



From fire to recovery: temporal-shift of predator–prey interactions among mammals in Mediterranean ecosystems

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Abstract

Fires are becoming increasingly frequent, intense, severe and prolonged worldwide, and such situation is worsening. As a result, extreme fire conditions will increase, with consequences for wildlife, including increased mass mortality and changes in trophic relationships in natural communities. This intensification is expected to be particularly pronounced in the Mediterranean ecosystems. In this scoping review, we summarized current knowledge and gaps in understanding the effects of fires on wildlife, focusing on predator–prey interactions. These interactions play a critical role in animal communities and their understanding is fundamental for appropriate management and conservation. Mammals were chosen as a model group because of their remarkable ecological role. We grouped and analysed the post-wildfire changes in the predator–prey relationships into three-time intervals: immediate, short- and long-term effects. This is relevant as vegetation restoration, by altering cover and habitat structure, may affect hunting strategies and anti-predatory behaviour. Our review showed that studies generally had several limitations, the most common of which were the lack of replication, the strong geographical bias, and the focus on few target species. Nevertheless, we could formally describe how fire affects predator–prey relationships in Mediterranean ecosystems through processes that exert different cascading effects at different times after the fire event. We encourage long-term studies on communities, including as many components of the food chain as possible, using an interdisciplinary approach, and prioritising investigations in high-risk ecosystems.

Keywords Climate change · Ecological succession · Habitat restoration · Predators · Trophic cascades · Wildfires

Introduction

One of the greatest global threats to wildlife is the alteration of fire regimes (Flannigan et al. 2013; Bowman et al. 2020). In fact, fires are becoming increasingly intense and frequent worldwide, even in less flammable environments, such as arctic circle and equatorial rainforests (Mariani et al. 2018). Consequently, the twenty-first century has been designated as “the age of the megafire” (Stephens et al. 2014). Recent

examples include megafires in Chile, California, Portugal, Amazon, and Australia, with ~ 15 million hectares burned (Gómez-González et al. 2018; Williams et al. 2019; Brando et al. 2020; Nolan et al. 2020; Geary et al. 2022). There are likely several causes of increased fire risk, such as abandonment of agricultural land, biomass accumulation, inadequate woodland management, depopulation of the countryside and expansion of cities (Moreira and Russo 2007; Pausas et al. 2008; Seijo and Gray 2012; Fernandes et al. 2013). In addition, there is increasing evidence that global warming played a key role (Bradstock et al. 2014; Abatzoglou and Williams 2016; Jones et al. 2020).

Consistently with the fire risk increase, climate models suggest that, under all scenarios, more frequent, intense, severe, and extended fires, and, ultimately, more “mega-fires”, may occur (Jolly et al. 2015; Bowman et al. 2020; Geary et al. 2022). Consequently, extreme fire conditions will be more common, with consequences for wildlife, including higher mass mortality, changes in trophic relationships among species and potentially cascade effects

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on animal populations (Williams 2013; Nolan et al. 2020; Nimmo et al. 2021). For instance, at least 1071 animal and plant species are classified as threatened by fire regime alteration (IUCN 2019; Kelly et al. 2020).

Mediterranean regions (Box 1) are particularly prone to fires, and intensification of fire regimes have particularly increased in recent decades (Moreira and Russo 2007; Turco et al. 2018; Geary et al. 2022). Furthermore, they are likely to be increasingly at risk in the future in southern Europe (Turco et al. 2018; Abatzoglou et al. 2019; Ancillotto et al. 2021). Considering the potentially increasingly catastrophic effects of fires on Mediterranean ecosystems, they need to be fully understood.

With this scoping review, we aimed to summarize knowledge regarding effects of fire on wildlife in Mediterranean ecosystems. However, considering the broad field of study, we set specific objectives. We focused on the effects of fire on predator–prey interactions (Box 2) with the purpose to identify existing knowledge gaps, particularly the influence of successional patterns in post-fire vegetation recovery on the shaping of the predator–prey relationships. Understanding how fires affect these relationships is essential for a more detailed comprehension of the role of fires in shaping biocoenoses (Doherty et al. 2022). Predator–prey interactions have critical roles in animal communities and understanding them is fundamental for appropriate management and conservation of species (Sih et al. 1998; Matter and Mannan 2005). In the age of megafire, these aspects will become increasingly crucial for biodiversity conservation (Geary et al. 2022). Nevertheless, knowledge on this issue is very fragmented, particularly in some areas of the

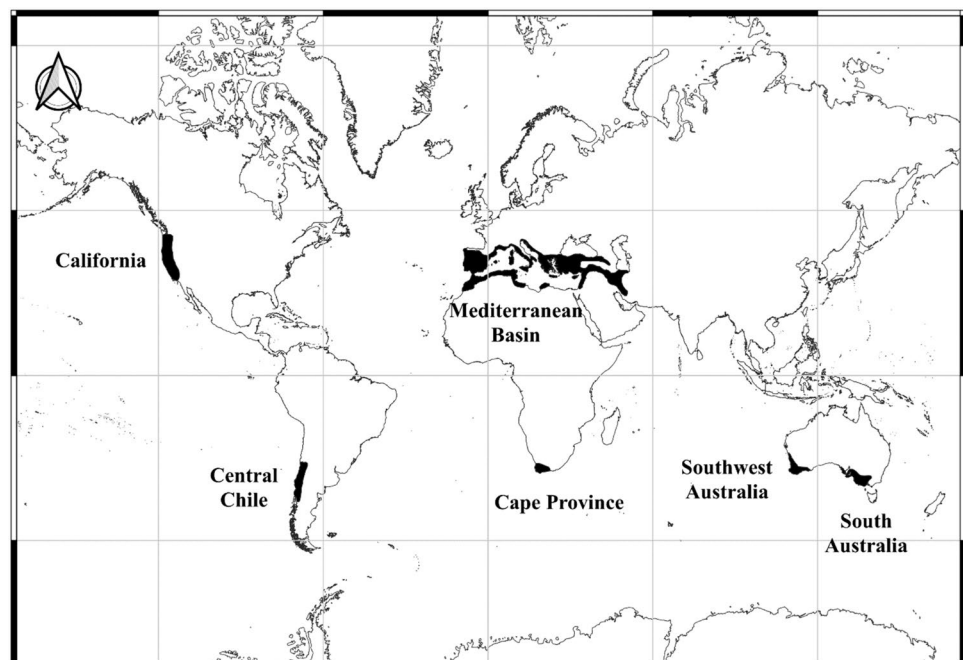
Mediterranean-type ecosystems, such as the Mediterranean basin, an area expected to become increasingly prone to fires (Bowman et al. 2017; Turco et al. 2018). This was an additional reason to focus the study of the effects of fires on predator–prey interactions in Mediterranean ecosystems. Mammals were chosen as the model group, given their important ecological role (Clutton-Brock 2009; Lacher et al. 2019).

Box 1 the Mediterranean-type ecosystems

In this review, we focused on the Mediterranean-type ecosystems (MTEs). These ecosystems are characterised by marked climatic seasonality. Winters are rainy and this rainfall exceeds the potential evapotranspiration of the plants, which results in a protracted winter-spring vegetation growing with high primary productivity (Keeley et al. 2011a). By contrast, summers are dry, making vegetation highly flammable (Moreno and Oechel 1994; Keeley et al. 2011a). This climatic condition is due to blocking incoming summer storms of western edges of the continents by a summer high-pressure cell of sinking dry air concentrated between 32 and 38 N or S latitude (Keeley et al. 2011a). In winter, this air cell migrates to the poles. Consequently, even though these areas cover only ~2% of the world's landmass, they are among the most fire-prone areas in the world and fires are widely acknowledged as drivers shaping local communities (Moreno and Oechel 1994; Keeley et al. 2011a).

Climatic conditions suitable for establishment of MTEs are present in only 5 areas: the Mediterranean Basin, the Cape Region of South Africa, Southwestern

Fig. 1 The 5 Mediterranean-type ecosystems (MTEs; black areas)



and South Australia, California, and Central Chile (Fig. 1) (Keeley et al. 2011a; Di Castri and Mooney 2012). However, there is no unanimity regarding their geographical boundaries.

Box 2 the predator–prey relationship

Predators and prey co-evolved over time, through steady “arms races” that led to a range of adaptations for both prey and predators. Usually, these races occurred in both spatial and temporal scales (Dawkins and Krebs 1979; Estes et al. 2011).

In response to predatory pressure, prey will attempt to exhibit adaptive behaviours to maximise their energetic intake (Lima and Dill 1990) and reduce mortality risk (Brown et al. 1999; Halle 2000). Consequently, this led to the develop of a series of anti-predatory behaviour by prey, like camouflage, use of warning signals and detection of the scent of predators (Kats and Dill 1998; Sherratt and Beatty 2003; Ruxton 2009; Laundré 2010; Palmer et al. 2017). In the spatial context, a prey species should try to avoid predators and high-risk sites, i.e. locations where the likelihood of encountering predators is elevated (Mandelik et al. 2003; Monterroso et al. 2013). In addition, prey should also seek sheltered environments, such as dense grasslands or shrublands (Mandelik et al. 2003). At the temporal level, prey should try to reduce locomotor activity overlap with their predators (Linkie and Ridout 2011). However, in cases where both predator and prey have nocturnal habits, certain prey have increased activity during the darkest nights, when predator hunting efficiency is lowest (Penteriani et al. 2013; Taylor et al. 2023).

Hence, predators can elicit a range of behavioural effects on prey species, with the mere instilling of fear being a significant factor, as proposed by the “ecology of fear” theory (Brown et al. 1999; Laundré 2010). These effects include reduction in activity patterns and home range size, changes in habitat use, deferment of the breeding season and increase in age at first reproduction of prey (Lima and Dill 1990; Kuijper et al. 2013). Consequently, these effects could reduce growth and reproductive rates, and body condition (Peckarsky et al. 2008).

By contrast, mammalian predators generally exhibit a tendency to adapt their habitat and time use to maximize encounters with their prey (Laundré 2010; Monterroso et al. 2013). Several mammalian predators hunt in ground open habitats, where detection of prey is easier, to increase hunting success (Leahy et al. 2016). Many mammalian predators are territorial species (Macdonald 1983); this behaviour is an essential point that permits predators and prey to coexist, as predators limited by

territorial fidelity cannot track the distribution shifts of prey in the short term, limiting their impact (Barbosa and Castellanos 2005). However, extra-territorial hunting expeditions are confirmed for certain mammalian species, like the red fox *Vulpes vulpes* (Tsukada 1997; Soulsbury et al. 2011) and spotted hyenas *Crocuta crocuta* (Cozzi et al. 2015).

The temporal dimension is also particularly relevant. For instance, several nocturnal predators are more active on bright nights, when visibility is optimal, thereby maximising hunting success (Prugh and Golden 2014). Furthermore, predators tend to adapt their locomotor activity to fit that of their prey through the diel cycle (Kronfeld-Schor and Dayan 2003). Naturally, the daily locomotor activity pattern is highly influenced by prey selection and feeding specialization. Whereas a generalist predator should not focus on a defined prey species, a specialist predator should be more inclined to synchronise its activity pattern with that of its preferred prey species, although factors like prey availability, ecosystem and evolutionary adaptations of both prey and predators play key roles. Overall, whereas prey will try to avoid predators, the latter will try to synchronise with them, in a cyclical relationship (Monterroso et al. 2013).

Materials and methods

This review was carried out in accordance with the PRISMA protocol (Moher et al. 2009), following standardized steps (Fig. 2).

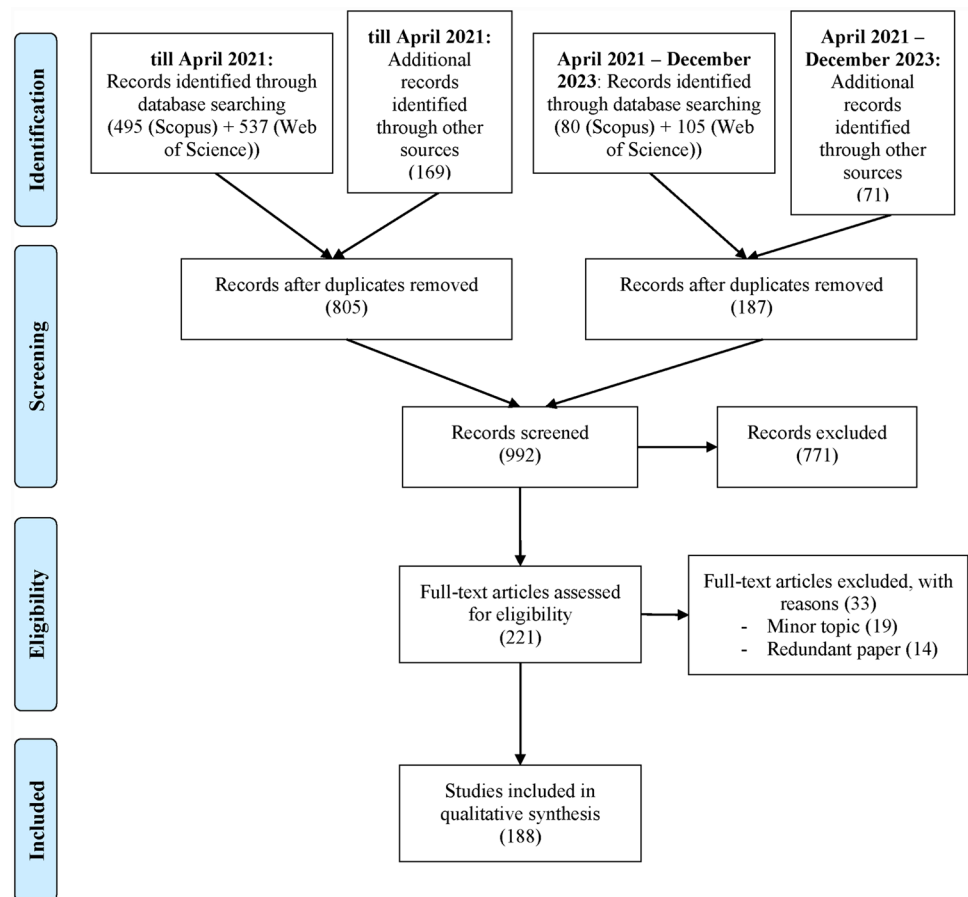
In April 2021 Scopus and Web of Science were scanned to identify existing papers, using the following string:

((prey* OR predator* OR predator–prey OR predation OR (predator PRE/0 prey)) AND (vertebrate* OR mammal*) AND (*fire* OR burn*)).

These sources were supplemented by further references that were considered relevant but not retrieved in the initial search. All identified papers were processed according to the PRISMA protocol, and 118 papers and books were selected.

In addition, the database was updated in December 2023 using the same approach and 70 studies were added to write this review. A total of 188 papers and books were then comprehensively analysed for this review.

Fig. 2 PRISMA flow diagram, from (Moher et al. 2009)



Discussion

Fires and their effects on Mediterranean biocoenoses

Structure and dynamics of natural communities can be significantly impacted by various disturbances (Sousa 1984; Johnson and Miyanishi 2007). Natural disturbances include flooding (Brum and Souza 2020), insect outbreaks (Flower et al. 2013), trampling (Pellerin et al. 2006), and wildfires (Bowman et al. 2009; Pausas and Keeley 2009). Among them, wildfires are particularly relevant because they alter structure and functions of ecosystems worldwide (Bowman et al. 2009). Fires exert both direct and indirect effects on wildlife (Engstrom 2010; Puig-Gironès et al. 2018). Direct effects include injury or death, although the magnitude of the effect varies greatly among species (Doherty et al. 2015). By contrast, indirect effects mainly are changes in soil properties, vegetation structure and composition (Monamy and Fox 2000; Banks et al. 2011; Bento-Gonçalves et al. 2012), affecting habitat elements like soil fertility and structure, availability of food, shelter, and microclimate. These environmental shifts can affect prey and predator abundance, distribution, and behaviour

in many ways (Letnic et al. 2004; Zwolak et al. 2012; Jorge et al. 2020), with the potential to modify predator–prey relationships (Paine 1980; Hradsky et al. 2017). In turn, predator–prey relationships are highly context-dependent relationships, which resulted mainly affected by the time elapsed since the fire and ecosystem type (Cherry et al. 2018; Doherty et al. 2022). An example is the reciprocal effects of predators on prey in terms of habitat use, abundance and/or activity (Hradsky et al. 2017; Puig-Gironès and Pons 2020; Doherty et al. 2022; Puig-Gironès 2023). For example, in a recently burned area, the stone marten *Martes foina* has been found to influence the foraging activity of small mammals (Puig-Gironès 2023).

In Mediterranean ecosystems, fires are a natural occurrence exerting an adapting force that has shaped the evolution of biocoenoses for millennia (Bowman et al. 2009; Pausas and Keeley 2009; Pausas and Parr 2018). As a result, flora and fauna are generally adapted to fires (Engstrom 2010; Pausas and Keeley 2014; Pausas and Parr 2018). However, implications of recent altered fire regimes (i.e. mega-fires) on the trophic network are unknown and could be disastrous, leading to biodiversity loss and resource depletion (Kelly et al. 2020; Geary et al. 2022; Nimmo et al. 2022). To understand the effects of fires on the predator–prey

relationship in these ecosystems, it is necessary to fully understand some key elements such as their impact on the ecosystem and post-fire successional stages. The impacts of fires on animal populations, as well as on their interactions, depend mostly on the vegetation succession, which in turn is related to the time passed since the disturbance (Monamy and Fox 2000; Keeley et al. 2005). In fact, the effects of fires may persist over time, even after the flames are extinguished. Hence, as the vegetation recovery is a crucial factor to understanding the impacts of wildfires on predator–prey relationships, we summarised the known effects by grouping them into 3 phases: (i) immediate effects, i.e., from extinguishing the fire to the first few months afterwards (Lees et al. 2022), when there is lack of vegetation (Moreno and Oechel 1994; Pausas and Keeley 2009); (ii) short-term, i.e., within a few years after the fire (Spencer et al. 2022), when the undergrowth is usually dense, but the arboreal cover is lacking (Trabaud 1994; Keeley et al. 2005); and (iii) long-term, i.e., many years after the fire (Soyumert et al. 2020), when the arboreal cover is also restored (Pausas et al. 2008; Keeley et al. 2011a). In the literature, these intervals do not have distinct thresholds and may vary according to specific ecological contexts. However, in this review we have used the phenological phases of the Mediterranean vegetation following a wildfire to define the limits of the intervals. A conceptual diagram of these effects is depicted in Fig. 3.

The immediate effects

By burning vegetation, a fire may exert many different effects, depending by factors like ecosystem type and fire regime. For instance, a mixed-severity fire essentially increases landscape heterogeneity, whereas a high-severity fire decreases landscape heterogeneity, leading the burnt area to a former successional stage (Pausas and Keeley 2009). However, many plants species in Mediterranean fire-prone areas are defined “fire-adapted” species and can survive fires through various strategies, including serotiny (i.e. an induced seed release system, common in *Pinus* spp.) and resprouting (i.e. post-fire activation of dormant vegetative buds to regrowth) (Trabaud 1994; Konstantinidis et al. 2005; Paula et al. 2009; Keeley et al. 2011b; Pausas and Keeley 2014). The effectiveness of these strategies depends on specific conditions, such as those defined by the fire regime (Keeley et al. 2011b). Although recurrent fires can, under certain circumstances, stimulate seed germination and reduce competition (Pausas 2004; García et al. 2016), they can also be particularly deleterious, because they can affect plants at earlier life stages, which cannot reach reproductive maturity and produce a seed bank (Díaz-Delgado et al. 2002; Baeza et al. 2007; Pausas et al. 2008). These alterations influence the ensuing ecological succession, with potential

to affect predator–prey relationships of species that enter it (Monamy and Fox 2000; Torre et al. 2022).

The direct effects of fires on wildlife are attributed to burning, asphyxiation, heat or physiological stress (Smith 2000; Michel et al. 2023). Specific fire events have variable impacts on wildlife, due to properties of the fire-regime, including intensity, severity, scale, season and time since fire, as well as habitat types and taxa affected (Engstrom 2010; Birtsas et al. 2012; Geary et al. 2020; Nimmo et al. 2021). However, while estimating direct effects of fire on fauna is complex and can be highly variable (Pausas and Parr 2018; Tomas et al. 2021), Jolly et al. (2022) in their systematic review have suggested that direct mortality is generally low (estimated as 3%).

In addition to the features of the fire regime, two key features that determine impacts of fire on various mammalian species are vagility and the kind of shelter employed (Smith 2000; Chia et al. 2015; Jolly et al. 2022). For instance, among small mammals, the most decisive impact is on taxa that are not very vagile and take refuge on the ground; some individuals of these species are usually killed by fires (Simons 1991). By contrast, individuals belonging to highly vagile species and/or those that shelter underground are more likely to escape or survive fires (Robinson et al. 2013; Jolly et al. 2022). Large predators for example, such as the wolf *Canis lupus*, are often regarded as having some degree of resistance to fire (Lino et al. 2019).

The effect of shelter location is particularly clear for small mammal assemblage. Although small mammals are generally considered very susceptible to fire, certain burrowing species suffer low direct mortality (Letnic et al. 2005). As expected, by contrast, mortality is usually higher in species that shelter above the ground (Simons 1991). The mortality of strictly arboreal species is poorly documented, especially in the Mediterranean ecosystem, but could be reduced due to their vagility (Koprowski et al. 2006).

For an herbivore, a first effect of fire is depletion in food resources (i.e., burnt vegetation). In turn, this decline can trigger a series of cascading effects, such as starvation, decreased reproductive success leading to population decline and emigration to unburnt areas, richer in food resources (Morris et al. 2011a, 2011b). However, the extent of this depends on the features of the fire regime and the trophic specialisation of the prey. After a fire, populations of specialist species, such as insectivorous, may be most affected by a decline in food availability since their main food resources may have been burnt (Recher and Christensen 1981; Sutherland and Dickman 1999; Driscoll 2007).

Another immediate effect on prey can be a reduction in cover and refugia availability, through the simplification of vegetation structure (Derrick et al. 2010; Robinson et al. 2013; Chia et al. 2015). This could lead to increased predation risk (Green and Sanecki 2006; Conner et al. 2011), then

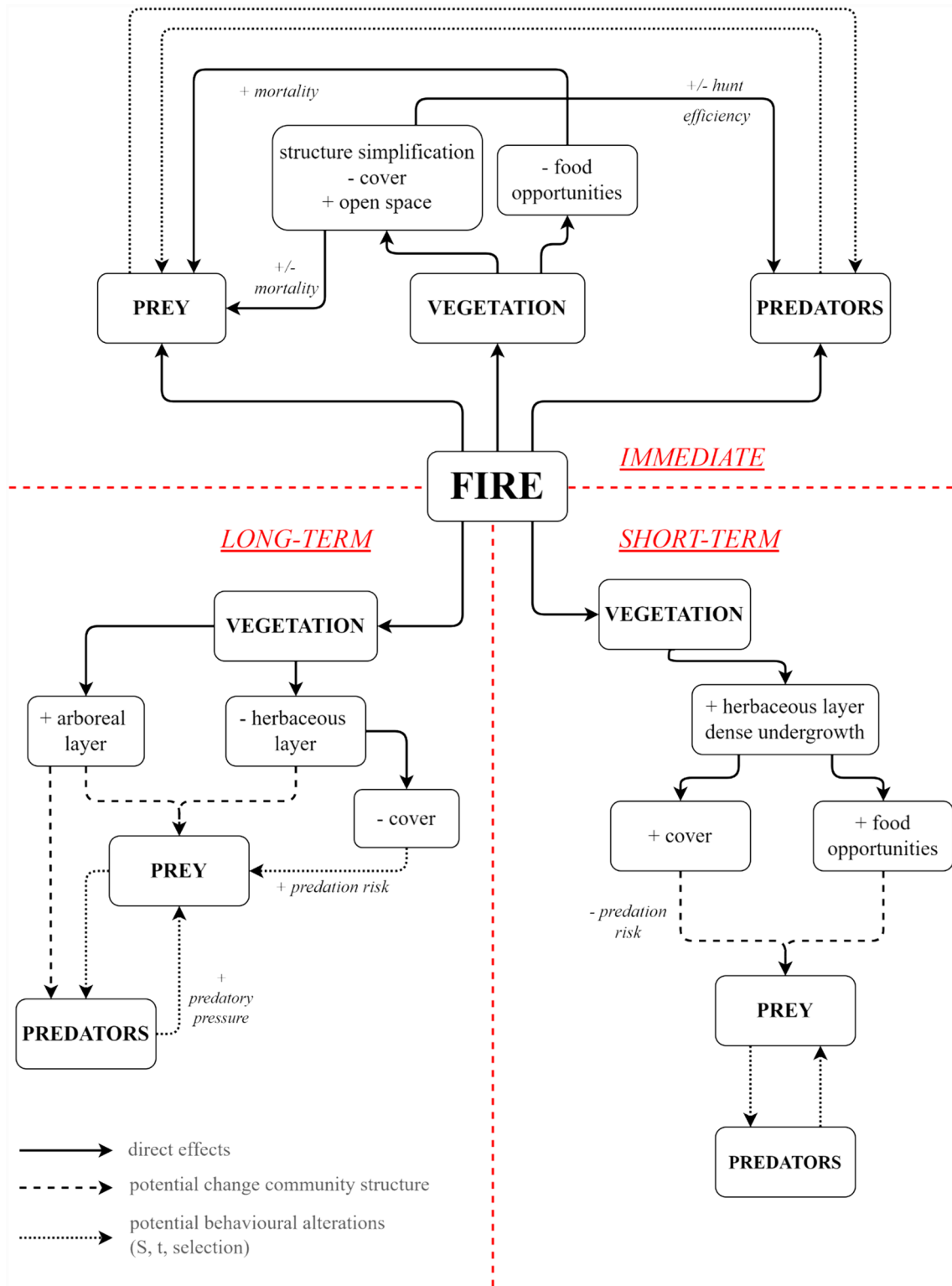


Fig. 3 Conceptual map of the effects of fires on predator–prey relationships in the Mediterranean ecosystem, divided into 3 temporal phases: immediate, short- and long-term effects. *S* alteration in space use; *t* alteration in time use; *selection* alteration in terms of resource selection

increased mortality, when prey vulnerability depends on habitat structure (Verdolin 2006). This is certainly relevant for small ground-based mammals; there is strong evidence that their mortality is positively correlated with increasing post-fire habitat simplification (Conner et al. 2011; González et al. 2022).

In the Mediterranean ecosystems, the period of highest prey mortality tends to occur shortly after the fire, especially during the first months after a high severity fire (Conner et al. 2011; Morris et al. 2011a; Leahy et al. 2016). However, specific fire regimes can also benefit certain species, based on their food habits and anti-predatory behaviour (Bleich et al. 2008; Jaffe and Isbell 2009; Bond 2015). For instance, the fox squirrel *Sciurus niger* seems to benefit from fires of low intensity, through stimulation of fungi and cone generation and creation of open foraging areas, that simplify squirrels movement (Karmacharya et al. 2013). Formation of open spaces also increases visibility, which can favour species that need to detect predators (e.g., bighorn sheep *Ovis canadensis*; Bleich et al. (2008) and vervet monkeys *Cercopithecus aethiops*; Jaffe & Isbell (2009).

Like their prey, predators can also become direct victims of fires, especially those of high severity and/or large size (Jolly et al. 2022). However, the impact on predatory mammals varies, and while it may be minimal for large, highly mobile species, such as large carnivores (Engstrom 2010; Lino et al. 2019), smaller predators like the stone marten may also face significant challenges (Birtsas et al. 2012). In addition, there appears to be a positive relationship between the home range size of predators and their resistance to fire. Indeed, extensive movements make them less dependent on local resources, which may be less or no longer available. Furthermore, it also allows them to exploit both resources available in the burnt area and the nearby unburnt area (Nimmo et al. 2019).

There are indications that the predator response to fire is highly species-specific as well, and it depends on factors such as environmental variables, progression of secondary succession, trophic and non-trophic interactions, and population dynamics (Smith 2018). For example, in a Mediterranean area in Macedonia, stone martens were not recorded in burned areas even three years after a fire (Birtsas et al. 2012), whereas in study areas in Spain this species was common even few months after fires (Puig-Gironès and Pons 2020; Puig-Gironès 2023), suggesting that differences even among areas of the same ecosystem type can strongly influence the predator response. Fires can increase habitat suitability for predators that could benefit from a reduction in vegetation, facilitating hunting (Conner et al. 2011; Leahy et al. 2016). In fact, several studies suggest that predators could increase their occurrence in newly burnt areas due to increased predation success (Leahy et al. 2016; Nimmo et al. 2019; Geary et al. 2020). However, if the predator species

needs cover to hunt, as in the case of ambush predators, predators tend to avoid burnt areas (Eby et al. 2013; Doherty et al. 2022).

The choice of prey species also depends on their availability. Therefore, a change in availability due to fire could influence the choice of prey species towards more available species (Green and Sanecki 2006; Hradsky et al. 2017). However, even non-trophic interactions such as intra-guild competitive interactions can also shape responses of predator species to fires (Geary et al. 2020). In fact, a usual apex predators' effect is the suppression of less competitive species (i.e. mesopredators), through competitive interactions (Palomares and Caro 1999; Geary et al. 2018). As a result, mesopredators tend to adopt prey-like behaviour in such scenarios, showing spatial and temporal avoidance of apex predators (Durant 1998; Vanak et al. 2013). Fires, by the creation of open habitat, can affect the habitat use and selection of apex predators. Consequently, mesopredators may avoid these environments, where they may also be more vulnerable to apex predators (Schuette et al. 2014; Geary et al. 2018, 2020). However, such responses may not always occur. For example, there is evidence that in certain situations mesocarnivores may not be competitively affected by apex predators, but rather may be facilitated, by capitalizing on the enhanced feeding opportunities resulting from carcasses left by apex predators (Ferretti et al. 2021; Rossa et al. 2021). The combined effects of fire, predation and competition are therefore difficult to generalise, then further research is needed.

Short-term effects

After a fire, plants gradually develop towards more mature conditions following their recovery processes (e.g., serotiny, resprouting, Keeley et al. 2011b; Pausas and Keeley 2014) and the natural stages of secondary succession (Trabaud 1994; Keeley et al. 2011a). In Mediterranean ecosystems, usually the first phase of plant recovery involves establishment of a dense undergrowth, with herbs and grasses often blooming in recently burnt vegetation (Gill and McMahon 1986; Moreno and Oechel 1994), although plant recovery differs among biomes due to biotic factors, e.g., plant community as well abiotic factors (topography, soil, rainfall and fire severity; Keeley et al. 2005; Puig-Gironès et al. 2017). The process is particularly quick in Mediterranean areas, where climatic conditions and adaptive traits of the plant species promote a rapid post-fire recovery (Trabaud 1994; Paula et al. 2009). Consequently, a few years after fire, the undergrowth could become even more dense in burnt than in unburnt areas (Torre and Díaz 2004).

For mammals, a widely accepted post-fire successional model is the Habitat Accommodation model (HAM; Fox 1982; Monamy and Fox 2000, 2010; Torre and Díaz 2004; Swan et al. 2015; Torre et al. 2022), derived from

facilitation, tolerance, and inhibition models (Connell and Slatyer 1977). The HAM can be used to predict the successional order of mammalian community following a fire, considering the essential habitat requirements of each species. This model proposes that an early species enters the post-fire succession and reaches maximum density when the habitat is at an optimal level for that species in terms of vegetation. As post-fire succession proceeds, vegetation will change, becoming less suitable for early species, which decrease in density, whereas other more suitable seral species will enter succession (Monamy and Fox 2000). For instance, in a pioneering study conducted in Lakes National Park (Australia), species like the New Holland mouse *Pseudomys novaehollandiae*, the eastern chestnut mouse *P. gracilicaudatus*, the house mouse *Mus domesticus*, and the slender-tailed dunnart *Sminthopsis murina* reached higher abundances in the early post-fire stages, when their habitat requirements were fulfilled, and they were then considered early successional species (Fox 1982; Monamy and Fox 2000). In contrast, species that required advanced forest maturity, such as squirrels, are considered late successional species (Koprowski et al. 2006; Mazzamuto et al. 2020). The key point of HAM is therefore the change in vegetation, and particularly its structure. Habitat Accommodation model has had strong experimental support in the small mammal assemblage (Torre and Díaz 2004; Swan et al. 2015; Torre et al. 2022), a fundamental prey group for many predators (Hanski et al. 2001; Posłuszny et al. 2007; Castañeda et al. 2022). Usually, the earliest small mammals are ground-foraging species, with herbivorous and/or granivorous food habits (Haim and Izhaki 1994, 2000), well suited to early-successional vegetation.

In addition to the vegetation structure, plant species also have important roles. For instance, black-footed rats *Mesembriomys gouldii* have been found to be particularly dependent on *Cycas* sp. in post-fire Australian forests, and the post-fire loss of these plants could lead to local black-footed rats extinction (Woinarski et al. 2005), with potential cascading effects on the whole ecosystem (Nimmo et al. 2019; Geary et al. 2020). Moreover, another hypothesis has been postulated, the Green Magnet Hypothesis (GMH; Archibald et al. 2005; Jorge et al. 2020), to explain why herbivores are inclined to visit recently burnt areas. According to GMH, herbivores are attracted to these areas because of the favourable feeding opportunities. However, this attraction takes perceived predation risk into account; consequently, herbivores do not always follow the GMH (Cherry et al. 2017, 2018). Thus, when the GHM is followed, density of certain prey species may become higher in burnt than in unburnt areas. In the Mediterranean basin, a good example is the small mammals assemblage (Torre and Díaz 2004; Puig-Gironès and Pons 2020). In a study in Catalonia (Spain) the authors reported that this assemblage was also particularly developed around boundaries of the burnt area

(Puig-Gironès et al. 2018), where the habitat structure and cover were more elaborate and thicker than in the inner parts of the burnt area.

As predators tend to adapt to the availability and distribution of their prey, changes in prey abundance can trigger shifts in predator behaviour and foraging strategies (Nimmo et al. 2019; Doherty et al. 2022, 2023). Predators may concentrate their hunting efforts in burned areas with higher prey densities, resulting in locally increased predatory frequencies (Geary et al. 2020; Puig-Gironès and Pons 2020; Doherty et al. 2022). For example, Puig-Gironès and Pons (2020) report that 15 months after fires there was an increment of rodent foraging activity, and 6 months later, an increasing of red fox occurrence. Conversely, occurrence of the stone marten was not affected by small mammals' abundance, presumably due to its generalist food-habits (Virgós et al. 2010; Puig-Gironès and Pons 2020). Shifts in predatory frequencies can have significant ecological effects. In fact, they may lead to a decline in prey populations, potentially triggering cascading effects throughout the food web. Changes in predatory behaviour might affect interspecific interactions, ultimately shaping community structure (Geary et al. 2018, 2020; Doherty et al. 2022). Furthermore, alteration of prey availability may also affect predators' locomotory activity pattern, as reported for the red fox from 1 to 3 years after a fire (Birtzas et al. 2012; Hradsky 2020; Spencer et al. 2022).

Long-term effects

In Mediterranean ecosystems, in the years following a fire, that post-fire successional outcomes can be highly variable due to factors such as fire intensity and recurrence, plant reproductive strategy and seed maturation (Retana et al. 2002; Pausas et al. 2008; Keeley et al. 2011b; Pausas and Keeley 2014). High intensity fires can lead to massive community collapse, resulting in prolonged recovery periods. Conversely, low intensity fires can facilitate more rapid vegetation recovery, through both survival and reproductive mechanisms and nutrient supply (Moreno and Oechel 1994; Keeley et al. 2011a; Caon et al. 2014). On the other hand, recurrent fires could be particularly detrimental to forest regeneration, leading to prolonged forest recovery time, or even to its conversion into a successional shrubland (Díaz-Delgado et al. 2002; Baeza et al. 2007; Pausas et al. 2008). However, usually succession proceeds with increasing tree cover and decreasing herbaceous one (Trabaud 1994; Keeley et al. 2011a). Consequently, strictly terrestrial and herbivorous animal species will be at least partially replaced by arboreal, omnivorous and/or insectivorous species, or those that feed on trees grown in the further seral stages (Prodon et al. 1987; Arrizabalaga et al. 1993; Torre

et al. 2022). These changes are consistent with Fox's Habitat Accommodation Model, as their succession follows a predictable pattern of vegetation succession. For example, the response of meso/large mammals to a wildfire in Turkey was studied over several years (Soyumert et al. 2020). Sites burnt since more than 30 years had lower species richness than those burnt 13 years before, but supported species that are usually absent in the short term after fire, such as brown bears *Ursus arctos* and wild goats *Capra aegagrus*. Similar results for small mammals in terms of specific richness were found by Torre et al. (2022) in Spain. If the predicted successional scenario is respected, for prey, predation risk and pressure could theoretically increase until the local abundance of the prey return to pre-fire levels. However, experimental evidence is still limited (Torre and Díaz 2004; Torre et al. 2022).

Predators preferring forested habitats with high tree cover (e.g., *Martes* spp.) are expected to be more common in these late-successional systems (Bond 2015).

As ecological restoration proceeds, the system could return to the pre-fire stage, or to a newly evolved state that reflects the restoration of the ecosystem (Chakraborty and Li 2009; Keeley et al. 2011a; Holl 2020). However, long-term data are the least available, probably due to the challenges of maintaining consistent monitoring efforts over time and funding constraints.

Drawing general conclusions is challenging, because of the intricate nature of ecological processes. For instance, there is variability in the post-fire response depending on the type of ecosystem affected and the features of fire regime (Lindenmayer et al. 2016; Lewis et al. 2022). In addition, the potential occurrence of other disturbances over time (e.g. additional wildfires, establishment of human activities), and long-term cascading effects due to successional dynamics and trophic interactions increase the complexity of the analysis (Lindenmayer et al. 2016; Geary et al. 2018; Smith 2018).

Concluding remarks and future perspectives

Limitations of studies on post-fire effect

Despite the many studies on responses of wildlife to fires, our scoping review highlighted many limitations. Most studies focus on fire-responses of a single species or taxon (e.g., Jaffe and Isbell 2009; Eby et al. 2013; Sokos et al. 2016; Lino et al. 2019; Mazzamuto et al. 2020; Nalliah et al. 2022). This is a standard starting point for ecological studies. However, to fully comprehend the ecological effects of fires, a more comprehensive viewpoint that considers interactions among different taxa at the community level is necessary. The selection of target species is contingent upon

the specific context, objectives and hypotheses formulated. Ideally, species from different functional groups should be included, e.g., at least one each of apex predator, mesopredator, and prey species.

Immediate and short-term studies can provide immediate insights about the fire effects on ecosystems, and long-term ones are needed to understand ecosystem dynamics over time. However, while the first ones abound (e.g., Hradsky et al. 2017; Puig-Gironès and Pons 2020; Spencer et al. 2022), the second ones are scarce (e.g., Sokos et al. 2016; Soyumert et al. 2020). Effects at one or two years after the fire are quite well-known for specific groups (e.g. rodents, Haim and Izhaki (1994); Puig-Gironès et al. (2018); Mazzamuto et al. (2020)), but long-term effects are poorly characterized. In order to mitigate the effects of fires, which will increasingly impact wildlife, it should be of primary importance to study the post-fire recovery period, which is highly variable depending on factors such as the ecosystem type and climate (Keeley et al. 2005, 2011a; Puig-Gironès et al. 2017).

Most of the studies were carried in North America and Australia (Geary et al. 2020; González et al. 2022). This geographical bias poses a significant challenge since it restricts the findings applicability to other continents. However, the studies on North American (e.g., Bleich et al. 2008; Schuette et al. 2014) and Australian (e.g., Hradsky 2020; Geary et al. 2022) Mediterranean ecosystems are useful for predicting the outcome of Mediterranean ecosystems on other continents, due to their shared temperate climate (Moreno and Oechel 1994; Keeley et al. 2011a). Nevertheless, it is imperative to underline the intrinsic diversity of the ecosystem's biocoenosis of each geographical region. These differences highlight the need to conduct additional research on the unique ecological conditions of each region. Regrettably, there are very limited studies about mammalian post-fire responses in the Mediterranean basin (Haim et al. 1996; Soyumert et al. 2010, 2020; Birtas et al. 2012), of which only three studies (Torre and Díaz 2004; Puig-Gironès and Pons 2020; Puig-Gironès 2023), conducted in Spain, included predator–prey relationships.

Another limitation in studying unpredictable phenomena is that many studies are not replicated under the same or even similar conditions. In fact, replicating the same fire regime features (e.g. spatial extent, fire intensity) and environmental conditions poses significant difficulties in achieving experimental control and standardisation. In addition, ethical considerations and safety concerns may limit the ability to conduct fire experiments. Consequently, as wildfire studies are often opportunistic and lack pre-treatment data, the conclusions that can be drawn are usually limited to that single system. By contrast, prescribed fires are manageable, allowing for study through appropriate sampling design (e.g. Before-After Control-Impact, BACI). Unlike

wildfires, prescribed fires are less intense, severe and extensive (Whelan 1995; Fernandes et al. 2013), then their impact on wildlife is very different from that of wildfires (Pastro et al. 2011). As a result, studying the effects of prescribed fire cannot serve as a surrogate for understanding the effects of wildfire, although it depends by factors like ecosystem and taxa affected (Converse et al. 2006; Morris et al. 2011a; Hradsky et al. 2017).

Mechanisms to be disclosed

The actual mechanisms behind the observed effects is usually unknown (Kelly et al. 2012; Zwolak et al. 2012; Leahy et al. 2016). For instance, although it is frequently well recognised that animal abundance varies in response to fires (Torre and Díaz 2004; Zwolak et al. 2012; Jorge et al. 2020), the demographic drivers behind these changes are often not clear. In fire ecology, wildlife studies are typically disconnected dots, due to the wide range of fire characteristics and ecological contexts studied. For instance, each study has a distinct set of features (natural/prescribed fire, low/high severity and/or intensity, different scale, seasonality, biogeographical region, species investigated). In addition, responses of a certain taxon to a fire in a certain part of the world could be completely different to that of the same taxon in a different biogeographical region (Geary et al. 2020), or after a fire with different severity (Bond 2015; Chia et al. 2015; Lewis et al. 2022). For example, fire severity effects have been observed in taxa such as rodents (Diffendorfer et al. 2012), bats (Buchalski et al. 2013), and marsupials (Chia et al. 2015). Therefore, with such specific information it is difficult to draw a general picture from which to attempt to draw overarching conclusions about the effects of fires on wildlife and predict its effects on prey and predators (Hradsky et al. 2017; Puig-Gironès and Pons 2020). To predict effects of fires on animal populations driven by trophic relationships, e.g., predator–prey relationship, is challenging, also considering the complexity of the predator–prey relationship itself. However, fully identifying the effects of fires on these relationships will be crucial to understanding effects of fires on wildlife, given their role in shaping population dynamics.

Establishing an international network that links together all available information from each future fire could be a possible solution. To date, information is still relatively scarce due to some of the limitations highlighted, but it is hoped that future studies will fill these gaps by elucidating the role of each factor in affecting the ecological system impacted by fire, as well as how these factors may interact and reverberate on the relationships among the different components of the system. For example, by clarifying the effects of individual components of the fire regime on vegetation regrowth, habitat availability, species mortality

and community dynamics, taking into account differences among different biocoenoses, is essential to this understanding. By analysing the fine interactions among these factors, we could gain a thorough understanding of their combined influence on many ecosystem components, ultimately leading to a deeper knowledge of how fire affects ecosystems. With this understanding, or a sort of framework for the impact assessment, it may be possible to identify patterns that make the effects of fires more predictable. Given the current megafires outbreak and their devastating effects on ecosystems around the world (Nolan et al. 2020; Geary et al. 2022), the development of predictive models of megafire occurrence and behaviour should be a priority task. Combining data and knowledge from various ecosystems and areas, such a network could improve our knowledge of megafire dynamics and make it easier the development of effective megafire management plans.

Applying this strategy, we suggest that future studies should characterise in detail some key aspects of the fires and their potential effects (Whelan et al. 2002; Keeley et al. 2011a; Geary et al. 2020) (Table 1). Among these, the fire regime, including the extent of the impacted area, the severity of the various zones and the intensity of the fire should be prioritized (Keeley 2009; Lewis et al. 2022). Additional aspects such as soil type, climate zone, topography, other disturbance sources and affected biocoenoses should also be characterised. As there is strong evidence that effects of fire on vegetation have a key role in the entire trophic network (Moreno and Oechel 1994; Keeley et al. 2011a), effects of the fire on the vegetation should be studied in detail, to assess the potential impacts on the animal community through alteration of key components and structures such as food resources and cover (Monamy and Fox 2000; Geary et al. 2018; Torre et al. 2022). A interdisciplinary approach to fire studies is therefore recommended. This recommendation stems from the recognition that fires are multifaceted phenomena with far-reaching consequences. Each aspect considered—from the physical characteristics of the fire to its ecological consequences—requires expertise from different disciplines (Whelan 1995; Pausas and Keeley 2009; Moyo 2022). Studies on components such as soil and vegetation should be primarily carried out as key ecological drivers of primary productivity. In fact, wildfires, through the burning of organic matter can reduce soil fertility, triggering cascading effects on the vegetation recovery (Keeley et al. 2011a; Caon et al. 2014). For this purpose, remote sensing monitoring systems could complement field studies, by monitor changes in vegetation over time (Parks et al. 2014; Allison et al. 2016). On the other hand, animal studies should involve community studies, including as many components of the food chain as possible, e.g., primary and secondary consumers, plus meso- and apex-predators (Geary et al. 2020; Doherty et al. 2022). In fact, the effects of fires

Table 1 Components of the fire regime that should be characterised after each fire. This would make it possible to build a large database capable to predict the effects of fires on ecosystems, and ultimately on the predator–prey relationship

Components	Description	How	Why
Type Intensity	Type of fire ignition setting and control “Measure of the heat energy released” (Rothermel and Deeming 1980). Data rarely available	Categorical, levels: prescribed, wild Flame length/rate of spread/residence time. Numerical	Strong effect on fire intensity and severity (Whelan 1995) Higher fire intensities correspond to a higher mortality rate of plants and wildlife hiding underground (Whelan 1995; Engstrom 2010)
Burn severity	“Estimate of the environmental impacts of the fires” (Bowman et al. 2020) by means of Relativized Burn Ratio (RBR) (Parks et al. 2014)	Remote Sensing. Categorical, levels: unburnt, scorched, light, moderate, deep (Keeley 2009)	Defines the impact of the fire on the vegetation, with significant consequences for the whole ecosystem (Keeley et al. 2011a)
Extent	Size of the burnt area	Remote Sensing (ha). Numerical	Effect on successional and recolonization patterns (Haim 2002; Lawes et al. 2015)
Season	Season of the year in which the fire occurred	Time of the year. Categorical, levels: the four seasons	Different effect on plant growing and dormant season (Brockway et al. 2002; Konstantinidis et al. 2005)
Fire interval	“Time between consecutive fires” (Whelan 1995)	Number of days. Numerical	Recurring fires are particularly impactful for vegetation restoration (Díaz-Delgado et al. 2002; Pausas et al. 2008)
Ecoregion (ER)*	Ecoregions classified by biomes and habitat types	Remote Sensing. Categorical, levels: ERs	Each ecoregion is composed of unique ecosystems, differently adapted to fires (Pausas and Keeley 2009; Pausas and Parr 2018)
Post-fire anthropic interventions*	Type of any post-fire interventions carried out in the area	Categorical, levels: several (e.g. clearcut, salvage logging)	Potential strong influence on ecosystem recovery (Lindemayer et al. 2012)

*Information not included in the usual fire regime definition, but nevertheless of interest

extend beyond individual species and may affect the entire ecological communities. By adopting a community perspective, researchers could investigate the dynamic interactions that occur among different species within an ecosystem and gain a broad overview that can be insightful in understanding post-fire dynamics (Whelan 1995; Morin 2011; Moyo 2022).

More emphasis should be placed also on changes in trophic and non-trophic relationships among species, which play key roles in shaping post-fire community dynamics (Geary et al. 2018; Smith 2018; Doherty et al. 2022). Trophic relationships, such as predator–prey dynamics, are known drivers of ecosystem structure and function (Estes et al. 2011; Terborgh and Estes 2013). Understanding how fire affects them is therefore essential for proper management and conservation of wildlife (Sih et al. 1998; Matter and Mannan 2005). In addition, non-trophic relationships, including competition, also have profound effects on community composition (Mayfield and Levine 2010; Morin 2011), although the effects of fire on these are still little investigated (Geary et al. 2018; McHugh et al. 2022). By prioritising the study of both trophic and non-trophic interactions, we can achieve a more comprehensive understanding of the multifaceted effects of fire on ecosystems, also encompassing the intricate web of relationships that collectively shape post-fire community dynamics (Leahy et al. 2016; Geary et al. 2018; Smith 2018; Doherty et al. 2022; Puig-Gironès 2023). Such research should follow ecological succession over time, to understand the actual impacts of a fire on wildlife, which most likely does not end within a few years of the event (Kelly et al. 2011; Soyumert et al. 2020). Thus, studies should begin soon after the fire and be continued for several years and possibly decades thereafter.

Finally, more attention should be paid to less studied but high-risk areas, such as the Mediterranean basin, where, although there has been considerable research on the effects of fires on several taxa (e.g., Santos and Cheylan 2013; Puig-Gironès et al. 2017, 2023; Ancillotto et al. 2021), there are surprisingly few studies investigating their effects on ecological interactions within mammalian communities (Torre and Díaz 2004; Puig-Gironès and Pons 2020; Puig-Gironès 2023).

As scientific research is often limited by economic resources, it may not always be possible to implement the proposed solutions. However, a more feasible alternative might be to choose one or more indicator taxa and study them intensively around the world (Geary et al. 2020). Studying the same taxa in different ecosystems allows data to be collected under a variety of environmental conditions. This may help to determine the role of specific factors and to generalise ecological patterns, thereby improving our comprehension of global ecosystem dynamics. A suitable indicator species could be the red fox, due to its extraordinary

ecological plasticity (Geary et al. 2020; Garcês and Pires 2021). This species is widespread in almost the entire northern hemisphere, plus parts of Australia, including three of the five Mediterranean areas: the Mediterranean basin, Australia and California. The red fox is both autochthonous predator (northern hemisphere) and invasive predator (southern hemisphere), consequently this relevant conservation element can also be assessed. As a mesopredator, it can play the trophic role of predator or prey, and it can undergo competitive interactions with apex predators (Geary et al. 2018; Garcês and Pires 2021; Rossa et al. 2021). Finally, there are already data on relationships between red foxes and fires, e.g., in Australia (Hradsky 2020; Nalliah et al. 2022; Spencer et al. 2022; Doherty et al. 2023). As a highly opportunistic species, it tends to adapt very well to fire-prone areas (Hradsky 2020; Doherty et al. 2023).

However, this approach has its drawbacks. Variability in habitat types, species interactions and environmental factors across ecosystems can introduce complexity and limitations to data interpretation. In addition, the influence of other factors, such as human disturbance and habitat fragmentation (Sousa 1984; Baeza et al. 2007; Ancillotto et al. 2021), cannot be underestimated, as they can confound research results and make it difficult to extrapolate findings to larger geographic scales.

Together with the red fox, the small mammal assemblages, as a key prey group, could be studied. Small mammals are distributed worldwide and are among the taxa for which we know most about the effects of fires on recovery (Banks et al. 2011; Puig-Gironès et al. 2018; Hale et al. 2022) and dynamics (Arrizabalaga et al. 1993; Haim and Izhaki 1994; Torre et al. 2022). Furthermore, their specific composition varies greatly at geographical scale, and include from early to late successional species (Fox 1982; Monamy and Fox 2010).

In summary, post-fire community research must be given top priority in order to gain a more comprehensive understanding of the ecological effects of fires on wildfire in Mediterranean ecosystems. It is necessary to apply an interdisciplinary approach to the study of these communities and give emphasis on the comprehension of ecological interactions. In the case this is not feasible, we suggest investigating at least the red fox/small mammals system as soon as the fire occurs, and to continue the research for as long as possible.

We believe that a large-scale application of this framework would yield significant insights of how fire affects predator–prey relationships in Mediterranean ecosystems. Given the ongoing of climate change and intensification of fire regimes, this knowledge may prove valuable in the future for managing and predicting changes in mammal communities. In this way, researchers can lead the way for more effective approaches to mitigate the ecological impacts of

wildfires and preserve the biodiversity of these threatened ecosystems for future generations.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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