 2018).

Fauna adapted to fire-prone habitats

There are many animals present in fire-prone landscapes and they have structural and phenotypic traits that contribute to adaptation to this habitat; that is, they benefit from the habitat generated by recurrent fires (Table 2). In some instances, they may be quite specialized in the sense that they require fire to create the appropriate conditions for growth and reproduction. Although these species may not show any apparent adaptation to survive or to avoid fire, their population size increases after fire, i.e., they are adapted to the

Table 1 Some key questions for improving our understanding of the evolutionary role of fire in animals

Scale/approach	Question
Among closely-related taxa	Can taxa (or populations) in fire-prone habitats detect, avoid and survive fire better than those in non-fire prone areas, and if so, how?
Population	To what extent are fire-related behavioural traits variable and heritable?
Population	To what extent have fire regime changes (e.g., fire exclusion, increased fire frequency, lengthened fire season) generated evolutionary shifts in these behavioural traits? i.e. how labile are these traits?
Population	Are (post-fire) colonization traits under strong selection in fire landscape mosaics?
Population	What fitness benefit is conferred by the use of fire directly or postfire habitats for species without any apparent fire-adaptation?
Community	Does the prevalence of species with behaviour that confer fire protection (e.g., burrowing behaviour) differ under contrasting fire regimes?

Table 2 Example of the possible benefits to animals of fire and fire-altered habitat

Benefit	Category	Fauna [references]
Fresh grasses, and leaves	Food resource	Herbivores, e.g., large mammalian grazers, insect herbivores, arboreal marsupials [1, 2]
Fire-released seed, and more exposed seeds in the soil	Food resource	Granivores including rodents, seed-removing ants [3]
Animals fleeing or dying	Food resource	Predators, scavengers (e.g., birds, kites, owls, ants)
Weakened and dead trees	Food resource	Bark beetles, cavity-dependent (hollow-nesting) animals like woodpeckers, other birds, lizards, possums [4]
Dead wood	Food resource	Saproxylic insects [5–7]
Flowers, post-fire blossom	Food resource	Insect pollinators [12–15], hummingbirds [16]
Meeting point	Mating cue	Saproxylic insects [8,9], smoke flies [10], mole crickets [22]
Synchronization of the emergence	Mating cue	Insects (some beetles; [11])
Reduced habitat complexity: increased visibility	Habitat alteration	Birds of prey; large herbivores, primates (easier to move and detect their predators [17]);
Reduced habitat complexity: movement through the environment	Habitat alteration	Grouse (gaps for mating: [18]), seed-dispersing ants (move further with fire [19])
Microclimate change	Habitat alteration	Ectotherms—e.g. thermophilous reptiles, insects [20] (warmer post-fire environment)
Reduction of parasites	Biotic interactions	Vertebrates [21]
Reduction of predators	Biotic interactions	Insects (e.g., reduction of insectivore vertebrates) [23]

By benefits (first column) we refer to the changes in resources and conditions generated by fire that can be used by the fauna groups mentioned (third column), and are aggregated in four categories (second column): Changes in food resources, mating cues, habitat alterations, and changes in biotic interactions. Note that the benefits have cascading effects affecting interacting species (e.g., predators, parasites, mutualistic partners). For instance, fire attracts many insects (e.g., bark beetles, saproxylic insects) that are the food of many birds (e.g., Hovick et al. 2017). Additional examples can be obtained from reviews like those in North America (Smith 2000) or in Australia (Whelan et al. 2002)

References [1] Lopes and Vasconcelos (2011), [2] Romme et al. (2011), [3] Andersen (1988), [4] Gibbons and Lindenmayer (2002), [5] Boucher et al. (2012), [6] Koivula et al. (2006), [7] Kiltie (1989), [8] Evans (1966), [9] Evans (2010), [10] Klocke et al. (2011), [11] Jacobs et al. (2011), [12] Bernhardt (1990), [13] Fulton and Carpenter (1979), [14] Prada et al. (1995), [15] Potts et al. (2003), [16] Contreras Martínez and Santana (1995), [17] Jaffe and Isbell (2009), [18] Hancock et al. (2011), [19] Parr et al. (2006), [20] Christian and Morton (1992), [21] Scasta (2015), [22] Howard and Hill (2007), [23] Pausas et al. (unpublished)

conditions generated by fire, and thus, dependent on a given fire regime (fire-dependent animals). In many cases, drivers other than fire, like human disturbances (e.g., clearing), can generate similar habitats and responses, however here we focus principally on cases in natural settings, where these conditions are mostly generated by wildfires (and in some cases, by prescribed fires too).

Some animals are directly killed by fire (by either heat or smoke), but it is generally thought that many escape from it by moving to safe sites. Because the postfire environment differs strongly to prefire conditions, some animals substantially alter their diet and behavior after fire (e.g., Stawski et al. 2015; O'Donnell et al. 2016). Other species can be negatively affected due to either starvation or increased predation in open conditions (indirect fire effects; e.g. Leahy et al. 2016). Fire-related mortality and the degree of habitat structural change largely depend on the characteristics of the fire (intensity, season, extent, patchiness); for example, high intensity crown-fires usually cause greater changes in the habitat and faunal communities than low intensity surface fires (see Smith 2000 for examples).

Among the animals that require habitat created by fires, there are those species that inhabit open conditions or large forest gaps (Table 2); these include large mammalian herbivores that feed on new high quality vegetation regrowth after fires. Many large herbivores are adapted to the grassy environment provided in flammable open habitats (Parr et al. 2014; Bowman et al. 2016) (e.g., tropical savanna, tallgrass prairies), and easily coexist and interact with the surface fires occurring in these ecosystems (Fuhlendorf et al. 2009). Although in many instances the benefits have not usually been framed in terms of fitness, there are exceptions. For instance, the availability of postfire regrowth in the early dry season has been shown to help sable antelope (*Hippotragus niger*) cope with the nutritional limits posed by the dry season, and is especially critical to lactating females (Parrini and Owen-Smith 2010). The evolution of some diets in animals (C4 diet specialists, e.g., grasses and sedges) has been linked to the evolution and spread of fire-prone grassy ecosystems (Edwards et al. 2010). In addition, herbivores may also modify fire regimes themselves (Pausas and Keeley 2014), and in some cases, there may be feedback processes between fire and animals in such a way that animals generate fire regimes more appropriate for their survival (niche construction); this includes large herbivores that maintain tree-grass ecosystems (van Langevelde et al. 2003), and animals that by removing litter, inhibit surface fires around them (e.g. ants and some ground-nesting birds, Carvalho et al. 2012; Nugent et al. 2014; Smith et al. 2017). Given that many parasites, including ticks, have a life stage in the vegetation, fire can also benefit some vertebrates by killing parasites and reducing the spread of diseases (Scasta 2015). Thus, the post-fire period can provide a window of health and opportunity for many vertebrates.

Some animals using the post-fire environment are opportunistic species that are widely distributed, while others are highly specialized to postfire conditions and seldom occur outside burned areas. For instance, there are many insects living in dead wood or weakened trees that benefit from (or depend on) fire and respond positively by increasing their populations after fire (Table 2). In fact, some populations of fire-dependent saproxylic insects have been reduced in northern Europe due to the suppression of natural fires from managed forests; prescribed burns are now being used as management strategy to aid their conservation (e.g., Wikars 2002). Among vertebrates, there are some emblematic examples of fire-dependent birds in different environments, including the black-backed woodpecker (*Picoides articus*) that inhabits severely burned coniferous forest of North America (Collard 2015); it feeds on wood-boring beetle larvae and nests in trees recently killed by fire. That is, fires may favour some species (e.g., the beetles in this case) and have positive cascading effects on other trophic levels (predators; Hovick et al. 2017) and interacting species. Other emblematic examples of fire-dependent animals include the migratory hummingbirds in tropical ecosystems that depend on post-fire flowers (Contreras Martínez and Santana 1995), or grouse (*Tetrao* species) that require open gaps in the boreal forest for mating (Hancock et al. 2011). Frill-necked lizards (*Chlamydosaurus kingii*) of northern

Australia occur at higher densities and have higher body mass on burnt as opposed to unburnt sites, because of greater prey accessibility (Corbett et al. 2003). Feral cats have been shown to travel long-distances to reach intensely burnt habitats where food is easier to detect (McGregor et al. 2016). Small prey must balance their increased risk of predation against the benefit of available resources (e.g. new plant shoots) in the burned area. The altered conditions postfire (light, soil nutrient availability, enhanced seed germination) often result in a bloom of flowers shortly after fire that benefits pollinators (e.g., Bernhardt 1990; Contreras Martínez and Santana 1995; Potts et al. 2003). This increase in pollination is likely to also benefit predators (Hovick et al. 2017; cascading effects), and to affect the whole structure of the web of interactions, but little research has been performed at this scale in postfire conditions.

There are other animals that appear to benefit from specific postfire successional stages; many are from forested environments where changes to the habitat following fire persist much longer than in grassy systems (e.g. savannas). Vegetation structure is a classical niche dimension (MacArthur and MacArthur 1961). There are many studies across a range of taxonomic groups documenting successional replacement of species over several decades as habitat changes following a fire (for a classical example, Fox 1982). Similarly, there are a number of studies reporting different animal communities depending on the different vegetation structure determined by different fire regimes. While many species may do well across different stages, in some cases the specialization is particularly strong. An iconic example is the Leadbeater's possum (*Gymnobelideus leadbeateri*) that was very rare in Australia and thought to have gone extinct after the extensive 1939 Black Friday fires burned their entire distribution range (Gibbons and Lindenmayer 2002). However, forest regrowth provided food, and large dead trees left still standing after the fires provided shelter and nesting allowing the Leadbeater's possum population to greatly expand from prefire conditions (Gibbons and Lindenmayer 2002). No obvious adaptation to survive fire can be seen in this creature, yet their habitat requirements are only provided by the occurrence of large infrequent fire. The existence of species adapted to different vegetation structures or to a mix of different postfire successional stages provides conservation value to landscape mosaic of different postfire age and has led to the use of "patch mosaic burning" for conservation (e.g., Legge et al. 2015; Berry et al. 2016). It is also the base of the idea that "pyrodiversity begets biodiversity" (Martin and Sapsis 1992; Parr and Andersen 2006; Bowman et al. 2016).

While some species can benefit from the habitat generated by recurrent fires, other animals also benefit from the fire itself, i.e., directly as it is occurring. It is common, for example, to see birds of prey (e.g., Bonta et al. 2017) and other opportunistic species (e.g., fork tailed drongos, *Dicrurus adsimilis*, in Africa; C.L. Parr, pers. observ.) catching insects fleeing the fire front, while other bird species (e.g., white storks, *Ciconia ciconia*; Corbett et al. 2003; and different egrets species, J.G. Pausas, pers. observ.) walk behind the fire feeding on recently charred invertebrates (fire-foraging). There is even some evidence of raptors intentionally spreading fire for increasing the availability of preys (Bonta et al. 2017). However, the contribution of this food source to their diet and survival during the dry season remains to be quantified (Table 1). Insects that have fire detectors and are attracted to the flames also benefit directly from fire (Schutz et al. 1999; Evans 2010; see below).

Overall there are many species that, in one way or other, are dependent on particular fire regimes for completing their life cycle. These species may not show any apparent fire adaptation, but almost certainly they would become very rare or even extinct in the absence of fires generating their habitat. Species in open fire-prone habitats may not necessarily be adapted to fire but to landscapes or biomes generated under a certain fire regime. In short,

we cannot imagine the great diversity of many open ecosystems, including the fauna they contain, without the existence of fires. This begs the question: to what extent do some of these animals show specific fire adaptations? This is relevant for understanding the evolutionary pressures shaping diversity, and has implications for land and fire management. Below we review evidence of putative adaptations to (a) survive fire, and (b) to survive and exploit postfire conditions.

On the search for fire adaptations in animals

Dealing with fire: fire survival adaptations

Many plants in fire-prone ecosystems persist after a fire thanks to morphological adaptive traits conferring survival (e.g., thick bark and resprouting structures; Keeley et al. 2012; Pausas 2015; Pausas et al. 2018). This is not necessary true for animals; their mobility and general lack of modularity means that behavioral traits are more likely to evolve. Because the direct fire impact is often detrimental to animals, developing or enhancing behaviors to rapidly detect fires (e.g., from the smoke or sound) and escape from them could be adaptive in recurrently burned ecosystems. However, it is not always easy to discern the role of fire from the role of predators in shaping those behaviors. Examples of fire-related behavior include the evidence that some bats and possums can detect smoke even when in torpor, and thus they arouse and move to a safe site (Scesny and Robbins 2006; Nowack et al. 2016). Behaviours that allow detection and avoidance of fire are especially important in less-mobile animals (Whelan 1995); for instance, some frogs appears to recognize the sound of fire and quickly move to less flammable habitats (Grafe et al. 2002). Newts have been observed rapidly crossing fire fronts to move to unburnt refuges; apparently, their skin secretion facilitates their survival (Stromberg 1997). Terrestrial tortoises are abundant in some fire-prone ecosystems (Ernst et al. 1995; Sanz-Aguilar et al. 2011); yet, little is known about their ability to detect fire and move to refuges (ground holes, bare patches), or to what extent recurrent fire may have selected for some morphological traits to increased protection. Some Australian lizards make use of holes in the soil for shelter in frequently burnt habitats but do not use them in habitats that experience lower fire frequencies (Braithwaite 1987). Many non-flying invertebrates (e.g. ants, stick insects, wingless nymphs of grasshoppers, spiders) appear to be able to detect fires well in advance of the front, presumably from smoke or sound; they attempt to shelter from fires by either moving into the soil, or by climbing to the tops of trees (Sensenig et al. 2017; Dell et al. 2017). Some animals in fire-prone ecosystems do not appear to show stressed behaviour in the presence of fire, but move calmly and search for a safe site or for a low flammability patch (Whelan 1995). Outstanding examples are the case of primates, including chimpanzees (*Pan troglodytes*), which through a complex suite of behaviours to avoid fire, including observing and predicting fire behavior, communicate to each other about the fire's occurrence, and move accordingly without showing signs of stress (Pruetz and LaDuke 2010). And after fire, they expand their home range to the burned area for food gathering, including eating "cooked" fruits (Herzog et al. 2014). Another putative behavioral adaptation is the case of those animals that evade the fire by actively excluding it, as some ants or the Australian lyrebird that, by consuming or moving litter, they inhibit surface fires around their nests (Carvalho et al. 2012; Nugent et al. 2014). Some species can enter torpor as food availability decreases and the exposure to predators increases postfire; this may also provide benefits in postfire conditions where resources are low. This is the

case of some small mammals that do not leave their home range after fire but remain hidden and reduce their activity by lowering their body temperature and increasing multi-day torpor (Stawski et al. 2015).

To what extent fire has contributed to shaping all these escape-avoiding behaviors in animals is unclear because most studies have not been framed in terms of fitness benefits (Tables 1, 3). It is likely that fire acts as a selection pressure in many of these animal behaviors, in a similar way to other changes in enemy pressure. For example, animals living on islands are less wary than those on the mainland, presumably because of the lack of predators (Cooper et al. 2014). Even over a short time scale, many animals modify their behavior in response to recent changes in predators (e.g., Samia et al. 2015; Geffroy et al. 2015; Mikolajewski et al. 2016; Dröge et al. 2017). Despite animal behavior being the product of multiple selective pressure (as many other traits), species living under long contact with fires may have evolved particular behaviours to increase fire survival (Table 3). The search for mechanisms driving putative fire adaptations in the animal kingdom is an open research area (Tables 1, 3).

Table 3 Examples of traits that may be adaptive for animals living in fire-prone ecosystems, and thus they are candidate traits that could be modified by natural selection (i.e., fine-tuned by fire) or could be over-represented, in fire-prone ecosystems

Trait	Type	Examples [references]
Ability to make a hole for protection	Behavioral	Small mammals, large arthropods
Ability to use a shelter for protection	Behavioral	Reptiles [1]
Ability to modify fuel continuity	Behavioral	Ground-dwelling birds [29, 30]
Burrowing live	Behavioral	Arthropods [28], reptiles
Non-panicked response	Behavioral	Primates [5], other mammals
Nesting deeper in the soil	Behavioral	Arthropods [28], reptiles
Ability to move long-distance	Behavioral	Mammalian predators [6]
Fire detection	Behavioral/ Morphological	Vertebrates [2–4]
Fire detectors	Morphological	Arthropods: beetles [7–13], ants [31]
Protective cover to body	Morphological	Tortoises [14–17], snails [25], newts [18]
Dark (cryptic) colour	Morphological	Lizards [19], mammals [20, 21], arthropods [22–24], birds (eggs)
Ability to enter in torpor	Physiological	Mammals [4, 26]
Thermophilia	Physiological	Ants [27]

Most traits confer survival during fire, except the last three traits that confer survival in postfire conditions. Examples of animal groups in which these traits could appear are also given. These traits and species groups require further research in an evolutionary context (Table 1)

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Adapting to survive and exploit postfire environments

There are some cases in which we find evidence of specific adaptations to survive the new environment or to exploit the newly available resources, and in this includes some morphological adaptations (Table 3). Perhaps the best-documented adaptation to fire in the animal kingdom is the presence of fire detectors in a number of insect species (Schutz et al. 1999; Evans 1966, 2010). This is not an adaptation to avoid fires but rather enables them to locate them and make use of new resources in the postfire environment. These pyrophilic insects are attracted to the flames of fires, often mate close to the fire (fire as a meeting point), lay eggs in killed or weakened trees, and their larvae feed on burned wood (specifically, fungi in burned logs) or on the phloem of weakened trees. The classical examples are the pyrophilous beetles of the genus *Melanophila* (Buprestidae, Coleoptera) that have infrared receptors (e.g., Schutz et al. 1999) and those of the Cerambycidae family (Coleoptera) that have smoke receptors (Table 2), although there are many other insects with a pyrophilous behavior from a range of taxonomic groups (Table 2). There are also some insects that remain dormant for several years in the soil as larvae, and when a fire occurs, it stimulates a synchronized emergence (Jacobs et al. 2011); to what extent this synchronization has been selected by fire remains unexplored, but it could be adaptive in fire-prone environments.

After a fire, in addition to changes in vegetation structure, the colour of the habitat alters dramatically too. Thus, another common adaptation of animals living in fire prone ecosystems, and especially animals that use recently burnt environments, is the development of cryptic colouration that provides camouflage in the new environment (Table 3). Dark colouration confers a selective benefit mediated by enhanced camouflage in recently burned areas (Forsman et al. 2011). For instance, the flightless Greater rhea (*Rhea americana*) that lives in the South American savannas (cerrado) subject to very frequent fires (i.e., several fires per decade), has a long neck with a black base; when it sits on the ground, it cannot be differentiated from a burnt stem. Similarly, in Africa there are several bird species that use recently burned ground for breeding (e.g. coursers, plovers, larks and night-jars): eggs are dark coloured and chicks possess heavily pigmented down, providing camouflage in postfire conditions (de Ronde et al. 2004). The Californian lizard (*Sceloporus occidentalis*) is also cryptically coloured matching the black stalks on burned shrubs (Lillywhite et al. 1977), and the abundance of melanic squirrels in North America is positively correlated with the fire frequency (fire melanism; Guthrie 1967; Kiltie 1989). Invertebrates too show colour modifications to increase fitness postfire; for example, the frequency of melanistic individuals of the pygmy grasshopper (*Tetrix subulata*) is higher after fire (predation is reduced) than in unburned areas (where they are more conspicuous). In this case, and given that grasshoppers complete their life cycle within a year, the proportion of melanistic individuals declines as vegetation recovers and ground cover changes; thus, under frequent fires, they show fluctuating selection associated to the fire (Forsman et al. 2011).

Concluding remarks

Plants have been the main focus for research on the evolution of fire-prone ecosystems, however, there remain great challenges and opportunities for studying the relation between fire and fauna in an evolutionary framework. Many animal species show a preference,

sometimes strongly, for habitats generated by fire (fire-dependent fauna), but few of them show specific adaptations facilitating fire or postfire survival (fire-adapted fauna). In part this may simply reflect the low number of studies that have attempted to look for adaptations. There remains significant scope for research on fire adaptations in animals, and especially in relation to the rich behavioral traits that allow persistence in fire-prone ecosystems (Tables 1, 3). These traits are poorly explored under the framework of the evolutionary fire ecology but may provide a rich source of fire adaptations. Discerning adaptations to fire survival from those adaptations to fire-generated habitats may provide clues on the mechanism generating biodiversity, and keys for land management. There is much to be done to unambiguously disentangle the evolutionary role of fire in animals—we are hopeful this paper will stimulate future research.

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