



Tamm reviews

The impact of fire on soil-dwelling biota: A review

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ARTICLE INFO

Keywords:

Belowground organisms
Biodiversity
Burning
Fire severity
Prescribed fire
Soil ecology
Thermal insulation
Wildfires

ABSTRACT

Fire has always been a driving factor of life on Earth. Now that mankind has definitely joined the other environmental forces in shaping the planet, lots of species are threatened by human-induced variation in fire regimes. Soil-dwelling organisms, *i.e.*, those organisms that primarily live in soil, suffer the numerous and different consequences of fire occurrence that are, however, often overlooked compared to those on vegetation and wildlife. Most of these organisms live in the uppermost soil layer, where fire-imposed temperatures on the ground are the highest insofar as they are lethal or dangerously upset natural habitats.

This contribution is a reasoned collation of findings from a number of works conducted worldwide that aims to gain insight into the immediate and longer-term impacts of single or repeated wild or prescribed fires on one group of soil-dwelling organisms or more.

In fire-prone ecosystems, fire is a controlling factor of soil biota biodiversity and activity, but also where it is infrequent its ecological footprint can be substantial and lasting. Generally, the immediate fire impact on soil biota is strictly related to the peak temperatures reached on the ground and their duration, and on a set of soil properties and water content. Vertebrates can escape overheating death by running away, searching for wet niches or burrowing deep into soil. Invertebrates and microorganisms, which have little or no mobility, succumb more easily to fire, but make up for this intrinsic vulnerability thanks to their greater fecundity at the population level.

Fire or burn severity, which can generally be defined as loss of organic matter aboveground and belowground, is the key factor of the indirect fire effects on soil-dwelling biota; whereas controlled burns do not often imply any substantial and lasting shift from the original situation, extreme and vast wildfires can have major consequences that may be severer than direct killing. In fact lairs are devastated, nutrient pools are heavily affected, food webs are upset, soil temperature and moisture regimes change, and toxic pyrogenic compounds remain in soil. All types of organisms can recolonise the burned area from their sanctuaries, provided that land use does not change, *e.g.*, to pastures or arable fields, and prompt enough vegetation re-sprouting and/or encroachment prevent substantial soil erosion. Each major taxon has genera or species with useful traits and behaviours to resist fire or to recover from its unwelcome environmental legacy sooner than others. If burned soil does not undergo other fires that occur too closely together for the typical fire regime of that particular area, most of its living components are generally capable of returning to pre-fire levels in times that depend on a series of factors, such as fire severity and post-fire rainfall.

1. Introduction

Fire is an upsetting event for terrestrial ecosystems upon which the most obvious impact is partial or total vegetation and litter removal, *i.e.*, fuel load. What especially draws the media's attention is loss of human life and property, but recent fire crises around the globe have also opened our eyes to the disastrous consequences for wildlife (Anony-mous, 2020; Pickrell and Pennisi, 2020). Kelly (2020) estimate that

human-induced modifications of fire regime, *e.g.*, the pattern, frequency and intensity of wildfires that prevail in an area over long time periods, including fire suppression in some protected areas, place the survival of at least 4,400 terrestrial and freshwater species from a wide taxa and habitats range at risk. In this respect, relatively less general interest is collected by soil-dwelling organisms, *i.e.*, those organisms that primarily, or for a substantial part of their life cycle, live in soil. Yet they include most of those smaller sized organisms that play fundamental and

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<https://doi.org/10.1016/j.foreco.2021.118989>

Received 15 October 2020; Received in revised form 21 January 2021; Accepted 26 January 2021

Available online 19 February 2021

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irreplaceable roles in ecosystem functioning.

Soil is “the biologically active, porous medium that has developed in the uppermost layer of Earth’s crust [...] through weathering processes driven by biological, climatic, geologic, and topographic influences” (Encyclopedia Britannica, 2020). Although several recent soil definitions tend to be as inclusive as possible to consider soils – including virtually lifeless substrates, like those from the driest areas on our planet, and even some of the loose blankets lying on the surface of Outer Space landmasses (Certini and Ugolini, 2013) – soil on Earth is actually a tremendous repository of genetic diversity (Orgiazzi, 2016), with soil organisms estimated to represent as much as 25% of the 1.5 million living species described worldwide (Decaëns, 2010). Fire can seriously endanger such a high-valued biotic heritage because of the temperatures it imposes on the surface or immediately below it, which are well above the few tens of degrees that are lethal for life. A large part of soil-dwelling organisms actually reside in the surface layer, where the organic fraction, which comprises mainly plant residue, animal remains and humic substances, often prevails over the inorganic one to, hence, form the “organic horizon”. This horizon, which is commonly indicated with the master letter O, is fuel and is, thus, the most dangerous place to stay in during fire (Swengel, 2001; Doamba et al., 2014). Below the O horizon, lethal temperatures are confined to a few top centimetres because “mineral” soil is a poor conductor of heat (Enninfu and Torvi, 2008). Nonetheless, the overall habitat can be so badly disrupted by fire that it becomes uninhabitable for most survivors for a variable time span (Massman et al., 2010). Possible hindrances to prompt soil biota recovery are various, e.g.: i) food shortage as the residual biomass from a fire is mostly scorched and charred and is a poor substrate for decomposer organisms, with a cascade effect on the whole soil food web structure (Gongalsky and Persson, 2013); ii) the persistent action of toxic compounds that form during fire, such as polychlorinated dibenzo-p-dioxins (PCDDs), dibenzofurans (PCDFs) and polynuclear aromatic hydrocarbons (PAHs), which are redistributed on the burned area and in its neighbourhood (Kim et al., 2003); iii) the net loss of nutrients in spite of the initial positive pulse in their availability (Andreu et al., 1996); iv) the collapse of organo-mineral aggregates and the subsequent clogging of soil pores, which lead to compaction and sealing (Mataix-Solera et al., 2011); v) the establishment of a new “pedoclimate”, i.e., soil temperature and moisture regimes (Harden et al., 2006). Additionally burned soil, made bare and often more hydrophobic by fire (Atanassova and Doerr, 2011), is vulnerable to erosion, which progressively removes the top most fertile layer (Shakesby, 2011; Vieira et al., 2015). Mass movements, which are also favoured in burned areas (Ziadé et al., 2014), sometime imply sudden substantial soil displacement. In such cases, the ecosystem’s complete recovery is very slow or even prevented (Thom and Seidl, 2016). On the contrary, where land use remains unchanged and no major erosional process or mass movement takes place, post-fire plant colonisation generally proceeds quickly because it is being favoured by the fertilisation of ashes rich in available nutrients at rates that depend on fire severity and environmental conditions, especially climate conditions. In parallel, immigration of heterotrophic organisms from surroundings and reproduction of survivors may fully or partly counterpoise losses due to mortality and emigration.

Fire usually creates a mosaic of soil patches burned with uneven severity, which can be operationally defined as “loss of or change in organic matter aboveground and belowground” (Keeley, 2009), possibly interspersed with other unburned ones (Fig. 1). Such spatial variability overlaps the already high original variability of each soil feature. Therefore, the interpretation of the overall soil response to fire is challenging, mainly for the soil-dwelling biota whose variability in amount, composition, and activity terms is even wider than those of soil abiotic components (Pietramellara et al., 2002). As stated by Neary et al. (1999), “the overall impact of fire on soil biota is complex, highly variable and at some degree unpredictable”. This is perhaps the reason why reviews on the fire effects on soil are generalist; e.g., Neary et al. (1999), Fisher and Binkley (2000), Certini (2005), Alcañiz et al. (2018), Neary

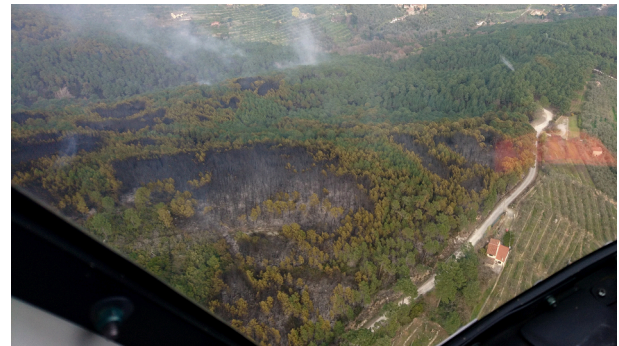


Fig. 1. A wildfire occurred on 24 February 2019 in a maritime pine forest in Vicopisano, central Italy, that created a mosaic of areas burned with uneven severity, interspersed with other unburned ones (picture by Cristiano Foderi).

(2019), along with those that focus on individual aspects – e.g., DeBano (2000) on fire-induced soil water repellence, Shakesby and Doerr (2006) about fire-induced changes to soil morphology and hydrology, González-Pérez et al. (2004) and Knicker (2007) regarding the impact of fire on soil organic matter. However, there is nothing that provides an overview of the fire impact on soil biota. One partial exception is the work by Pressler et al. (2019), which is a meta-analysis of many observations made from several empirical studies to investigate the fire effect on soil mesofauna (essentially arthropods and nematodes) and microorganisms (fungi and bacteria), and includes the total biomass and indices of abundance, richness, evenness, or diversity as measured response variables. This study convincingly, and surprisingly, highlights that neither the burned biome type (forest, shrubland, or grassland) nor fire type (wild vs. prescribed) succeeds in explaining much variation in soil biota responses.

The literature about the fire impact on specific groups of soil-dwelling organisms has increased substantially in recent years and is now ample enough to perform a comprehensive review. The purpose of this work is to provide reasoned insight into the commoner ramifications of fire on the main taxa, ranging from mammals to bacteria (Fig. 2), and to make inferences on fire as a possible driving factor of soil biology. Some major gaps in research on the subject are also highlighted.

2. Soil-dwelling vertebrates

Vertebrates spending much time on or in soil comprise small mammals and herpetofauna which, in turn, comprises reptiles and amphibians. Given their relatively high mobility, soil-dwelling vertebrates can potentially escape the fire by fleeing or hiding (the “refugia strategy”, *sensu* Pausas, 2019); in fact they are expected to be more exposed to negative effects on their shelter, food and breeding requirements than the direct impact of high temperatures or toxicity from smoke and/or oxygen depletion. Nevertheless, such conventional wisdom is disputed by Engstrom (2010), who reviewed a wide range of direct or “first-order” fire effects (killing or serious permanent injuries) on terrestrial vertebrates, and concluded that they were generally no less important than indirect or “second-order” effects (e.g., through shortage of food, freshwater and shelters).

2.1. Small mammals

Small soil-dwelling mammals include mainly rodents: moles, rats, mice, squirrels, hamsters, porcupines, etcetera. As fire approaches, they run away or move through tunnels. Those sleeping or hibernating in burrows are protected from direct fire effects (Dawson et al., 2019), but when they return to the burned surface, exhausted by long fasting, they may die because of forced changes in the diet composition or higher predation pressure. In fire-prone environments, some species have

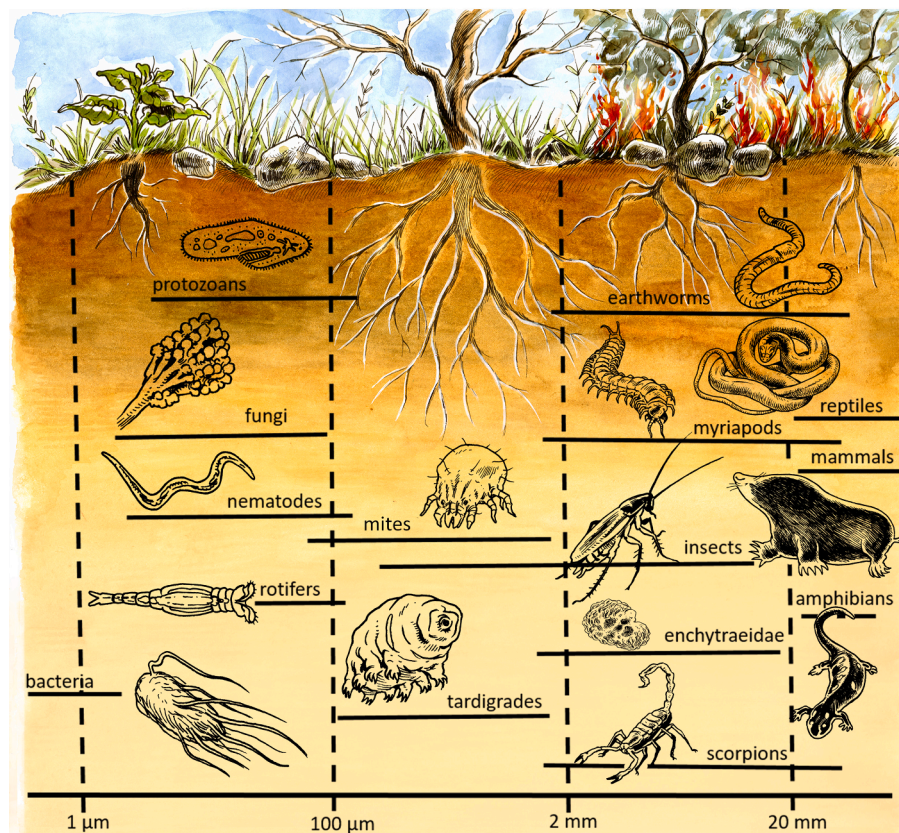


Fig. 2. A schematic representation of the major representatives of the variegated underground living world, classified according to body range size for each group (background and organisms drawn by Gianluca Borgogni). Note that the figure accounts for neither the physical distribution of organisms according to depth nor the usual thickness and features of the surface O horizon.

developed peculiar traits or behaviours to resist fire and/or survive on inhospitable post-fire landscapes (Fig. 3). One such example is the yellow-footed antechinus (*Antechinus flavipes*), a small terrestrial and arboreal marsupial from Australia which, despite being mainly insectivorous, may eat small vertebrates, eggs, nectar and flowers. This species can survive both fire, probably by hiding deep in rocky crevices, and desolate post-fire landscapes, by decreasing its daytime activity and



Fig. 3. Interface between a mixed Mediterranean forest and a burned portion of it 2 days after a severe fire that removed litter and the tangled understory, and almost completely the overstory (Orentano, central Italy; picture by Giacomo Certini). The burned area is a desolate environment where food and shelter are limited, and temperature and moisture extremes increase stress for the surviving organisms.

using torpor frequently to save energy (Matthews et al., 2017). Torpor is actually a physiological adaptation that plays a key role in the post-fire survival of small mammals, and can substantially increase in order to cut foraging requirements and exposure to predators, as demonstrated by Stawski et al. (2015) for brown antechinus (*Antechinus stuartii*), another small insectivorous marsupial from Australia. Specific morphological or behavioural adaptations make favour some animals over others in fire resistance or post-fire recolonisation terms insofar as fire is actually functional to them to remove competitors for the same ecological niche (Pausas and Parr, 2018).

Fire may have deleterious effects on the physiology of small mammals by, for example, making their reproduction difficult, as demonstrated in Australia by Begg et al. (1981) in four species: *Dasyurus hallucatus*, *Antechinus bilarni*, *Zyzomys argurus*, and *Zyzomys woodwardi*. In fact major habitat changes destabilise animals in delicate phases, such as courtship, gestation and caring for young (Banks et al., 2007).

The time required for mammals' recovery, if any, varies and depends on species and environmental conditions. One major driving factor in this regard, at least in temperate and semi-arid environments, is stochastic events like rainfall, which also control both erosion and vegetation recovery (Pastro et al., 2011). This is true of any other group of soil-dwelling organisms and will, thus, not be emphasised hereafter. After a first obvious depopulation period, if serious erosion does not occur and plant recolonisation quickly takes place, a new environment resembling the *status quo ante* may form, and possibly also show positive features (e.g., removal of pathogens or plant species beyond the context). In this case, the assemblage of post-fire small mammals can be the same, or even more abundant and diverse, than the pre-fire one, as assessed by Yarnell et al. (2007) in a South African grassland ecosystem. In an oak-dominated forest in Pennsylvania, Kirkland et al. (1996) found that

4–12 months after fire, small mammals were significantly less abundant in burned than in unburned forests, and two arvicoline rodents – the meadow vole (*Microtus pennsylvanicus*) and southern red-backed vole (*Clethrionomys gapperi*) – were still missing in the burned area. In a burned 15,000-hectare area in Arizona, Bock et al. (2011) assessed that the family Cricetidae of rodents declined because of fire-induced multi-year grass canopy reduction and returned to preburn levels only after 6 years. Fox and McKay (1981) monitored how small mammal abundance and diversity in portions of a eucalypt forest in Australia recovered after fire had occurred from 9 years to 1 month previously. A replacement sequence in time was observed for species reaching their maximum abundance (*Pseudomys novaehollandiae* and/or *Mus musculus* → *Sminthopsis murina* → *Antechinus stuartii* → *Rattus fuscipes*), which was interpreted as species occupying stages in the succession when their optimal habitat requirements were fulfilled. Regeneration age had the strongest effect on the biomass of *Rattus fuscipes*, the most abundant species, which displayed logistic growth in biomass, i.e., no resident populations established in the first 3 years, followed by a rapid increase on the plateau after 8 years.

Post-fire land management can significantly affect small mammals' recovery, as demonstrated by Lee et al. (2008), who examined the densities of three small rodent species – Korean field mice *Apodemus peninsulae*, Korean large-toothed red-backed vole *Eothenomys regulus* and black-striped field mice *Apodemus agrarius* – in a pine forest partially burned 4 years earlier. The mean number of small rodents captured in the unburned forest was significantly bigger than in the burned area. Nonetheless in the latter, there were fewer rodents where damaged trees were removed compared to where scorched trees were left unharvested, which suggests evaluating the opportunity to perform post-fire practices in those forests that host some protected animals.

Prescribed fire is expected to have minor effects, if any, on small mammals by virtue of its typical limited extent, short duration and low intensity. Actually, after studying mixed conifer forests in Sierra Nevada over a 3-year postfire period, Monroe and Converse (2006) found negligible impacts of prescribed fires on deer mouse (*Peromyscus maniculatus*) and lodgepole chipmunk (*Neotamias speciosus*) populations, and total small mammal biomass. Greenberg et al. (2006) captured eight species during an experiment designed to determine effects of three fuel reduction techniques on rodent species in the Appalachian Mountains. White-footed mice (*Peromyscus leucopus*), which composed ~ 80% of all the captures, did not undergo any statistically significant reduction in abundance, fitness (body weight), and demography (age or sex ratios) due to mechanical understory felling followed by prescribed fire. However, the survey done in the plots that underwent mechanical understory felling and prescribed fire alone was inconclusive. The review by Darracq et al. (2016) on the ramifications of prescribed fire with small mammals (and amphibians) in the longleaf pine (*Pinus palustris*) ecosystems to the southeast of the USA noted no significant difference in the number of species across burn frequencies, i.e., high (1–3 years), moderate (>than 3–5 years), and low (>than 5 years), which suggests a minor role of the fire return interval. Nonetheless, other studies on this subject performed in other environments are needed to obtain a consistent pattern.

Interestingly, we found no studies that pay attention to the fire impact on moles, which are the mammals that spend the most time in soil, although they very likely circumvent all direct fire effects.

In summary, wildfire generally has a significant impact on small mammals, and more in relation to the changes imposed on their habitats, with consequences in diet, predation and physiology, than in relation to direct killing or serious debilitation. The prescribed fire impact on the same class of animals seems negligible.

2.2. Herpetofauna

Herpetofauna resorts to many mechanisms to save itself from fire, mainly running and burrowing. The post-fire environment is

inhospitable to the herpetofauna, particularly for those species that require leaf litter or another surface cover that has been burned. Crucial undesired fire ramifications are soil erosion/sedimentation for amphibians, and increased vulnerability to predators for reptiles. In the longer term, however, fire can create a variegated environment capable of supporting a higher diversity of herpetofauna (Bury, 2004).

Several studies have dealt with fire impact on both reptiles and amphibians, but by almost exclusively from the controlled burning perspective. They are herein discussed, while the studies about only reptiles or amphibians are discussed in two subsections. Prescribed fire effects on herpetofauna have been comprehensively reviewed by Russell et al. (1999) in both upland and aquatic habitats. These authors concluded that such a fire type generally has barely any direct effect on most reptiles and amphibians, especially in fire-prone ecosystems where they have behaviourally adapted to avoid direct mortality by fire. In sandhill pine- and oak-dominated associations of the southern USA, Mushinsky (1985) assessed how burning even increased the diversity and abundance of reptiles and amphibians, and that some fire periodicities were better than others for maintaining high diversity. In fact, the diversity of herpetofauna on plots burned every year or every 7 years was higher than in the plots burned every 2 years, where a dense layer of grasses and herbaceous plants prevented occupation by the herpetofauna, at least until it had been reduced over time. Langford et al. (2007) composed an inventory of reptiles and amphibians in wet slash pine savannas on the Coastal Plain of Florida, where frequent fire is needed to suppress hardwood encroachment and to remove ericaceous understory vegetation. These authors found larger numbers of individuals in burned than in unburned stands. In an oak/hickory forest in Kentucky, Hromada et al. (2018) analysed the responses of herpetofaunal communities to prescribed fires applied twice to a 1,000-hectare area 1 year and 4 years prior to sampling. They observed that fire created an available vegetation structure gradient that induced a taxa-specific response by reptile communities. Positive effects were found for some lizard and snake species, while the amphibian community did not seem substantially impacted. Nonetheless, some amphibians showed moderately higher abundances in unburned sites, plausibly due to the availability of aquatic breeding habitats. In fire-maintained rosemary scrub sites in Florida, Ashton and Knipps (2011) reported how herpetofaunal communities did not vary with fire frequency, but abundances of some species did. In *Pinus rigida* or *Quercus* spp. stands of the southern Appalachians, North Carolina, Ford et al. (1999) documented that high-intensity prescribed fires had very little effect on the herpetofauna, namely a series of newts, salamanders, frogs, skinks and snakes (and some small mammals, mostly shrews and mice) 2 and 14 months after burning. Once again in North Carolina in an upland oak-dominated forest, Greenberg et al. (2018) did not document any adverse effects of prescribed fire on reptiles and amphibians during either the growing season or the tree dormant season, which suggests that season of burn *per se* is not pivotal for the herpetofauna's response. Finally, McLeod and Gates (1998) found that salvage cutting and prescribed burning were negative for the distribution and abundance of reptiles and amphibians in mixed pine-hardwood stands on the Atlantic coastal plain of Maryland. Adults of four amphibian species, young-of-the-year of five amphibian species (*Bufo woodhousii*, *Rana catesbeiana*, *R. clamitans*, *R. palustris*, *R. utricularia*), and three reptiles (*Carpophis amoenus*, *Storeria dekayi*, *Thamnophis sirtalis*) were in fact significantly more abundant in unburned than in burned areas. The main reason for such fire-induced decrease, at least for amphibians, was the removal of the thick leaf litter and dense pine canopy, which kept the ground cool and moist.

Overall, it would seem that prescribed fire is mostly harmless for the herpetofauna, but no strict rule can be drawn on the basis of such a few and partly conflicting findings.

2.2.1. Reptiles

Reptiles are evidently affected by wildfires, and both directly and indirectly, but perhaps less than amphibians. In particular, their

recovery seems faster. This is closely linked with vegetation recovery (e.g., rapid grass cover formation and its extent) and more marginally to some fire variables. Indeed in northern Portugal, Pinto et al. (2018) found that fire frequency and time since fire only partially explained the abundance, diversity and richness of some reptile communities, and apparently played less important roles than other factors, such as land-use type and vegetation structure. Similarly, by investigating a wide range of vegetation types spanning from sedge land to temperate rainforest in Australia, Lindenmayer et al. (2008) recorded 15 reptile species from five families, and found no significant relations between reptile species richness and the number of fires over 35 years, the time since the last fire, or a major fire severity.

Fire effects on reptiles have been investigated especially as regards snakes, lizards and turtles, but not widely enough to draw general conclusions about any of these groups.

Snakes have the formidable ability to escape fire, as verified by Rudolph et al. (1998) by endowing *Pituophis melanoleucus ruthveni* specimens with radio-transmitters. Nevertheless in fast-spreading wildfires, several individuals may succumb to flames (Fig. 4). Community recovery can be quite fast, in the order of 1 or a few years. Setser and Cavitt (2003) compared annually burned and long-term unburned tall-grass prairies in Kansas to find that two snake species, *Coluber constrictor* and *Thamnophis sirtalis*, were less frequently captured on recently burned prairies, but frequency was apparently the same beyond a single growing season. Snake species associated with moist, cool microclimates or leaf litter are significantly less abundant in burned areas, as demonstrated by McLeod and Gates (1998) in pine-hardwood forests of Maryland. Eating habits can also prove fatal in post-fire environments. Webb and Shine (2007) analysed 16 years of mark-recapture data about the endangered broad-headed snake (*Hoplocephalus bungaroides*) and the small-eyed snake (*Cryptophis nigrescens*) from burned areas in Australia. They noted that wildfire did not apparently affect the first species, but the latter's population decline was 48% eight months after the wildfire and 37% some years later. The authors attributed this discrepancy to both species' different foraging modes and how they affect their predation, with the small-eyed snakes being very active and, thus, more vulnerable to avian predation than broad-headed snakes, which are ambush-foragers that spend long periods in retreat-sites.

Lizards possess great motility and the excellent ability to burrow, and often succeed in avoiding injuries or death by fires, but might find it difficult surviving in bare burned areas. Fenner and Bull (2007) ascertained that a grassland fire, which burned throughout the area of a population of the rare pygmy bluetongue lizard *Tiliqua adelaidensis*, neither killed adult lizards, nor affected females' subsequent fecundity. Nonetheless, it implied significant reductions in activity and foraging,



Fig. 4. The scorched body of a snake in a freshly burned South Africa savannah (picture by Stefan Doerr).

and even a declining body condition. Pianka and Goodyear (2012) studied a species-rich lizard assemblage's population and community responses to fire in an arid environment of inland Western Australia to find that military dragon (*Ctenophorus isolepis*) abundance lowered due to fire, as it did in five species of *Ctenopus* skinks – *C. ariadnae*, *C. calurus*, *C. hanloni*, *C. pantherinus*, and *C. piankai*. On the contrary, the netted dragon (*Ctenophorus nuchalis*) and the termite-specialised nocturnal gecko *Rhynchoedura ornata* were found quite frequently during the short-term post-fire period, but became rare once the vegetation cover was virtually continuous again. Lizard diets changed significantly during the course of a 16-year fire succession cycle by them returning to near pre-burn conditions at the end of the monitored period. Chergui et al. (2019) used generalised linear mixed models to examine the influence of fire, forest type (cork oak and pine), habitat structure and climate factors on reptile-community abundance and species richness at several sites in the African rim of the Western Mediterranean, which was burned a few months to 10 years earlier. Abundance did not change with fire in cork oak forests, but increased for pine, while species richness was greater with oak and increased from unburned to burned areas. Two of the five commonest lizards in the region, *Acanthodactylus erythrurus* and *Podarcis vaucheri*, responded positively to fire in pine forests, but did not change in oak forests, which suggests that forest type had some effect on recovery. Schrey et al. (2011) demonstrated that different reptile species, including lizards, may experience distinct fire consequences for their local genetic diversity because of varying microhabitat preferences. In particular, fire increased the genetic diversity of the Florida scrub lizard (*Sceloporus woodi*), which peaked at more recently burned sites, while the opposite was true for the Florida sand skink (*Plestiodon reynoldsi*) and the six-lined racerunner (*Aspidoscelis sexlineata*).

Turtles are slow and, thus, vulnerable to flames. Actually, in the Mojave and Sonoran Deserts, Esque et al. (2003) found the desert tortoise (*Gopherus agassizii*) to be much more susceptible to direct (and indirect) wildfire effects than 11 other faster reptile taxa. Nevertheless, the desert tortoise is fond of its range, even when it burns, and tends to come back (Lovich et al., 2018). Breininger et al. (1994) reported in scrub and pine flatwoods of Florida that gopher tortoise (*Gopherus polyphemus*) densities did not show any relation with time since fire to vegetation classes (3 years or less, 4 to 7 years, and more than 7 years), which implies relatively fast recolonisation.

Overall, indirect fire effects on reptiles, e.g., disturbed habitat and increased predation, are by far stronger than direct ones, and the recovery of populations closely follows that of their habitat.

2.2.2. Amphibians

Amphibian mobility is generally less than that of mammals and reptiles and, hence, their direct mortality from fire is assumed to be higher. However, much depends on the season during which fire occurs. In fact under dry summer conditions, most amphibian species are relatively safe either underground or in water, but in spring, pond- and some stream-breeding amphibians migrate to water to reproduce or disperse from breeding sites, which makes them particularly vulnerable to flames (Pilliod et al., 2003). Late summer and autumn burning can be problematic for those amphibians that settle under leaf litter to overwinter, while winter fires are the least harmful to amphibians because they do not interrupt their breeding.

The amphibian population's post-fire recovery is variable as it depends on a number of factors. First of all, amphibians do not tolerate temperatures over 25–30 °C (Pilliod et al., 2003), which can represent a marked crisis in bare burned landscapes. Other indirect fire effects on amphibians include increased vulnerability to predators, changes in water temperature associated with canopy loss (which particularly affects eggs and larvae in aquatic life stages), changes in water chemistry and increased sedimentation in water bodies (which especially affect amphibian reproduction and recruitment). However, amphibians are so taxonomically and ecologically diverse that consequences of fire are expected to widely vary among species and geographic regions. Some

species may even increase in burned areas. Indeed a few months following a wildfire, in an oak-dominated forest of Pennsylvania Kirkland et al. (1996) counted significantly more individuals of American toad (*Bufo americanus*) and salamanders *Plethodon cinereus* and *P. glutinosus* in burned sites than in unburned ones. However, these authors did not identify the reason for this positive fire effect.

Terrestrial salamanders are somewhat protected from direct fire-induced mortality by being fossorial animals, but very little is known about their post-fire response. Gade et al. (2019) worked on this subject, specifically on red-legged salamander, *Plethodon shermani*, and observed its precipitous declines in burned upland forests of North Carolina, as well as loss of juvenile size classes with only the largest adult individuals remaining 18-months post-fire. The fact that no apparent negative effects were noticed in riparian forests of the same area suggested them to be buffered from wildfire effects, and the salamander populations inhabiting such an environment were at less risk of declining than those in exposed habitats.

An expectedly similar wildfire response to that of salamanders, which has barely been studied, is that of frogs. In mixed wood forests of Alberta, Constible et al. (2001) assessed that the fire impact on the frogs *Rana sylvatica* and *Pseudacris triseriata maculata* was comparable to that of harvesting, and very much depended on leaf litter, ground cover and soil moisture. Using empirical genetic data to deal with the frogs *Litoria ewingii*, *L. paraewingii*, and *L. raniformis* by stochastic population modelling in a range of fire-frequency scenarios in fire-prone environments of south-eastern Australia, Potvin et al. (2017) indicated that population size decreases and the probability of extinction increases with higher fire frequency. Nonetheless, these effects substantially differed among species.

Prescribed fire is typically less damaging for amphibian populations, as for any other group of organisms, by virtue of its relatively low severity. However, Schurbon and Fauth (2003) demonstrated its tangible impact by monitoring assemblages at 15 temporary ponds in South Carolina with different burn histories. Here, the immediate fire effects respectively explained 10.8% and 12.8% of variation in the abundances of amphibian in general and of anurans in particular. Instead the short-term fire effects explained 31.8% and 24.6% of variation in amphibian species richness and evenness, respectively. Prescribed fire impact on a woodland population of the Cow Knob salamander (*Plethodon punctatus*), a talus specialist and a species of much conservation concern, and the eastern red-backed Salamander (*P. cinereus*), a widespread habitat generalist, was investigated by Jacobsen et al. (2020) in the Appalachian Mountains. The mean *P. punctatus* abundance was lower at the burned sites, but no strong burn effect for *P. cinereus* was found. Overall, preventive management using prescribed burning altered microhabitat conditions, such as canopy cover, leaf litter depth and vegetation groundcover, which are important for woodland salamanders. Once more in the Appalachian Mountains, Ford et al. (2010) did not find any change in woodland salamander assemblage (seven different species) and very few differences in adult to juvenile ratios of salamanders prior to burning or afterwards. Their observations suggest that woodland salamanders are somewhat tolerant to two prescribed fires with close temporal proximity. Conversely, by radio-frequency identification O'Donnell et al. (2015) assessed that prescribed fire may significantly alter the surface activity and behaviour of the terrestrial western slimy salamander (*P. albagula*).

Although available data demonstrate wide variability, amphibians appear among the classes of soil-dwelling organisms that are most impacted by fire passage, which chiefly depends on fire severity and season.

3. Soil-dwelling invertebrates

Invertebrates comprise the majority of soil-dwelling animals and can be conveniently divided on a size basis, i.e., macro- meso- and micro-fauna, even though their size varies somewhat depending on the

ecosystem and contingent environmental conditions. Other than this convenient subdivision, we herein focus on the major taxa of arthropods, earthworms, enchytraeids, tardigrades and rotifers, nematodes, protozoans (Fig. 2).

Apparently the literature reports contradictory fire effects on invertebrates, which is partly explained by the different methodologies followed to count individuals or species, e.g., searching for them in predetermined areas or attracting them by traps (Swengel, 2001). Fire and sampling seasons are other causes of variability among various studies (Swengel, 2001). Finally, there are obvious differences in reaction to fire between epigeic organisms (living on the soil surface and unable to burrow) and endogeic organisms (burrowers), as emphasised by Coyle et al. (2017). The fire impact on soil invertebrates can be evaluated as changes in total biomass, abundance of individuals, community composition, or richness and diversity of the lowest taxonomic groups (Malmström, 2010; Kral et al., 2017). However, assessments are often limited to higher taxonomic levels (orders or families), which are also due to restricted expertise. In these cases, both total abundance and taxonomic diversity can be unsatisfactory measures of recovery (Moretti et al., 2006; New, 2014). A reliable option with such studies is to categorise species into trophic guilds rather than according to phylogenetic patterns, which can also allow easier comparisons to be made among different biomes (Moretti et al., 2006; Malmström, 2010).

3.1. Direct effects of fire on soil invertebrates

Invertebrates easily succumb to fire, but some insects possess considerable mobility. In a *Pinus sylvestris* forest in Sweden, Wikars and Schimmel (2001) determined that the immediate outcome, i.e., one single day later, of controlled moderate-severity burning that had removed the whole above-ground vegetation was an approximate 90% reduction in total soil invertebrates due to both mortality and forced emigration.

Lethal temperatures for invertebrates are no higher than they are for other organisms. For many soil arthropods, death can occur at around 40 °C, but prolonged exposure to slightly lower temperatures can be lethal (Malmström, 2008). This mostly depends on the anatomical features of individuals, which are also linked with the development stage and their habitat. The presence of a thick protective cuticle means, for example, that some arthropods (e.g., Oribatida, Elateridae) are relatively fire-resistant (Busse et al., 2005; Moretti et al., 2006). The soil surface is the most exposed part to direct fire damage for invertebrates, and also proportionally to the amount of forest floor, as demonstrated by a burning experiment conducted by Gongalsky et al. (2012) in a boreal conifer forest. Flying surface dwellers can escape the fire, while organisms that are inextricably linked with soil, such as earthworms and some arthropods, may migrate more deeply to avoid fire-related heat (Gongalsky et al., 2012; New, 2014).

In addition to fire intensity and severity, direct mortality of soil invertebrates depends on the burning season, which can actually fall in critical phases of invertebrates' phenology, such as diapause or the reproductive period. For instance, in Mediterranean environments, where wildfires preferentially occur in hot and dry summers when all biological activity is very slow, spring blazes are extremely detrimental for arthropod communities and population dynamics (Radea and Ariannoutsou, 2012).

3.2. Indirect fire effects on soil invertebrates and post-fire recovery

Indirect fire effects on soil invertebrates are often more serious than direct ones (Busse et al., 2005; Kral et al., 2017). In the short term, the destruction of food resources is the most significant limiting factor, especially for herbivores. A post-fire decrease in detritivores, such as litter-dwelling oribatid mites, millipedes and lumbricids, is usually recorded (Zaitsev et al., 2014). In grasslands of southern New Mexico, Killgore et al. (2009) found much fewer burrows of wolf spiders,

Geolycosa spp., and a significantly smaller area of termite galleries (approximately 80% less than the pre-fire situation in both cases) 4 months after a low-intensity prescribed burn. For spiders, this reduction could be due to changes in food resources, particularly the availability of small arthropods, while loss of grass cover could have been the cause for termites as termite galleries form primarily around the base of old or dead grass stems and on woody litter. The removal of vegetation cover implies higher diurnal temperatures on the ground (due to both lack of protection from solar radiation and reduced albedo by darkening) and lower soil moisture (from enhanced evaporation) which, along with a generalised rise in pH imposed by released ash, are real upheavals for the habitats of soil-dwelling invertebrates (Xu et al., 2012).

The post-fire recovery of invertebrates depends on the quantity and quality of the litter layer (Zaitsev et al., 2014). Korobushkin et al. (2017) found that the saprophagous soil fauna generally avoids the surface layer of burned soil, possibly due to the paucity of suitable resources and unfavourable hydroclimatic conditions. These conditions last until new plants establish and start to form a litter layer first, and then a more mature organic horizon (Moretti et al., 2006; Malmström, 2010; Radea and Arianoutsou, 2012).

Once vegetation has slightly recovered, mobile phytophagous become the main component of the soil faunal community, thanks also to the minor predation occurring in the first colonisation stage (Gongalsky and Persson, 2013). Some diet-generalists feeding on plants, such as grasshoppers, crickets, aphids, cicadellids and thrips, in burned areas may be more abundant than they were before the fire (Kral et al., 2017; Koltz et al., 2018). In a successive phase, soil-dwelling predators and microbe-detritivores enter the burned area (Zaitsev et al., 2014). Some animals can adapt to the harsh post-fire environment by altering their diet and behaviour. For example, Peterson et al. (2008) reported how termites were able to feed on charcoal, although it could not be the only food source.

Post-fire recovery gradually proceeds from outside to the centre of the burned area, and is firstly carried out by highly mobile species (Gongalsky and Persson, 2013; Van Mantgem et al., 2015). Hence, for instance, carabids' recolonisation occurs sooner than that of soil-dwelling macrofauna (Zaitsev et al., 2016), while arachnids, earthworms, molluscs and myriapods are rather slow colonisers (Gongalsky and Persson, 2013). Unburned patches of land, even with a diameter of a few tens of centimetres, can support the restocking of soil invertebrates in burned areas better than unburned surroundings (Gongalsky and Zaitsev, 2016), and unburned corridors across burned areas are fundamental for the least mobile soil invertebrates (Zaitsev et al., 2014). In any case, complete invertebrate community recovery after a single fire can take years, or even decades, and chiefly depends on fire severity and the burned area width (Moretti et al., 2006; Malmström, 2010). Inferring any temporal law for invertebrates' recovery is hard because fire severity is a variable that is often not consistently accounted for in papers (Malmström, 2010), and there are very few long-term studies about this (Zaitsev et al., 2016). Meso- and macro-fauna recoveries from a wildfire of about 30–40% in 5–10 years have been reported for boreal forests by Zaitsev et al. (2014) and Gongalsky and Persson (2013), while full recovery of soil invertebrates in this environment has been found by Zaitsev et al. (2016) to require even 80 years. Actually, arthropod species characteristics of old-growth habitats (e.g., dead wood) are attracted no sooner than several post-disturbance decades (Buddle et al., 2006). Soil molluscs, such as snails and slugs that feed on litter, are perhaps the most heavily fire-impacted invertebrates because of their high physiological demand for humidity (Hylander, 2011) and feature among the organisms that need the longest times to completely recover (Kiss and Magnin, 2003).

Fire creates new habitats, where some rare species can be favoured over others and new exogenous species come to settle (Moretti et al., 2010). Open burned areas attract some pioneer soil-dwellers that feed on abundant resources in fire-injured ecosystems, such as scorched trees or herbaceous sprouts. Moreover, some invertebrates are well adapted to

frequent low-intensity fires, and their abundance and richness typically increase rapidly after each event (New, 2014). For example, the rare prairie mole cricket (*Gryllotalpa major*), which is confined to relict grasslands in Oklahoma, Kansas, Arkansas and Missouri, has been shown by Howard and Hill (2007) to have a non-random distribution, and tends to emerge on recently burned patches, which are suitable advertising arenas for reproductively-active males. In theory, a fire-adapted landscape with a patchwork of habitats corresponding to different successional stages and sites where fire occurs with distinct intervals would support the widest species variety (Gandhi et al., 2001).

All in all, fire frequency ultimately determines the fate of invertebrates, and most species recover better from a single severe fire than repeated less severe ones (Gongalsky and Persson, 2013), and a very quick fire return may not allow vegetation assemblage and the invertebrates community to completely reform.

3.3. Fire-adapted and pyrophilous invertebrates

Many invertebrates possess behavioural and/or physiological adaptations to fire. For instance, termites build fire-resistant mounds, while ants burrow nests to use them as shelters whenever necessary (Wikars and Schimmel, 2001; Doamba et al., 2014). Leaf-cutter ants (*Atta* spp.) remove litter and woody debris from the surface to prevent low-intensity fires from spreading to the understory around their nests (Carvalho et al., 2012). Other fire-adapted species have developed special abilities to look for safe places during fire or to promptly recolonize the least impacted ones after fire has passed (Gongalsky and Persson, 2013; New, 2014; Koltz et al., 2018). There are even some species, called "pyrophilous", that take advantage of burned environments. Uncommon in undisturbed areas, they base their long-term persistence on prompt fire return (Saint-Germain et al., 2008). Pyrophilous invertebrates comprise those "saproxylic" insects that live in dead wood, which may objectively benefit from fire occurrence (Swengel, 2001; Moretti et al., 2010; Boucher et al., 2012). They can also give rise to a positive cascade effect on other trophic level by, for instance, representing food for other invertebrate species that are not pyrophilous *per se* (Koltz et al., 2018). Effective fire suppression can cause the contraction, or even extinction, of a series of species that depend on fire at different levels, as demonstrated by Gongalsky and Persson (2013) in Fennoscandia.

The environment's proneness to fire may be reflected in the proportion of functional traits that is typical of a fire-adapted faunal community (Korobushkin et al., 2017), such as specific sensors that make several species of ants, flies, stick insects, beetles, grasshoppers and spiders capable of detecting fire well in advance (New, 2014; Milberg et al., 2015). The beetle *Calosoma frigidum* (Carabidae) is enabled, thanks to its temperature detectors, to synchronise its emergence from underground burrows as the albedo of soil significantly decreases, which also happens with fire-darkened soils (Jacobs et al., 2011).

3.4. Arthropods

Soil arthropods range in size from microscopic to several centimetres long, and include insects like beetles, ants, and termites; arachnids, such as spiders and mites; crustaceans, such as sowbugs; myriapods, like centipedes and millipedes; springtails and scorpions. Arthropods are generally vulnerable to fire, especially in their larval stage, when they lack mobility (Fig. 5). However when reviewing their response to fire, Kral et al. (2017) underlined that it is varied, and some groups like Orthoptera (grasshoppers and crickets) and Coleoptera (beetles), react much better than others, like Arachnida (spiders) and Homoptera (leafhoppers and aphids); for several other taxa, such as those of Hemiptera, Diptera and Hymenoptera, available information is still scarce.

Saprophagous arthropods and litter-dwelling groups (Isopoda, Formicidae, and some Coleoptera families like Curculionidae) are generally impacted very strongly by fire, and both directly and later because of lower litter availability (Korobushkin et al., 2017). After monitoring the



Fig. 5. The killed grub of a scavenger scarab beetle in the middle of charred litter in a freshly burned eucalyptus forest in Australia (picture by Stefan Doerr).

dynamics of litter-arthropod populations for nearly 2 years, Vasconcelos et al. (2009) recorded a general declining arthropod abundance, and the abundance and species richness of individual taxa, in a burned area of a woodland savannah in Brazil. However in forests of the Swiss Alps, Moretti et al. (2004) found that species richness for a wide spectrum of taxonomic invertebrate groups was significantly higher in the sites that underwent repeated surface winter fires than in unburned forests. In particular, a positive fire effect on species richness was observed for ground beetles (Carabidae), hoverflies (Syrphidae), and spiders (Araneae), while only isopods and weevils (Curculionidae) were found to be negatively impacted, in terms of species number or abundance. In the same region, Moretti et al. (2006) assessed that arthropod communities are vulnerable to recurrent fires, which also induces a dominance hierarchy among species.

Post-fire arthropods' colonisation can start very shortly by those species looking for burned areas to carry out some of their life phases. For example, the beetles *Atomaria pulchra* (Cryptophagidae) and *Corticaria rubripes* (Latridiidae) have been found to colonise a forest one day after burning (Wikars and Schimmel, 2001). Post-fire conditions may immediately favour heliophilous and thermophilous insects, such as Neuroptera, Heteroptera, Cerambycidae, Lucanidae, and Buprestidae (Moretti et al., 2010). Muona and Rutanen (1994) studied the immediate fire-induced changes in beetles at three sites in coniferous forests of Finland, and noticed that the number of individuals and species had generally increased. In fact several were attracted to burned sites, including soil- and litter-dwelling groups like Carabidae, Byrrhidae and some Elateridae. However, Cholevidae that live in rodent nests and many litter-dwelling Staphylinidae were drastically reduced by fire and did not recover until after 2 years.

As with other animals, prescribed fires by virtue of their typically lower severity are less harmful than wildfires for soil-dwelling arthropods. Martikainen et al. (2006) assessed how carabid beetles are well-adapted to prescribed fires in *Pinus sylvestris*-dominated forests of Finland, to the extent that a relatively high fire frequency is essential to maintain their population. Again in Finland, harvesting and burning was found to improve the abundance and richness of both saproxylic and non-saproxylic beetles in some forests (Toivanen and Kotiaho, 2007), even implying benefits for some red-listed rare species. Yet early season low-intensity prescribed fires (single or recurrent) in mixed forests of south-eastern USA devastated leaf-litter arthropod abundance, albeit diversity was not affected (Coleman and Rieske, 2006). Population resurgence was not evident until the second growing season in multiple-burned areas, which demonstrates that in this environment a fire frequency higher than 2 years is required if full litter layer recovery is a primary burn objective. In a mixed-conifer forest of Sierra Nevada (USA), Apigian et al. (2006) found that prescribed burning was slightly

less invasive, especially in terms of Coleoptera species richness, than two "fire surrogate" treatments; i.e., overstory thinning with understory mastication, and combined thinning and burning. Auclerc et al. (2019) showed that in some areas subjected to common cut and burn treatments conducted within 6- to 26-year intervals in a deciduous forest in northern USA, the invertebrate community composition varied with time and species distributions could be associated with the structural attributes of their habitats. For example, millipedes and the ground beetle *Calosoma externum* displayed early succession preference, while the dominant species in the oldest stands were the beetle *Stelidota octomaculata*, an acorn dweller, and the spider *Agroeca ornata*, which is usually associated with coarse down woody debris.

3.4.1. Macro-arthropods

It is customary to distinguish arthropods as macro-arthropods and micro-arthropods, although there is no real size limit between both groups because the smallest macro-arthropods overlap the largest micro-arthropods. This distinction is rather practical, with macro-arthropods alone being sampled as individuals, or functional macro-arthropods being able to relocate large amounts of soil, whereas micro-arthropods passively occupy existing spaces (Coleman et al., 2004).

Insects, myriapods, larger spiders and beetles are the most well represented macro-arthropods to deal with mineral soil and the overlying litter layer, whereas ants and termites are more actively involved in their structuring and functioning.

Ants (Hymenoptera: Formicidae) have been studied relatively often in terms of fire effects (Fig. 6). Different ant taxa can be regarded as 'fire-tolerant', 'fire-intolerant' or 'fire-neutral'. An experimental fire conducted in California was found to efficaciously control the invasive Argentine ant (*Linepithima humile*) by immediately halving its population, probably because this species nests near the surface (Sanders, 2004). Many other ant species, such as the Mediterranean *Aphaenogaster gibbosa*, normally nest at a depth of 30–40 cm, where they avoid direct heat during fire (Lázaro-González et al., 2013). Based on the studies carried out in California native shrubland, Van Mantgem et al. (2015) concluded that the ant species in this fire-prone ecosystem generally did not suffer any substantial fire-induced impacts. More or less the same conclusion was reached by other authors who studied savannahs in South Africa and Australia, where the abundance of some species was even promoted by burning (e.g., Hoffmann, 2003; Parr et al., 2004; Parr and Andersen, 2008). Tavella and Cagnolo (2019) investigated the macro- and microscopic structure of ant interaction networks in central Argentina, finding fire-induced changes in ant communities, but not in their whole structural patterns. By a meta-analysis of the data collected from 50 studies conducted in different environments, Vasconcelos et al. (2017) concluded that the fire effect on ant diversity varied very much



Fig. 6. Ants belonging to the species *Crematogaster castanea* (Red Cocktail ant) on a dead branch on the ground pictured a few minutes after a prescribed burning in the Kruger Park, South Africa (picture by Giovanni Mastrodonato).

among several vegetation types, and was extremely negative where fire was uncommon and minor, or insignificant where fire was frequent, as in savannahs and some grasslands. The same analysis revealed that only in forests did wildfires have a stronger negative effect on ant diversity than prescribed fires.

Termites (Isoptera) are insects that have occasionally been studied for their response to fire. They are common in fire-prone systems and usually remain protected from intense heat inside their highly structured mounds. In a study conducted in southern Australia that encompassed 560 sites clustered in 28 landscapes selected to represent different fire mosaic patterns, [Avitabile et al. \(2015\)](#) detected 12 termite taxa, but obtained very little evidence that their occurrence frequency was related to fire, and no evidence at all that habitat heterogeneity generated by fire influenced termite species richness. Nevertheless, [Killgore et al. \(2009\)](#) reported in desert grassland in New Mexico that at 4 months post-burn the number and size of termite gallery-sheeting were significantly reduced, chiefly because termites in most cases make their galleries around the base of old or dead grass stems. The recovery rate of termites in fire-affected areas is substantially conditioned by food supplies, as proven by [Benzie \(1986\)](#) in African savannahs, where harvester termites increased 4- to 5-fold over 2 years in fire-protected plots as a result of increased dead grass availability.

The response to fire of sowbugs and scorpions is virtually unknown. Only one study by [Parmenter et al. \(2011\)](#) has found a few months after a wildfire that the number of scorpions *Vaejovis* spp. (Vaejovidae) had increased in desert grassland in New Mexico compared to the unburned situation, along with those of acridid grasshoppers, carabid and tenebrionid beetles, and also the sun spiders (*Eremobates* spp.; Eremobatidae).

3.4.2. Micro-arthropods

Soil arthropod diversity and abundance are dominated by micro-arthropods, which are visible to the human eye or with some magnification and include chelicerates (mites, small spiders and pseudoscorpions), myriapods (centipedes, millipedes and symphylans), springtails, and many species of smaller-sized insects. Edaphic micro-arthropods are effective bio-indicators of environmental changes, including fire-induced ones ([Mantoni et al., 2020](#)), and have measurable impacts on the main pathways of soil organic matter formation and dynamics ([Soong and Nielsen, 2016](#)). The studies that have dealt with the fire impact on micro-arthropods are limited, perhaps because fully efficient sampling methodologies for such a group of organisms are lacking ([André et al., 2002](#)). In any case, it is known that fire significantly reduces the micro-arthropod community and changes its composition in the short and mid terms, mainly because the majority of their resources and habitats is lost, i.e., above-ground vegetation and the organic horizon ([Broza and Izhaki, 1997](#); [Rutigliano et al., 2013](#)). In this regard, a rise in soil pH can be crucial, as demonstrated by [Haimi et al. \(2000\)](#) with a wood-ash fertilisation experiment under Scots pines in Finland. Similarly, [Henig-Sever et al. \(2001\)](#) found very good negative correlations between the ash layer pH and the micro-arthropod community size, and proposed the latter as a fire severity index.

Micro-arthropod abundance and biomass have proven to be more fire-affected than species richness ([Gongalsky et al., 2012](#)), with some groups (e.g., Pseudoscorpiones) being more sensitive than others ([Lisa et al., 2015](#)). Fire frequency is a controlling factor of micro-arthropod abundance according to [Dress and Boerner \(2004\)](#), who found that this abundance in oak-hickory (*Quercus-Carya*) forest ecosystems in Ohio was significantly lower in an annually burned watershed than in periodically burned or unburned watersheds. The recovery rate of soil micro-arthropods (both quantity and quality) varies according to the environment type and post-fire conditions, and is especially bound to the vegetation recovery rate, which provides not only sources of energy inputs in the form of dead organic matter, but also a canopy that moderates the microclimate of the forest floor ([Marra and Edmonds, 2005](#)). [Abbott \(1984\)](#) assessed 3 years after a moderate-intensity fire in the

jarrah forest of Western Australia how the majority of the invertebrates inhabiting soil and litter did not show any significant difference in density between burned and adjacent unburned areas. However, there were still more centipedes (Chilopoda), silverfishes (*Zygentoma*) and cockroaches (Blattodea) in the unburned surroundings, while millipedes (Diplopoda) occurred at significantly higher densities in the burned area.

Mites (Acari) are perhaps the most widely studied group of micro-arthropods in terms of fire effects. They are abundant everywhere on Earth, especially in soil and related habitats (moss cushions, fallen wood, grass tufts, ant and termite nests) ([Ponge, 1993](#)). Their proximity to the surface and low mobility make mites prone to direct fire effects, although the solid exoskeleton of moss mites (Oribatida) somewhat reduces this proneness ([Gongalsky et al., 2012](#)). [Kamczyc et al. \(2017\)](#) demonstrated a significant effect on Mesostigmata mite density of both fire and forest age, with more individuals in unburned and mature Scots pine forests (83–101 years vs. younger ones of 9–40 years old), while mite diversity significantly differed between forest ages, but not between burned vs. control. In a tropical rainforest of Nigeria, [Badejo \(1994\)](#) reported the densities of juvenile cryptostigmatid mites to be higher in an area burned 6 months earlier than in an unburned counterpart, which suggests fire-promoted reproductive activity. Nevertheless, densities of some dominant mite genera, such as *Haplozetes*, *Scheloribates*, *Nothrus* and *Carabodes*, were still lower in the burned area. This author attributed such a selective influence of burning on mite taxa to their differences in feeding requirements, phenological patterns and life history tactics. Mites have been shown to recover from burning with discrepant speed also in a completely different environment; namely, a boreal conifer forest in Sweden, where [Malmström et al. \(2008\)](#) found faster recovery for Mesostigmata compared to Oribatida.

Concerning the immediate and short-term effects of prescribed fire on soil mites, [Grabczyńska et al. \(2009\)](#) revealed that they were modest in a pine mixed forest in Poland in both density and taxonomic diversity terms. Although the values recorded in the burned plots immediately after fire significantly differed from those in the unburned surroundings, 60 days later mite abundance was similar in both treatments, and were equal after another 30-day period. This finding demonstrates a certain recovery speed after low-severity disturbances. In the Mediterranean maquis of Italy, [Rutigliano et al. \(2013\)](#) performed monitoring 245, 364 and 728 days after an experimental fire, and found that oribatid mites showed the highest abundance and species density on the latest date, while the highest species density for springtails was observed 245 days after fire, concomitantly with peaks in soil water content, total and active fungal mass, and abundance of culturable total, xerotolerant and heat-stimulated fungi.

Springtails (Collembola) are other numerous micro-arthropods in soil, which have sometimes been studied in fire impact terms, but not sufficiently to draw any definite conclusion. [Brand \(2002\)](#) compared the species richness, frequency and density of springtails in burned and unburned areas of an arboretum in Illinois. In burned areas, there were significantly fewer springtail species and the frequencies of eight of the 10 commonest species were lower. However, the fire effect varied markedly for the 30 species identified in that study; for example, *Isotoma notabilis*, *Lepidocyrtus* spp., *Neanura muscorum* and *Tomocerus flavescens* showed significantly higher frequency and density in unburned areas, unlike *Isotoma viridis* and *Xenylla grisea*. In the Russian taiga, [Saifutdinov et al. \(2018\)](#) assessed that total springtail abundance depended on the forest subregion, and not on burning, while fire reduced the abundance of sexually reproducing epiedaphic springtails by an average of 40%. This decrease positively correlated with fire severity and negatively with both litter thickness and soil water holding capacity. [Huebner et al. \(2012\)](#) studied contiguous sites with a differing fire history to explore the post-fire succession of springtail communities in a maple-oak forest of southern Québec, and noted that the species found after high-intensity fires were smaller in size than in unburned areas. Other character states (eyeless, unpigmented) suggested that these species were

endogeic versus epigeic, and that fire-induced litter loss was most probably the main driver behind community compositional changes.

3.5. Earthworms

Earthworms (Oligochaeta), along with termites and ants, serve as “soil engineers” by translocating large volumes of matter, altering soil physico-chemical properties and influencing resources availability to other species (Lavelle et al., 2016).

Earthworms can be divided into those that dwell in surface litter, in mineral soil, and in both, which are respectively called “epigeic”, “endogeic”, and “anecic”. The first ones are expected to suffer the direct impact of heating more than the other two. In spite of their fundamental importance for soil ecology and fertility, works that have focused on fire ramifications in earthworms are not as abundant as expected, and almost always deal with controlled burning. The only study found on wildfires is perhaps that by Bhadauria et al. (2000) who, in a mixed oak–pine forest of the Himalaya, found a significant immediate post-burn decline in the population density of *Eutyphoeus nanianus* and *Octolasion tyrtaeum* which, however, proliferated after 4 months. Four months later, *E. nanianus* had returned to more or less pre-fire levels, while *O. tyrtaeum* density was still significantly lower than it was originally. Collett et al. (2013) found that two spring short rotation prescribed fires in dry sclerophyll eucalypt forests of west-central Victoria, Australia, had no discernible effect on arthropods, but substantially reduced earthworms, which recovered to their original levels no earlier than 3 years. Once more in the jarrah forest of Australia, Abbott (1984) recorded no significant changes in earthworm density almost 2 years after a moderate-intensity fire. James (1988) reported how the biomass of native tallgrass prairie earthworms *Diplocardia smithii* and *D. verrucosa*, collected in Kansas more than 1 year after burning, had increased by 135% and 67%, respectively. Such a positive response reflected an 11% increase in soil organic matter in burned areas, which suggests a positive fire effect in resource-based terms. On the contrary, the introduced exogenous earthworm *Aporrectodea turgida* declined because of fire, which demonstrated its poor adaptation to such disturbances. In line with this, Ikeda et al. (2015) proved that prescribed fire was effective in managing the earthworm *Amyntas agrestis*, a non-native earthworm that proliferated in the topsoil of North American forests, by reducing the viability of cocoons and the survival rate of juveniles through the removal of their preferred food resource, i.e., litter. If we summarise these relatively few, but partly contrasting findings, low to moderate controlled burning in fire-prone ecosystems appears to have some transient impact on indigenous earthworms, which can be pseudo-permanent in exogenous non-adapted earthworms.

3.6. Enchytraeids

Enchytraeids resemble small earthworms and mainly include species that live in highly organic terrestrial environments. They are vulnerable to fire and often live in the upper few centimetres of fuel-rich soils. Changes in enchytraeids abundance and activity affect many other living components of the soil environment because of their key role in organic matter decomposition and mineralisation (Didden, 1993). A very negative fire impact on enchytraeids, which is even higher than that on the majority of soil-dwelling organisms and strictly linked with litter removal, was recorded by Zaitsev et al. (2017) in boreal conifer forests of Russia. In quite a similar environment in Sweden, Malmström et al. (2009) assessed how burning reduced enchytraeid abundances by between 30% and 65%, and these reductions lasted a couple of years. The species *Cognettia sphagnetorum*, which in that study made up 98–99% of all enchytraeids, was revealed by Liiri et al. (2002) to be negatively affected by wood ash release to soil, and thus suggests the transient change in pH as the main controlling factor of the post-fire recovery of enchytraeids.

3.7. Tardigrades and rotifers

Tardigrades are 0.1- to 1.5 mm-long and eight-legged segmented animals that inhabit most terrestrial, freshwater and marine environments. They can be essentially considered aquatic animals as terrestrial species also live within layers of water that are thick enough to house them. This and their ability to survive extreme conditions, such as lasting drought, suggest high heat resistance. However, the few studies carried out on tardigrades reveal their vulnerability to fire. In New Zealand, mountain snow-tussock grassland was involved in a controlled spring burning, and Yeates and Lee (1997) found drastic tardigrades losses in population density terms that persisted up to 30 months later. Five years after the clear-cutting and burning of a mature mixed stand of *Pinus sylvestris* and *Picea abies* in central Sweden, Malmström et al. (2009) counted only half the original numbers of tardigrades, which partly explained such failure to recover by declining forest mosses as many tardigrades are moss-dwellers. In a Mediterranean forest of Portugal that was burned at low severity, Vicente et al. (2013) demonstrated that tardigrades required at least 10 years to recover their pre-fire numbers, which was not enough time for diversity if fire severity had been higher.

Rotifers are 0.1- to over 2 mm-long animals. They are divided into more than 2,000 species that are common in freshwater and soil environments worldwide, and feed on particulate organic detritus, dead bacteria, algae, and protozoans. They are thought to be highly sensitive to heating because this can dry soil. However, the actual fire effects on soil rotifers are unknown. The above-cited comprehensive work by Yeates and Lee (1997), carried out in a New Zealand mountain snow-tussock grassland burned 16 and 30 months earlier, did not record any significant changes in rotifer population density on both dates compared to the pre-fire condition. However, the only study to have focused on such a taxon in fire impact terms, that by Chittapun (2011), was performed in rice fields of Thailand and revealed that post-harvest residue burning had a substantially negative effect on rotifer biodiversity. Patoine et al. (2002) discovered that the rotifers living in water bodies close to burned areas may experience a reduction in their species richness because of ash drift.

3.8. Nematodes

Nematodes are one of the most numerous and diverse faunal groups on Earth, which live in wet hotspots in soil, and particularly concentrate in the rhizosphere. The indirect fire effects that nematodes suffer seem to be by far more important than direct ones, especially in environments where soil moisture is a limiting factor, and differences in overall abundance and trophic composition are mainly due to water availability. In an arid juniper savannah in New Mexico, Whitford et al. (2014) found that taxonomic diversity, ecological indices and abundance of trophic groups of soil nematodes (bacteria-feeders, fungi-feeders, omnivore-predators) were lower for at least 3 years in the soil portions that underwent prescribed fire, most probably due to the removal of plant canopies and litter layer, which reduce water loss from soil. In a forest of *Pinus elliotii* in Florida, where the original nematode community consisted of 26–39% herbivores, 28–40% fungivores, 29% bacterivores, 3–4% omnivores and 1% predators, McSorley (1993) found that within 6 weeks of controlled burning, omnivores and predators had increased, while herbivores remained unchanged. In particular, the fungivore *Aphelenchoides* declined after burning, while *Acrobeloides* increased, which was initially the most abundant bacterivore. Such discrepant behaviour was assumed to be a consequence of fungi’s higher sensitivity to heat than bacteria. One noteworthy work is that by Butenko et al. (2017), who studied the fire impact on nematode diversity, abundance and biomass in areas burned 5 years earlier, located along a 3,000 km-long south-north transect in European Russia that covers five main forest types, from Mediterranean forests to the boreal taiga. In soils historically subjected to fire occurrence, they generally

detected a few hyphal-feeding, plant associated and plant-feeding nematodes, and a bigger biomass of bacterial-feeding nematodes, of which the latter is associated with the growing ratio between bacterial and fungal biomass. Conversely, Pen-Mouratov et al. (2012) found in the woodlands of Israel 1 year after a wildfire that eight of the thirteen species of omnivore-predator nematode genera, and some bacteria-feeding species, were less numerous in burned soils, while no apparent fire effect on fungi-feeding nematodes was observed. Two originally missing omnivore-predators were found in burned soils, but with very low abundances. Here, finally, a couple of bacteria-feeding nematode genera (*Cephalobus* and *Acrobeloides*) were more frequent than in the unburned surroundings. Some indirect shift in nematode biomass and diversity could derive from fire-induced changes to “nematophageous fungi,” i.e., carnivorous fungi able to successfully trap and consume nematodes. This has been suggested in the study by She et al. (2020) who, in mountain forests in China, proved that a considerable amount of such fungi types was killed by a severe wildfire in the top 10 cm of soil, and their vacant niches were subsequently replaced with nematophageous fungi that were originally distributed in deeper soil. In particular, the dominant *Arthrobotrys* genus, endowed with excellent saprophytic ability, was substituted for *Dactyloctenella*, which displayed better capturing ability, with plausible implications for the nematode community. In a spruce forest ecosystem in Slovakia, Renčo and Čerevková (2015) found that 8 years after a wildfire, the mean number of nematode species was still significantly lower than the original number, although ecological and functional indices and metabolic footprints indicated that the soil ecosystem had fully recovered with even moderately higher nutrient levels.

All in all, wildfires seem to have a significant and lasting impact on nematodes, even though it differs among various genera and species. The impact of prescribed fire seems much less. In fact while making censuses of soil nematodes at 99 burned and unburned forested sites in Mississippi, Matlack (2001) concluded that, in the long run, prescribed fire does not significantly affect the nematode community in either number of individuals or diversity terms.

3.9. Protozoans

Protozoans are single-celled eukaryotes that are either free-living or parasitic, and form an independent kingdom that is distinct from animals (Ruggiero et al., 2015). The protozoans frequently found in soil are ciliates, heterotrophic flagellates, and naked or testate amoebae. These voracious bacterial predators play central roles in the soil fertility, accumulation and stabilisation of soil organic matter, and in hormonal effects on roots as well as in microbial diversity. The few studies to have dealt with fire effects on soil protozoans are insufficient to gain plenty of insight into the topic. However, there are some clues of a substantial fire impact. In peatlands from north-eastern China, 3 days after a wildfire Qin et al. (2017) recorded major changes in testate amoebae composition. Turner and Swindles (2012) illustrated clear differences in testate amoebae communities among three zones of a UK moorland characterised by contrasting fire histories. In particular, they found that *Hyalosphenia subflava* dominated those communities living in mosses and had colonised the surface after intense wildfire. In a savannah in Brazil, Pierozzi et al. (2016) sampled soil several times throughout one year after a non-specified fire, and recovered 102 protozoan morphospecies divided into 12 taxonomic groups with ciliates and amoebae. There was no apparent direct fire effect on the protozoan community, rather an indirect one through drought intensification and biomass removal. Protozoans appeared adapted to that fire-prone environment as no significant change in richness was durable and diminished abundance lasted only a short time. Wanner and Xylander (2003) found that total biomass and species inventory of testate amoebae in east German pine forests were considerably reduced by controlled burning, but returned to their original level within 1 year. In sphagnum-dominated mires of Poland, Marcisz et al. (2016) showed that functional traits of testate

amoebae, such as mixotrophy (the combination of autotrophic and heterotrophic nutrition) and small hidden (“plagiostomic”) apertures, were strongly connected with fires of the past 2,000 years, which suggests that these traits can be used as palaeo-ecological proxies of past burnings.

4. Microorganisms

Microorganisms are by far the most numerous living beings in soil. Hence each reduction in their biomass, activity and diversity may result in multiple ecosystem functions declining (Wagg et al., 2014). The literature about fire effects on soil microorganisms is larger than that on bigger organisms, which allows robust conclusions to be reached. Based on meta-analyses, Holden and Treseder (2013) and Pressler et al. (2019) concluded that fire causes significant reductions in soil microbial biomass by generally depressing more fungi than bacteria. Regarding this last point, however, some authors have recorded a stronger impact on bacteria, such as Brown et al. (2019) in the top ~ 15 cm of duff and soil from mountain forests in Tennessee and North Carolina. Despite various examples of relatively fast recovery (e.g., Acea and Carballas, 1996), the meta-analyses by Dooley and Treseder (2012) and Pressler et al. (2019) showed that the fire impact on soil microorganisms often persists over a decade and they are generally less resilient to fire than initially assumed. Types of fire and burned biome, and burning depth, appear to be poor predictors of soil microorganisms’ recovery rate (Pressler et al., 2019), but this area still contains wide knowledge gaps and, thus, avenues for future research.

Compared to wildfires, prescribed fires are known to have a less marked and shorter impact on the soil microbial community (Pourreza et al., 2014; Akburak et al., 2017; Giuditta et al., 2020). Investigating pine forests in Spain that are periodically submitted to low- to moderate-severity prescribed fires, Fonturbel et al. (1995) observed that total microbiota and single groups, such as heterotrophic bacteria, filamentous fungi and algae, underwent changes that were all in all modest and ephemeral. Choromanska and DeLuca (2001) even proved that preventive low-intensity fire may predispose the microbial community to the impact of wildfires and, thus, limits damage. In some cases fire is functional for preserving soil microbial ecology, and perhaps even the steady state of the whole ecosystem. For example, Wardle et al. (1998) assessed how continued fire suppression led boreal forests of *P. sylvestris* to late secondary succession under which microbial activity in soil declined, probably due to excessively high concentrations of phenols. Periodic burns, on the contrary, encouraged such activity by releasing freshly charred materials on which phenols were adsorbed and inactivated.

4.1. Direct and indirect fire effects on soil microbes

The direct effects of wildfires on microbes are generally more marked than those on bigger soil-dwelling organisms because of their virtual immobility. The obvious outcome is a significant reduction in microbial biomass on the surface, where temperatures during fire far exceed deadliness. In a pine forest of Galicia, a temperate humid region of Spain, Prieto-Fernández et al. (1998) assessed immediately after a wildfire that microbial biomass had almost disappeared on the surface layer (0–5 cm) and dropped to 50% just below (5–10 cm). In their review on the topic, Pingree and Kobziar (2019) undermined the validity of the traditionally accepted metric of 60 °C for a 1-minute duration as the threshold of microorganisms’ death and provided relevant models for real temperature-duration microbial responses to explain why high survival occurs in very intense, but fast fires and, conversely, poor survival while enduring relatively low temperatures. Moreover, the direct fire impact on soil microbes depends on soil water content (see Barreiro et al., 2020, and references therein). Along these lines, Choromanska and DeLuca (2002) observed in a mixed conifer forest in Montana that soils at three different moisture levels (0.03, 1.0, 1.5 MPa) underwent

different fire-induced declines of microbial biomass C. The highest one was observed in the moistest soil, perhaps because of faster heat transmission, as water is a better conductor than air. On the other hand, a lot of thermal energy during fire is spent on evaporating water, and overall higher temperatures can be reached in drier soils (Busse et al., 2005).

Indirect fire effects often surpass direct ones. Fire changes soil properties like pH, organic matter amount and quality, nutrient availability and moisture retention, which control the recovery rate of microbial populations (Prendergast-Miller et al., 2017). One year after a large-scale wildfire that burned endangered *Araucaria araucana* forests in Chile, Fuentes-Ramirez et al. (2018) measured a marked increase in bacteria and fungi abundances, which were respectively 4- and 7-fold higher than in unburned areas on average. Such microbial proliferation was not casually associated with substantially larger amounts of available N, P and K in burned soil. Pietikäinen et al. (2000) revealed that changes in the chemical properties of dry humus from a mixed stand of *Pinus sylvestris* and *Picea abies* induced by heating at 230 °C were capable of causing a substantial shift in the microbial community structure. Whitman et al. (2019) worked on a wide range of soils and burn severities in boreal forests of Canada, and found that burned communities became more and more dissimilar to unburned ones with increasingly severe fires, and some globally abundant taxa were identified as significant positive fire responders, including the bacteria *Massilia* sp. (64-fold more abundant with fire) and *Arthrobacter* sp. (35-fold), and the fungi *Penicillium* sp. (22-fold) and *Fusicladium* sp. (12-fold). Hamman et al. (2007) investigated the belowground impact of high and relatively low severity wildfires that had affected mid-elevation forests in Colorado 14 months earlier to find no significant change in microbial biomass, but in both cases with structurally different communities from those at the unburned sites. All in all, the indirect response of soil microorganisms to fire appears to be vastly diverse, depending on a plethora of factors of which fire severity and post-fire environmental conditions are perhaps the most important, with some others that may even still remain unknown.

When summarising the mechanisms by which fire impacts soil microorganisms, Hart et al. (2005) convincingly advanced that where frequent fire had shaped the evolutionary history of a forest, indirect fire effects on soil microbial communities could be mediated primarily by changes in vegetation. Knelman et al. (2015) demonstrated in high altitude Ponderosa pine forests in Colorado that a crucial role in driving the soil bacterial community structure in burned landscapes is played by the type of association of colonising plant species in secondary succession, which vastly varies according to fire severity. It is known that severe fires generally promote N-fixing plants (Newland and DeLuca, 2000), which can counterbalance the large N losses that burned ecosystems undergo (Johnson and Curtis, 2001). Nevertheless, severe burning also alters the composition and activity of symbiotic fixers, and affects the canopy interception of precipitation to such a degree that it is difficult to predict the net effect of fire on the N cycle (Smithwick et al., 2005). There is compelling evidence that post-fire microbial immobilisation is a key process in N-conservation by limiting the substrate available for nitrification and, therefore, loss of inorganic N from the system via leaching (Weston and Attiwill, 1990). As far we know, there is no study that has aimed to unravel fire ramifications in soil microbiota by changes in the N cycle.

Microorganisms can suffer from fires in terms of activity, as well as biomass and diversity. Basal respiration and enzyme activity are the variables most widely used to account for soil microbial activity and related changes following disturbances (Staddon et al., 1999). Both experience significant and durable decreases because of severe blazes (Hernández et al., 1997; Dove et al., 2020), while the impact of low-intensity prescribed fires is usually lesser and short-lasting (Fritze et al., 1993; Fioretto et al., 2005). A meta-analysis by Wang et al. (2012) showed that prescribed fires had much less marked effects on soil microbial respiration (and biomass) than wildfires, although recovery from the latter can be relatively fast in fire-prone ecosystems, such as

Mediterranean forests of Aleppo pine (Hedo et al., 2015).

Basal respiration and microbial biomass are generally well correlated (Holden and Treseder, 2013), but not always in the event of fire. In this regard, Pietikäinen and Fritze (1995) found that a prescribed fire actually decreased both soil microbial biomass C and basal respiration in a *Picea abies* dominated stand in Finland, but the two variables did not change proportionally, possibly because the specific respiration rate (CO₂ evolved per unit of microbial C) was higher in burned areas than in unburned ones. Soil basal respiration recovery strictly depends on the vegetation recovery rate and fresh organic matter input. In Mediterranean sclerophyllous vegetation, Bárcenas-Moreno et al. (2011) measured the highest microbial respiration rate (µg CO₂ h⁻¹ g⁻¹ dry soil) 4 days after a wildfire, which then sharply dropped and did not return to the original values within the next 32 months. Such a trend was associated with, and is perhaps explained by, the abundant dissolved organic C in the immediate post-fire, which was later progressively consumed. Once more in a Mediterranean environment and under three distinct plant covers (holm oak, black locust, grass), 1 year after a severe fire Panico et al. (2020) still measured lower respiration rates than the pre-fire ones in spite of higher organic matter mineralisation rates, i.e., the ratios between the C respired by microbes and whole soil organic C. Low-intensity burns slightly decrease soil organic matter, but have been proven to leave it more vulnerable to microbial degradation (Dicen et al., 2020).

Enzyme activities are the direct expression of the soil microbial community to metabolic requirements and available nutrients. Soil enzymes are, thus, formidable biomarkers of the functional ability of the soil community and, indirectly, of soil quality (Caldwell, 2005). Soil enzyme activities are closely related to the cycles of nutrients and, hence ultimately, to the fate of soil organic matter (Zhang et al., 2005). Fire has a consequence on soil enzyme activity, which is mostly an immediate net reduction proportional to severity (Lucas-Borja et al., 2018; Pérez-Valera et al., 2020). Fairbanks et al. (2020) studied the activity of seven hydrolytic enzymes involved in key nutrient transformation steps in a conifer-covered watershed of the Rocky Mountains in New Mexico 3 weeks after a wildfire. They found an overall decrease only for β-1,4-glucosidase, β-D-cellobiohydrolase, and nitrogen (N) β-1,4,N-acetylglucosaminidase activities, moreover confined to the 2 cm uppermost soil. Interestingly, these authors disentangled a significant control of topography on the catchment scale, with higher potential enzyme activities in convergent zones, which correlated primarily with higher soil moisture, clay content and vegetative cover. The post-fire recovery of enzyme activity is tied to plant cover recovery, with roots being the main substrate resource for enzymes, such as acid-phosphatase and urease (López-Poma and Bautista, 2014). In an oak-hickory forest of Missouri undergoing a long-term fire experiment, Eivazi and Bayan (1996) measured significantly reduced activity for soil arylsulphatase, acid phosphatase, α- and β-glucosidase and urease over the background seasonal variability for both plots burned annually and for plots burned every 4 years compared to unburned plots. In a Mediterranean mixed pine-oak forest, Borgogni et al. (2019) observed a drastic immediate fire-induced decrease in total enzyme activity that disappeared 10 months later when some enzymes, i.e., beta-glucosidase, leucine aminopeptidase and alkaline phosphatase, showed fully restored or even greater activities than the original ones. Boerner et al. (2005) seasonally monitored burned and unburned areas in Quercus-dominated forests in Ohio 2 years after a prescribed fire, and did not notice any significant differences in the activity of acid phosphatase, α-glucosidase, phenol oxidase, chitinase, and l-glutaminase. This could have been due to both the long time span available for recovery and an effective low impact of prescribed fire.

Each microbial group possesses specific resistance to heating and the ability to recover from damage (Vázquez et al., 1993; Docherty et al., 2011). Consequently, hereafter we deal separately with three big taxa that are hyperpresent in soil, which are three of the seven most recently recognised kingdoms (Ruggiero et al., 2015), i.e., fungi, bacteria, and

archaea.

4.2. Fungi

Fungi are essential decomposers in the soil food web as they convert recalcitrant organic matter into easier-to-digest forms that other organisms can use. Another crucial role that fungi play in soil is binding mineral particles together into stable aggregates by their long hyphae (Fig. 7) to enhance soil porosity and permeability.

The vast majority of the several tens of thousands of fungal species occur in the soil environment at least in some stage of their life cycle. By a meta-analysis, Pressler et al. (2019) found fungi to be less resistant to fire than bacteria. Another meta-analysis by Holden and Treseder (2013) did not highlight any substantial difference in this regard between the two groups. However, both reviews prove that soil fungi overall undergo a sudden significant decline because of burning. Cairney and Bastias (2007) reviewed the fire impact on the fungal community of forest soils, and concluded that such an impact and its duration were very site- and (or) fire-specific, and more pronounced where repeated burning occurred. A phospholipid fatty acid (PLFA) analysis allowed Bååth et al. (1995) to demonstrate that a *Picea abies* dominated forest in Finland was substantially poorer in soil fungi 14 months after a prescribed fire following clear-cutting, and proportionally much more than in bacteria. On the contrary, again according to a PLFA analysis, Docherty et al. (2012) assessed that general fungi and arbuscular mycorrhizal fungi had not significantly changed 9 months after a fire, and not even after 21 months, in annual grasslands in California. In a *Picea mariana*-dominated forest in east-central Alaska burned 3 years before at different severities, Bergner et al. (2004) found that light fire had no effect on fungal and bacterial abundances in soil, while severe fire only decreased fungal abundance, which supports the hypothesis of greater fungi sensitivity compared to bacteria.

Wildfires significantly reduce the number of basidiomycetes (“mushrooms”) species and fruit body biomass (Hernández-Rodríguez et al., 2013; Vázquez Gassibe et al., 2014), with obvious ramifications in animal diets. The abundance of some pyrophilous species (Fig. 8) increases in the short term (Martin-Pinto et al., 2006; Pilz et al., 2004), but most of the major species like *Russula* and *Amanita* are associated with mature trees and organic horizon, and therefore do not germinate well under early-successional conditions (Visser, 1995). However, basidiomycetes represent a fairly modest fraction of the vast and varied fungi kingdom. McMullan-Fisher et al. (2011) reviewed the literature on fire and fungi in Australia by collating studies that included sites with different times since fire or distinct fire histories. They concluded that



Fig. 7. A fungal species of the genus *Phoma* isolated from the ash layer of a burned pine forest in Tuscany, Italy (picture by Giovanni Mastrodonato and Paola Nipoti).



Fig. 8. The basidiomycete *Lyophyllum atratum* (Fr.) Singer born in the charcoal-rich ground of a Mediterranean pine forest of Liguria in Italy. This species is typical of burned areas, where it fruits in large numbers a few months after fire (picture by Matteo Carbone).

fire effects on fungi are extremely variable, mostly depending on soil and vegetation type, and fire severity and frequency.

Burned areas often undergo a flush of fruit bodies of pyrophilous macrofungi, the most famous of which is perhaps the genus *Pyronema* of Ascomycetes (Bruno et al., 2020), due to a mixture of heat, stimulating spores germination, little competition and a marked tolerance of post-fire conditions. Another genus of Ascomycetes, whose occurrence in burned areas is quite typical, is *Anthracoobia*, which forms extensive mycelial mats and masses of fruit bodies, particularly at heavily impacted microsites where they perform an important prompt antierosive function (Claridge et al., 2009). Some fungi cannot be considered fully-fledged pyrophilous, but show marked heat-tolerance or the ability to take advantage of post-fire conditions, like the genus *Gelatinospora*, whose spores need a treatment of temperature, chemicals, or a combination of both, to initiate germination. In fact, in a *Pinus contorta* forest in Canada, Widden and Parkinson (1975) found such a genus of fungi to occur only in burned areas where, on the contrary, species belonging to *Trichoderma* and *Penicillium* were less frequent because chemical burning products inhibited spore germination and growth. A reduction in *Penicillium* species frequency was recorded by Bissett and Parkinson (1980) 6 years after a moderately severe fire in a Canadian subalpine coniferous forest, while other taxa (i.e., *Cladosporium*, *Phoma*, *Botrytis*) were more frequently observed in burned soil patches than in unburned counterparts. Sun et al. (2015) investigated a fungal community along a boreal coniferous forest fire chronosequence (2 to 152 years) in Finland to find that richness and diversity were higher at the most recently burned forest sites, while at the 152-year site there were low diversity and evenness. However, functional gene diversity did not differ between the two extreme post-fire forest development stages, which suggests that their fungal communities shared similar gene profiles. In a different environment, i.e., the Mediterranean maquis, Rutigliano et al. (2013) highlighted marked differences in fungal species while comparing plots that had undergone low- and high-severity burning with unburned plots on three post-fire dates. *Penicillium waksmanii* was detected only in the control plots, whereas *Aspergillus ustus*, *A. wentii*, *Gilmaniella humicola* and *Torula herbarum* were found only in burned soils. In soil affected by low-severity fire, *A. ustus* and *A. wentii* even became the dominant species 245 post-fire days for the former and 364 post-fire days for the latter. *Gilmaniella humicola*, a known heat-tolerant fungus, was detected only in the soil exposed to high-severity fire, while several other species like *Neosartorya fischeri*, *N. spinosa*, *Penicillium canescens* and *P. roseopurpureum*, were noted in all soils, regardless of being burned and unburned.

The fragile symbiosis between vascular plants and fungi in mycorrhizae generally suffers considerably from fire, which can severely

disturb the hyphal network and reduce the quantity of fungal propagules that survive on the soil surface, and finally cause a substantial decline in fungi density in the field (Pattinson et al., 1999; Castaño et al., 2020). In a mycorrhizal association, the fungus colonises roots either intracellularly as in arbuscular mycorrhizal fungi or extracellularly as in ectomycorrhizal fungi. Generally, fire effects are stronger on the latter. Accordingly, Treseder et al. (2004) investigated boreal forests in Alaska burned 3, 15, 45, and 80 years earlier, and concluded that dominant mycorrhizal groups shifted from arbuscular to ectomycorrhizal fungi as succession progressed because fire did not noticeably reduce the abundance of arbuscular mycorrhizal fungi in contrast to ectomycorrhizal colonisation, which had to wait up to 15 years to return to pre-fire levels. The legacy of wildfires in ectomycorrhizal fungi terms depends on the heating and combustion of the uppermost organic layer, which directly correlate to the mortality of mycorrhizas and inversely to their growth potential (Dahlberg, 2002). Fire severity is actually a main driving factor in this regard, as assessed by Owen et al. (2019) when following fungal recovery for 13 years in a burned ponderosa pine forest in Arizona subject to frequent fires. Patches burned at moderate severity showed different sporocarp and ectomycorrhizal community compositions, wider dispersion and larger ectomycorrhizal species pool-colonising pine seedlings compared to those pieces of land where fire had high severity. In the latter, coloniser ectomycorrhizal fungi were from genera *Rhizopogon*, *Cenococcum* and *Wilcoxina*, which are known to survive high heat. Overall, these authors' findings also supported the notion that fungal communities had evolved within that fire-prone forest, and had somehow adapted to it. Such a notion is supported also by the findings of Smith et al. (2021), which also indicate the likely centrality of fire-adapted soil fungal communities in restoring the structure and functions of fire-prone ecosystems.

Post-fire resumption of mycorrhizae from hyphal regrowth from root segments or viable propagules is often relatively fast, in the order of months (Bellgard et al., 1994; Rashid et al., 1997; Alem et al., 2020). However in a Mediterranean pine forest in Spain, 1 year after a wildfire Vilariño and Arines (1991) found that burned plots still had lower viable propagule densities and less intense vesicular–arbuscular colonisation of herbaceous vegetation than the unburned control. Moreover, the spores of *Acaulospora laevis* (the dominant species before burning) from the burned plots showed low germination rates. Generally speaking, even if fire has negatively impacted mycorrhizal root infection, it does not necessarily imply a decline in seedling survival and plant growth (Busse et al., 2005).

4.3. Bacteria

Bacteria are the smallest and most diverse organisms in soil (Schloss and Handelsman, 2006), whose resistance to heat varies. For example, *Pseudomonas* is very sensitive, while other genera, such as *Bacillus* or *Clostridium*, produce resistant spores that allow them to survive at 100–120 °C (Theodorou and Bowen, 1982). Bacteria generally resist better direct fire effects than fungi (Hart et al., 2005), and also take advantage of the post-fire higher soil pH (Rousk et al., 2010) and the lower C/N ratio of substrates (Pourreza et al., 2014) to predominate them.

Fire can significantly modify the taxonomic structure of the soil bacterial community and does so in proportion to severity. Lucas-Borja et al. (2019) evaluated the impact of two fire severities (low and high) in an outdoor experimental controlled system consisting in soil monoliths extracted from Aleppo pine stands supporting living vegetation and insulated from external conditions. Seven days after burning, the severely-burned soils showed significant changes in the composition of bacterial communities compared to the control plots. The genera of the phyla Firmicutes and Proteobacteria (e.g., *Firmicutes*, *Paenibacillus* and *Proteobacteria*, *Phenylobacterium*) were relatively more abundant in the monoliths burned at high severity, even compared to the low-severity burned ones, while many others had declined. Although the

immediate fire-induced changes in bacteria abundance and diversity often are substantial, recovery can be relatively fast by virtue of these organisms' frantic reproductive capacity. A fire-induced increase in soil of Proteobacteria and Firmicutes, and a decrease in Acidobacteria and Bacteroidetes, were recorded by Rodríguez et al. (2018) in Mediterranean forest ecosystems at 2–3 years post-burning. Adkins et al. (2020) assessed how 3 years after fire, Bacteroidetes abundance had increased, while Acidobacteria abundance had decreased along a burn severity gradient in a Sierra Nevada mixed conifer forest, which was chiefly due to persistent differences in soil pH. Moreover, overall bacterial phylogenetic diversity was negatively related to severity and was driven by differences in both nutrients and soil texture. In a spruce-dominated boreal forest of Alberta, Canada, Smith et al. (2008) found that beta-Proteobacteria and members of the genus *Bacillus* were highly characteristic of areas involved in a severe wildfire 1 year before. Further north in the Yukon and Northwest Territories, Zhou et al. (2020) compared bacterial communities and their potential functions across a chronosequence (>100 years) of burned forests in a continuous permafrost zone. Fire had promoted a marked increase in active layer thickness, and 3-year post-fire soil bacterial community compositions and potential functions were still altered, although only on surface layers and not on the near-permafrost layers. In particular, there were fewer alpha-Proteobacteria and beta-Proteobacteria than in unburned forests, while the relative abundance of Ktedonobacteria (*Chloroflexi*) was higher. Li et al. (2019) worked in a *Pinus tabulaeformis* forest in China and assessed how, 6 months after a high-severity wildfire, the relative abundance of some bacterial phyla was still substantially modified, and total and ammonium N and pH (even more) were the driving factors of the new bacterial community structure. The same variables, soil ammonium and pH, were found by Yeager et al. (2005) to be pivotal for the proportion of nitrogen-fixing and ammonia-oxidising species in a mixed conifer forest of New Mexico burned 14 months earlier. Under holm oak in Spain, Cobo-Díaz et al. (2015) explored the consequences of a wildfire on the rhizospheric bacterial communities involved in the N cycle, and measured a significant increase in gram-positive phyla, particularly Firmicutes and Actinobacteria. This was most probably an ecosystem strategy whose aim is to conserve N in the ecosystem by the first phylum playing a major role in N fixation and the latter in other potential pathways of the N cycle associated with the holm oak rhizosphere. A positive mid-term fire impact on the abundance of not only Actinobacteria, but also of Proteobacteria and Firmicutes, was observed by Prendergast-Miller et al. (2017) in Australian fire-prone environments. Actinobacteria (former Actinomycetes) often proliferate via sporulation in harsh post-fire environments, where they can take advantage of other groups by virtue of their ability to attack poorly biodegradable compounds, such as hydrocarbons, lignin and humic substances. Such a favourable condition is evidently not ephemeral, according to what Bárcenas-Moreno et al. (2011) found in a pine-dominated mountain forest in Spain where, after an initial wildfire-induced decrease, Actinobacteria significantly augmented and their colony-forming units 8 months later were about 8- to 15-fold higher than the reference values. Later on in the second and third post-fire years, colony units decreased to approximately, but did not equal, the original values. Xiang et al. (2014) proved substantial resistance to fire or fast recovery of Actinobacteria in a larch forest in northeast China, where the relative abundance of all the investigated bacterial phyla in soil (Alphaproteobacteria, Acidobacteria, Betaproteobacteria and Bacteroidetes), except Actinobacteria, were significantly shifted both 1 year and 11 years after the burning, and regardless of the severity of this. When reviewing the pyrogenic organic matter effects on soil bacterial community composition, Woollet and Whitman (2020) found that specific genera belonging to Actinobacteria and Proteobacteria, i.e., *Nocardioideis*, *Noviherbaspirillum*, *Phenylobacterium*, *Sphingomonas* and *Microvirga*, generally increased in soil following both burning and charcoal addition, which suggests that their positive response to fire might be partly related to soil charcoal enrichment.

Cyanobacteria are Gram-negative bacteria capable of performing photosynthesis and, in many cases, of fixing N. They are pioneer settlers on rock debris and sedimentary deposits, which they enrich and inoculate by preparing the ground for successive eukaryotic flora invasion and expansion (Golubic et al., 2000). The cyanobacteria population in soil is drastically depressed by fire, but responds positively to such a disturbing factor in the long term (in the order of years), when it can even exceed the one in the unburned surroundings (Vázquez et al., 1993). On diversity, in a xeric shrubland of Florida burned more than 10 years before, Hawkes and Flechtner (2002) did not record any major taxonomic changes in cyanobacteria communities compared to pre-fire levels. Cyanobacteria plausibly play a critical pioneering role in fire-affected soils as a consequence of improved light conditions (Warren et al., 2015), and some clues hint that their inoculation may be a valid approach to limit erosion in severely-burned areas (Aceá et al., 2001; Chamizo et al., 2020) thanks to their capability of promoting the formation of stabilising bio-crusts and acting as biofertilisers to accelerate secondary succession.

4.4. Archaea

Archaea are single-celled prokaryotes initially classified as bacteria that were named *archaeobacteria*, and were then considered a real kingdom in their own right. The archaeal domain includes the most heat-resistant living organisms owing to their particular cell wall and membrane lipid structure (Rothschild and Mancinelli, 2001), although the archaea commonly found in soil are not “hyperthermophiles”.

Fewer research works have been conducted about the reaction of soil archaea to fire than those about fungi and bacteria. The only study to have entirely focused on archaea is perhaps that by Jurgens and Saano (1999) in a boreal conifer forests in Finland. They applied a molecular approach to assess that clones taken from soils 1 or 2 years after clear-cutting and controlled burning were similar to one another, but differed from those isolated from undisturbed areas. Moreover, the sulphur-dependent thermophile phylum Crenarchaeota peculiarly dominated treated soils. In a Mediterranean mixed oak-pine forest in Spain, Rodríguez et al. (2017) recorded higher diversity for archaea (and bacteria) domains in burned soils than in the control, while Mikita-Barbato et al. (2015) found in a pine-oak forest in New Jersey that the archaeal community from the top organic horizon showed a large shift in composition between 2 and 13 months post-fire and, albeit less marked, this composition still significantly differed from the original one 25 months post-fire. This missing complete recovery seems to be linked with reduced N, P, and Ca availability. Actually evidence for an indirect effect of nitrate-N and DOC in modifying the genotype of at least ammonia oxidisers archaea in soil was found by Long et al. (2014) in a wet sclerophyll forest of Australia after a long-term prescribed fire. The day after burning a fire-prone shrubland under controlled conditions, Goberna et al. (2012) assessed shifts in the archaeal community structure, which were unrelated to any of the measured several physico-chemical soil variables. However, such shifts were by far lower than those for fungi and bacteria and, contrarily to these two major groups, they did further not increase later.

5. Research needs

From all that herein stated, it is clear that fire effects on soil-dwelling biota widely vary, and depend on lots factors, mainly the types of organisms, fire severity and vegetation recovery rates. Although the topic is “hot” and a growing number of related articles are published, the complexity of the phenomenon is such that many other studies and robust data are needed to infer universal laws, if indeed there are any. In particular, what is actually missing is long-term and continuous post-fire soil biological community monitoring, possibly in different environments and involving as many taxa as possible, in order to finally understand what the recovery path of each one is, the reciprocal

interactions between taxa in that delicate phase, the edaphic and environmental factors that most affect the recovery and its discrepancy among organisms, and the possible usefulness of human interventions to promote this recovery. For this purpose, all future studies dealing with fire occurrence in the environment should measure and describe in detail every site-specific physical, chemical and biological characteristic and mechanism that may plausibly play some control role on soil biota responses to fire and recovery rates. Actually, the fact that they are often missing in the literature renders any inference or meta-analytical outcome in this regard to be of limited reliability. In studies based on experimental fires, soil moisture and its spatial variability should be carefully measured, along with soil temperature peaks and their duration using constant-recording thermocouples.

Zaitsev et al. (2016) highlighted that studies into the impact of wildfires on soil organisms are fewer than those about other forest disturbance types, and argue that this is due mainly to practical difficulties in investigating wildfires. In fact these are unexpected events (at least for scientists) that do not allow full control over their variables. Moreover, wildfires impose a biological spatial variability on the ground that can be quite different from the original one. Such a discrepant overlap makes it difficult to draw conclusions on the real fire impact (Gongalsky and Zaitsev, 2016; Gorbunova et al., 2017). Hence, some pieces of land that are carefully studied and mapped in soil biology terms can be employed for scientific purposes with a burn that mimics the uncontrolled and intense ones (as in Santín et al., 2016), and with all the necessary precautions and with maximum safety, so as to acquire knowledge over time on soil biota recovery and the recolonisation process. However, the obvious limitation of surfaces that have been so sacrificed to fire could not account for the impact and recovery dynamics that occur in mega-fires.

Another weak point of the present corpus of literature on the topic is that focuses mostly on the outcome of a single fire event, while many ecosystems are prone to recurrent fire and at a frequency that is currently increasing as a result of climate change (Halofsky et al., 2020). In these cases, the long-term response to fire of living beings is the number of consequences of some previous fires, which are indecipherable as a plethora of environmental factors interact to determine the ecosystem’s ultimate response. Fire history is commonly missing in papers despite it being crucial information that is potentially able to account for some apparently unexpected results. Hence study areas in fire-oriented research should be selected from those with a well-documented fire history.

Works that determine the amount and persistence in burned soils of those toxic compounds, such as polycyclic aromatic hydrocarbons, dioxins and hydrogen cyanide, produced under some conditions by the combustion of the biomass or synthetic materials present as infrastructure or waste on ground, are desirable for the future and are virtually absent today. In particular, toxicological works are needed to highlight any long-term ramifications in the vitality and reproductive capacity of surviving or recolonising soil-dwelling organisms.

Finally, some taxa have been almost ignored in terms of their immediate response to fire and their fate in fire-shaped environments, and thus deserve being paid more attention by future research: striking examples of this are moles, scorpions, and rotifers.

We feel that the following are priorities for future works in this research field: *i*) measure as many variables as possible in burned and adjacent unburned areas to build large enough databases to disentangle the most significant factors that injure soil-dwelling biota or promote its recovery; *ii*) standardise the plethora of diverse methods followed to determine the abundance and diversity of various taxa to reliably compare studies; *iii*) narrow the time frame to perform experimental burns and sampling as the time of year when both occur is known to strongly influence findings; *iv*) extend research to those taxa and biomes that are taken into account less than others; *v*) run long-term experiments or monitor naturally-burned areas to check the fire effects and post-fire recovery of as many soil-dwelling organisms as possible (and

not only these).

6. Conclusions

The papers collected to compile this review about fire effects on soil-dwelling biota are so varied in terms of studied ecosystems and their proneness to fire, fire occurrence along the year, fire severity and frequency, extent of burned area, post-fire climatic conditions, sampling date during the year, and also in relation to sample size and type, monitoring period and methods, and investigated taxa, that it is challenging to reach general conclusions.

It is clear enough that, at first, fire always has several negative effects on soil biota and these effects can be direct and indirect. The prevalence of the former on the latter is directly related to fire propagation speed, and is inversely related to the mobility of organisms or their ability to create defence works from fire. Fire severity and frequency also strongly affect the resistance and resilience of soil biota.

Prescribed or controlled burnings are of limited extent, low-severity and slow compared to the vast majority of wildfires, and intend to remove only part of the understory and litter. Soil-dwelling organisms do not usually suffer substantial and lasting damage from this fire type, and most vertebrates are able to run away or retreat to deeper soil, while small-sized organisms easily amend their possible major losses by fast reproduction of survivors or migrating from unburned surroundings.

Fire impact is definitely more serious with wildfires, which can reach temperatures on the ground up to 600–700 °C and above, and they leave ample surfaces bare and defenceless against erosion. The vertebrates that are particularly susceptible to wildfires are amphibians, which possess less mobility than mammals and reptiles, and suffer more from higher temperatures and lower humidity, which are typical of exposed darkened areas. Numerous and contrasting ramifications of fire in invertebrates are reported in the literature, mostly because of such organisms' vast variety, their diverse niches and preferred habitats, and the different methodologies followed to count individuals or species. The organic (O) horizon is completely removed or, at least, substantially reduced and modified by charring and incineration. The destruction of food resources is the most serious fire legacy, and population recovery is strictly bound to return vegetation and consequent litter layer formation. This is especially true for invertebrates, which are herbivores, pollinators and detritivores and, in turn, represent high-protein food for a number of other beings. Hence they are a key factor of ecosystem recovery. Earthworms are crucial invertebrates to terrestrial ecosystem functioning and soil fertility, and fire does not seem to imply substantial abundance and diversity consequences for them. More attention has been paid to microorganisms, particularly bacteria and fungi as the two main taxa, than other soil-dwelling beings in terms of fire effects, although very few robust enough conclusions have been reached: *i*) wildfires cause significant immediate and short-term reductions in microbial biomass and activity; *ii*) fungi usually decline more because of burning than bacteria; *iii*) the impact of prescribed fires is lesser. Recovery times, apparently longer for fungi than bacteria, vary and depend on a series of factors, such as soil pH and available nutrients. Cyanobacteria, a phylum of photosynthetic bacteria, play a critical pioneering role in recently burned soils by promoting bio-crusts formation, which are functional to limit soil erosion. The archaea kingdom, which comprises some of the most "thermophile" organisms, is susceptible to fire as regards soil taxa, although apparently less than fungi and bacteria.

Invertebrates and microorganisms both comprise a minority of pyrophilous species, *i.e.*, those that take advantage of post-fire environments, and fire-adapted species, those that develop functional behaviours or morphologies to survive in burned areas.

Few studies have recorded the long-term (perhaps permanent) fire-induced removal of specific soil-dwelling organisms. Nevertheless, the time required for the complete recovery of some taxa is frequently substantial, of the order of several years or even decades. It has been proved that fires create a mosaic of areas burned at different severities

that are possibly interspersed with other unburned ones depending on the scale, and such a patchwork may even increase biodiversity by providing the organisms unable to compete in undisturbed soils with temporary refuges.

All in all, extremely severe blazes are real biological casualties, especially when they vastly extend to environments that have never, or very rarely, been affected by fire. In most other cases, fire neither implies irremediable damage to soil-dwelling biota, nor generalised (less likely) extinction, but can instead be a tremendous driver of ecosystem biodiversity. Nevertheless, using fire in ecosystem management requires profound soil ecology knowledge and carefully evaluating each possible consequence. In the epoch we live in – the *Anthropocene* – it is particularly important to understand that climate change and other generalised human-induced variations in fire activity are threatening species with extinction, likely including some soil-dwelling ones. Thus it is necessary to implement fire management actions and novel strategies in order to primarily preserve biodiversity.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

Acknowledgements

We thank Gianluca Borgogni for the drawings in Fig. 2, Cristiano Foderi, Stefan Doerr and Matteo Carbone for providing the beautiful photographs, Davide Mastrolonardo for helping prepare the graphical abstract, Patrizia Sacchetti, Tercia Strydom and Paola Nipoti for offering useful tips and, last but not least, two anonymous reviewers for constructive criticisms that have greatly improved the quality of this review.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.118989>.

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