The role of decomposer communities in managing surface fuels: a neglected ecosystem service

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ABSTRACT

Surface fuel loads are a key driver of forest fires and the target of hazard reduction burns to reduce fire risk. However, the role of biota in decomposition, or feedbacks between fire and decomposer communities are rarely considered. We review the evidence that decomposer organisms play an important role in surface fuel regulation and how this role is affected by fire. First, we outline the contribution of decomposer organisms to the breakdown of surface fuels. Next, we consider the three distinct phases through which fire regulates decomposer communities and how this may affect decomposition and future fire regimes. Finally, we consider interactions between global change and decomposer–fire feedbacks and the implications for fire management. Evidence indicates that decomposer organisms are important in regulating surface fuels and we propose that the biological basis and dynamic nature of fuel load control require greater attention. This includes better understanding of functional redundancy among decomposer organisms, the impacts of global change on the biota that drive decomposition and the factors that limit decomposer persistence and recolonisation following fires. By filling these knowledge gaps, we will be better armed to conserve and manage these functionally critical taxa in fire-prone ecosystems in a changing world.

Keywords: biodiversity, climate change, dead wood, decomposition, ecosystems, fuel, invertebrates, leaf litter.

Introduction

Ninety gigatons of terrestrial plant biomass, amounting to 90% of annual production, enters the global pool of dead organic matter each year (Cebrian 1999). The biomass is transformed into inorganic forms via complex decomposition steps or exits the pool through consumption by fire. While biological decomposition transforms organic material into microbial mass or stable humic substances, dead organic material consumed by fire is mostly lost to the air as carbon dioxide and methane (Schimmel and Granstrom 1996; Aerts 1997; Miyanishi and Johnson 2002; Van Wagtendonk 2006). Fire is a necessary process in many ecosystems, shaping the distribution of biomes and maintaining the structure and function of fire-prone communities (Bradstock et al. 2002; Bond and Keeley 2005; Bowman et al. 2009). Fires generally start with the ignition of dead organic matter in the surface layer. These surface fuels include fine fuels such as leaves, twigs and bark lying on the ground (Hines et al. 2010), as well as fallen branches and shorter vegetation (Scott and Reinhardt 2001). Across many ecosystems, the spread of fire is driven primarily by the fine fuel component of surface fuels (as well as weather and topography) (Raison et al. 1983; Catchpole 2002).

While the role of biodiversity in fire regimes is increasingly acknowledged, recent work focuses on vegetation (Duff et al. 2017), largely ignoring the role of other biota. Fire not only consumes surface fuels, but also disrupts communities of organisms that decompose those fuels. Invertebrates and microbes are the key players in the decomposition of surface fuels in many ecosystems, yet their role in decomposition is not well studied in the context of fire (Brennan et al. 2009; Buckingham et al. 2015) and
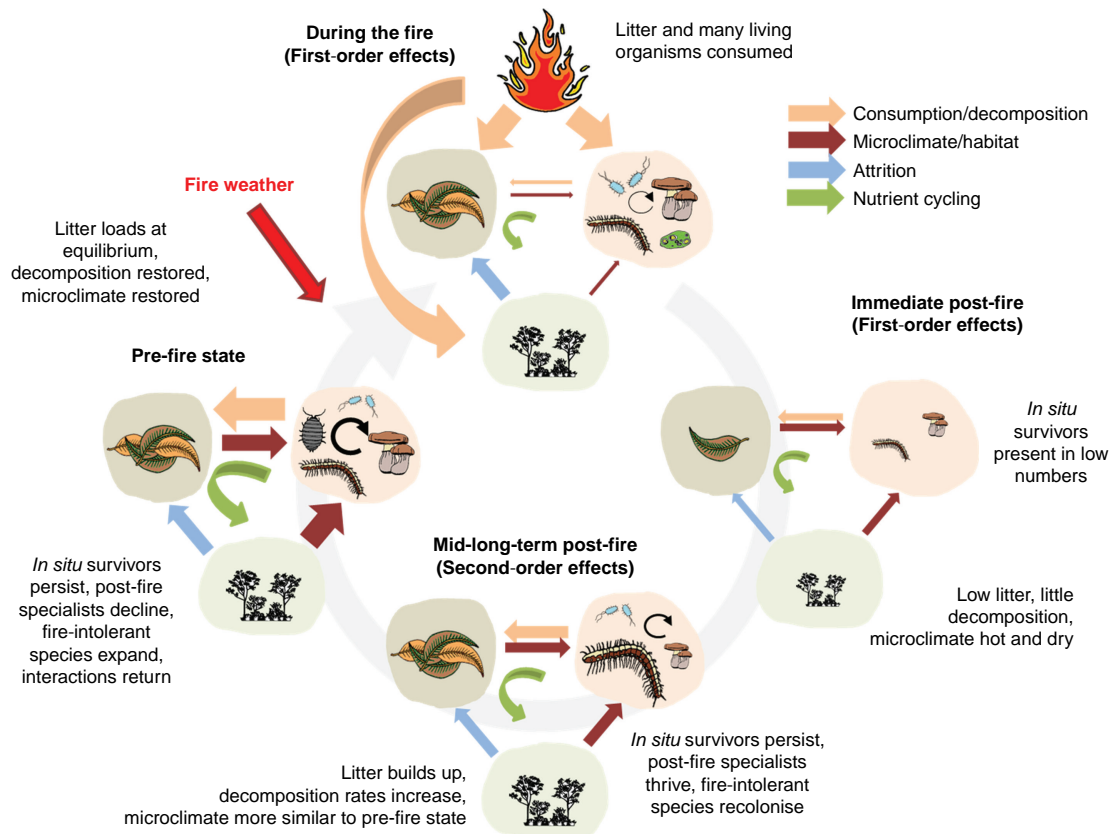
Fig. 1. Feedbacks among fire, decomposers, litter and vegetation throughout the fire cycle. Fires consume surface fuels (leaf litter, bark and woody debris), decomposers (invertebrates, fungi and bacteria associated with surface fuels) and live vegetation and alter the microclimate for biota. The surface fuels consumed by fire also act as habitat and food for decomposers. Decomposers affect vegetation through nutrient cycling, while vegetation alters the microclimates available for decomposers and the quality of litter. Vegetation produces surface fuels (senescence), but fuels may also inhibit colonisation by plants. Live vegetation also acts as a fuel when fires are hot enough. Throughout the fire cycle, decomposer communities and their interactions (represented by the black curved arrow) change in response to fire, resources and opportunities for recolonisation, eventually returning to a state similar to that prior to the fire.

invertebrate decomposers were considered only briefly in a recent review of animals as agents of fire (Foster *et al.* 2020). We propose that decomposer-driven changes in the fire-available fuel have the potential to alter fire frequency, extent and severity, thus creating a feedback cycle among decomposers, surface fuels and fire (Fig. 1). For example, increased fire frequency creates hotter and drier climates, which inhibits litter consumption by decomposer organisms, therefore increasing fuel loads (Hernández and Hobbie 2008; Brennan *et al.* 2009; Toberman *et al.* 2014). Further, changes in fire regimes due to global change are likely to have significant impacts on the decomposer species that evolved with natural fire regimes. Despite the potential importance of these feedbacks and the significant economic cost of attempts to control fire, little is understood of the ability of ecosystems to regulate litter and dead wood build-up naturally through the biodiversity of decomposer organisms.

Decomposition is primarily a biological process, driven by decomposer organisms, which are affected by the same anthropogenic perturbations (e.g. climate change and habitat fragmentation) that control the persistence of any species. Accurate predictions of fuel loads and their trajectories through time must therefore incorporate an understanding of the biological nature of decomposition, particularly in wetter ecosystems, where biological decomposition is more important (García-Palacios *et al.* 2013). Here, we review the contribution of decomposer biodiversity to regulating surface fuel dynamics across biomes and consider how decomposer biodiversity and the function of decomposition are influenced in three distinct temporal phases: (1) during the fire; (2) the immediate post-fire environment (both considered first-order effects); and (3) the long-term regenerated environment (second-order effects). We argue that feedbacks between decomposer biodiversity and fuel loads have the potential to affect the flammability of

environments, but that gaps in knowledge prevent us from determining the importance of this effect. Further, we consider the potential impacts of anthropogenic change on the complex relationship between fire, fuels and decomposer organisms. We conclude by considering how fire management programs might better conserve the function of decomposition, thereby allowing biodiversity to better regulate the accumulation of fuels.

Decomposer organisms and their ecosystem service

At a global scale, the decomposition of surface fuels is driven by a range of factors, with climate, litter quality and the soil and litter biota critical in regulating decomposition (Coûteaux *et al.* 1995; Zhang *et al.* 2008; García-Palacios *et al.* 2013). The impacts of soil biota on decomposition are regulated by climate and litter quality and therefore differ substantially among biomes (García-Palacios *et al.* 2013). The effect of soil fauna exclusion is most pronounced in wetter climates (González and Seastedt 2001) and a meta-analysis suggested that unexplained variation in large-scale decomposition models could be reduced by including biome-specific fauna effects on litter decomposition (García-Palacios *et al.* 2013).

Both invertebrates and microbes are important in litter decomposition. Invertebrates are directly responsible for an average of 37% of litter loss and up to 20% of wood loss on the forest floor annually across the globe (García-Palacios *et al.* 2013; Ulyshen 2016). Leaf litter decomposes considerably faster than woody debris (Gessner *et al.* 2010) and most studies examining the role of decomposers have focused on litter, with few examining woody debris (see Kampichler and Bruckner 2009; García-Palacios *et al.* 2013; Ulyshen and Wagner 2013). However, the breakdown of wood often requires specialised invertebrate species, which are linked to specific tree traits (Cornwell *et al.* 2009; Weedon *et al.* 2009; Zuo *et al.* 2016; Dossa *et al.* 2018). Functionally, although there is overlap in roles, invertebrate detritivores can be classified in three general ways: bioturbators that ingest and mix organic matter in the soil (e.g. earthworms and termites), shredders that physically fragment organic matter including transforming it into faeces (e.g. macroinvertebrates, including amphipods, woodlice, millipedes, dipteran larvae and saproxylic beetles) and grazers that consume microbes on detritus (e.g. microinvertebrates, including nematodes, mites and springtails) (Anderson 1988; David 2014; Hoang *et al.* 2017; Joly *et al.* 2018; McCary and Schmitz 2021). Bioturbation accelerates decomposition by transporting organic matter to a moister environment and bringing it into closer contact with other decomposers (Ashton and Bassett 1997; Lavelle *et al.* 2006; Coulis *et al.* 2016). In addition, it affects soil structure in numerous ways, including creating and degrading soil aggregates and pore formation, which increases decomposition by improving soil hydraulic properties and creating habitat space for smaller decomposers, especially microarthropods (Lavelle 1997; Lavelle *et al.* 2006; Hoang *et al.* 2017). Recent work shows that millipede, isopod and snail faeces improve decomposition rates relative to intact litter (Joly *et al.* 2020). This is likely driven by increasing organic matter lability and consequent leaching, rather than enhanced microbial activity, which is often lower in faeces (after an initial increase) (Joly *et al.* 2020). In Mediterranean shrubland, burial of millipede faeces led to further improvements of decomposition rates, suggesting possible synergistic effects with bioturbation (Coulis *et al.* 2016). Assimilation of organic matter consumed by invertebrates ranges from <10% (e.g. some millipedes) to >50% (e.g. some isopods, dipteran larvae), indicating that some taxa are capable of direct litter mineralisation (Dangerfield 1998; David 2014; Abd El-Wakeil 2015; Frouz 2018). Microarthropods, dominated by Collembola and Acari (springtails and mites), contribute to decomposition by moving organic material, which impacts soil aggregation and creates microbial hotspots (Chamberlain *et al.* 2006; Maaß *et al.* 2015; Soong and Nielsen 2016).

Although decomposition is often facilitated by invertebrates, the remaining 70–80% of annual decomposition is generally performed by the soil microbiota, which break down recalcitrant compounds such as cellulose and lignin. For example, fungi from the Agaricomycetes are the only organisms that produce enzymes capable of substantial lignin degradation, making them keystone taxa in the decomposition of woody debris (Floudas *et al.* 2012). Bacteria also contribute to wood and leaf litter decomposition and are capable of producing enzymes for cellobiose, pectin and even lignin degradation (Schink *et al.* 1981; Brown and Chang 2014; Lladó *et al.* 2016). While bacteria may not be as proficient at wood decay as fungi, anaerobic taxa such as *Acetivibrio*, *Clostridium* and *Ruminococcus* are primarily responsible for cellulose decomposition in anaerobic ecosystems such as peatlands (Boer *et al.* 2005). Bacterial nitrogen fixation (N-fixation) is known to occur in decaying wood and may assist in stimulating the decomposition process by replenishing nitrogen in a system that naturally has a high C:N ratio (Johnston *et al.* 2016; Bani *et al.* 2018). N-fixing bacteria from the order *Rhizobiales*, *Rhodocyclales*, *Pseudomonadales*, *Rhodospirillales*, *Sphingomonadales* and *Burkholderiales* have all been associated with decaying wood. Litter decomposition studies focusing on bacterial communities have revealed clear successional patterns. In general, leaf surface (phyllosphere) bacteria are present in the first stage of the decomposition but are rapidly replaced with taxa producing proteolytic and cellulolytic enzymes. In the later phase, the most common bacterial taxa are *Bradyzhorium*, *Streptomyces* and *Burkholderia*, the latter of which is strongly associated with the presence of fungi and can utilise fungal hyphae as migratory routes (Johnston *et al.* 2016; Purahong *et al.* 2016; Tláskal *et al.* 2016; Bani *et al.* 2018).

Interactions among species affect decomposition rates (Gessner *et al.* 2010). For example, the joint effects of woodlice (Isopoda) and earthworms (Annelida) are stronger than the sum of single-species effects on alder litter, but weaker on oak litter (Zimmer *et al.* 2005). Decomposition can also be enhanced by multi-trophic interactions (Hedlund and Öhrn 2000) and altered by litter disturbance or predation by vertebrates (Wyman 1998; Nugent *et al.* 2014) or herbivory by invertebrates prior to leaf fall (Kay *et al.* 2008). Although microbes are responsible for the majority of decomposition (by mass), their function is mediated by invertebrate decomposers (Lavelle *et al.* 1995): microbial breakdown is governed by accessibility, which is often enhanced by the action of litter-dwelling invertebrates, which mix the litter and shred and bore into plant matter, increasing the surface area available to bacteria and fungi (Beare *et al.* 1995; Wolters 2000; Dungait *et al.* 2012). Invertebrate detritivores may directly consume microbes and commonly have a symbiotic microbe community to assist in digestion of dead plant material (Zimmer and Topp 1998; Ulyshen 2016). The preferential grazing of soil fungi by litter-dwelling insects has been shown to alter fungal community competition dynamics, increasing fungal diversity (Crowther *et al.* 2013). Further, invertebrates are likely to be vectors for bacterial and fungal detritivores, but these phoretic relationships are poorly understood (but see Persson *et al.* 2011; Aylward *et al.* 2015; Jacobsen *et al.* 2017). This is particularly relevant in the context of recolonisation following disturbances, where insect-mediated transport has the potential to accelerate the recovery of microbe-driven decomposition.

Interactions among microbes may also be critical in the decomposition process: fungi facilitate bacterial penetration into leaves and wood (Boer *et al.* 2005), while wood decay proceeds at a greater rate when fungi are associated with N-fixing bacteria than when they are not (Blanchette and Shaw 1978; Hoppe *et al.* 2014). Bacteria enhance decomposition rates by consuming fungal decomposition products, thus stimulating fungi to upregulate their own production of degradative enzymes (Boer *et al.* 2005; Christofides *et al.* 2019). Alternatively, bacteria capable of lysing fungal hyphae, either to consume as a food source (mycophagy) or to avoid direct competition for cellulose, may reduce rates of wood decay (Tolonen *et al.* 2015). The variety of potential interactions among decomposer organisms serves to highlight the complexity of the community that drives decomposition.

Given their significant diversity, the most feasible approach to understanding decomposer communities and variation in their rates of decomposition may be trait-based because this allows us to understand the broader patterns despite limited knowledge of the biology of individual species (McCary and Schmitz 2021). This may be a particularly pertinent approach for microbial decomposers, for which the ability to link genes with function is progressing rapidly (e.g. Langille *et al.* 2013). For example, genes encoding degradative enzymes and bacterial N-fixation are potential targets for studying decomposer–fire–climate interactions. For invertebrates, dispersal traits have been linked with recolonisation following fire (Langlands *et al.* 2011; Buckingham *et al.* 2019). Fewer studies have attempted to link invertebrate decomposer traits with decomposition, but the feeding traits of detritivores covary with the palatability traits of leaf litter (Brousseau *et al.* 2019; Raymond-Léonard *et al.* 2019) and determine their impact on decomposition (e.g. detritus shredders, bioturbators and detritus grazers increase decomposition by 28, 22 and 15%, respectively, McCary and Schmitz 2021). Further, trait dissimilarity within detritivore assemblages is positively correlated with decomposition rate as more dissimilar species are more likely to have complementary (rather than redundant) effects on decomposition (Heemsbergen *et al.* 2004).

Effects of fire on decomposer composition across ecosystems

Fire-prone ecosystems cover a spectrum from fuel-limited to climate-limited ecosystems (Agee 1993; Noss *et al.* 2006; Pausas and Paula 2012; Steel *et al.* 2015). In fuel-limited ecosystems, frequent fires consume mostly live and recently dead herbaceous vegetation and litter, where flaming and residence times are short, there is little organic soil and minimal soil heating and most regrowth occurs through resprouting. In contrast, in climate-limited ecosystems, fire-return intervals and succession periods are longer, with greater fuel loads (including duff) accumulating. Across this spectrum, the characteristics of fire range from high frequency and low severity to low frequency and high severity, resulting in different interactions between fire and the decomposer community, depending on the ecosystem. Many species are adapted to natural fire regimes (Gill 1975), resulting in a cyclical change in species communities. Fire impacts decomposer communities through both physical and chemical changes to habitats and substrates, in three distinct temporal phases: (1) during the fire (first-order); (2) the immediate post-fire environment (also first-order); and (3) the longer-term regenerated environment (second-order) (Fig. 1). The extent of the changes to biodiversity wrought by a single fire and length of each of these phases vary among biomes.

First-order effects – during the fire

The immediate effect of fire on decomposer communities depends mainly on severity and duration (DeBano *et al.* 1998). Heating during fire causes the loss of nutrients and carbon via volatilisation and combustion of litter and soil organic matter, which may have long-term impacts on the ecosystem. The direct and immediate impacts of fire on soil- and ground-dwelling organisms vary among ecosystems. Radiation provides enough heat to combust surface fuels

and often kills organisms in the upper soil layer (Wikars and Schimmel 2001). Soil temperature during a fire depends on soil moisture (lower in moister soils; Burrows 1999; Busse *et al.* 2005), fuel load and soil composition, including rock and moisture content (e.g. Bradstock and Auld 1995; Stoof *et al.* 2011). High soil temperatures may be short-lived and heat intensity declines with depth, but heat penetration varies among ecosystems (Humphreys and Lambert 1965; Raison *et al.* 1986; Miranda *et al.* 1993; Schimmel and Granstrom 1996; Yoshikawa *et al.* 2002; Carrington 2010; Wanthongchai *et al.* 2011; Cawson *et al.* 2016). For example, soil temperatures in cerrado fires in central Brazil do not exceed 38°C below 2-cm depth (Miranda *et al.* 1993), whereas they may reach up to 80°C at 15-cm depth in jarrah forests in western Australia (Burrows 1999). Depths of 2–10 cm are generally sufficient to avoid lethal temperatures (of 30–60°C) for most invertebrates (Hoffmann *et al.* 2013; Grubb 2019), suggesting *in situ* survival is possible. Individuals buried deeper in the soil may stand a very good chance of survival: for example, Thom *et al.* (2015) showed that butterfly pupae buried deeper than 1.75 cm, where soil temperatures remained ~40°C or lower, had a 50% chance of survival, even where surface temperatures reach 500°C. Further, short heating residence times in fuel-limited savannas and woodlands may have little direct effect on microbes (Hansen *et al.* 2019) or the abundance and diversity of soil biota (Oliver *et al.* 2015; Semenova-Nelsen *et al.* 2019; Hopkins *et al.* 2020).

The quality of surface fuels also impacts the survivorship of soil organisms: for example, coarser fuels (e.g. charcoal) can increase the duration for which peak temperatures are held within the soil by up to 10 min, which is long enough to sterilise spores even of pyrophilous fungi (Bruns *et al.* 2020). In shrubland, fire experiments show that soil temperatures can be lowest where fuel loads are highest, probably owing to greater upwards heat transfer and decreased flame residence time (Stoof *et al.* 2013). While communities of soil biota may thus suffer a decrease in diversity and biomass during the fire, the impact of fire is spatially heterogeneous (Tangney *et al.* 2018), and variable among ecosystems (DeBano *et al.* 1998; Neary *et al.* 1999; Certini 2005; Pressler *et al.* 2019).

The mechanisms through which decomposer organisms survive fire *in situ* have received little attention. For invertebrates and microbes, avoidance usually involves escape to or existence deep in the soil or in unburnt refuges in less severe fires (e.g. in *Xanthorrhoea*, Brennan *et al.* 2011; under soil, Dell *et al.* 2017; or up trees, Sensenig *et al.* 2017). Survival may be enhanced by extreme temperature tolerance (Kassen 2002) and morphological and behavioural adaptations that allow escape underground. Further, plant endophytic microbial communities can be aerosolised during the combustion and burning of vegetation, which may assist in their survival, dispersal and reestablishment (Moore *et al.* 2021).

The presence of invertebrate species with limited dispersal capacities after severe fire likely results from *in situ* survival in burrows or other refuges (e.g. ground-nesting bees, Love and Cane 2016; amphipods, Menz *et al.* 2016). Low-severity fires can even increase microbial activity in the top 0–10 cm of soil in the short term, owing to warming effects (Bogorodskaya *et al.* 2010). In Mediterranean ecosystems of south-eastern Australia, amphipods burrow deeper in the soil to avoid desiccation in hotter months (Friend and Richardson 1977; Menz *et al.* 2016), potentially enhancing survival at the time of year that wildfires occur, but not necessarily protecting against hazard reduction burns in cooler times of year. The recovery of the detritivore community from fire is critical for the resumption of their important role in reducing subsequent fuel loads, so we would benefit from a better understanding of the potential for populations to survive fires *in situ* and how it varies with ecosystem, fire severity and season.

First-order effects – immediate post-fire environment

Most studies of the impacts of fire on biodiversity in general focus on the period between the fire event and re-establishment or resprouting of the vegetation, which can occur within a fraction of the burning season (e.g. Eva and Lambin 1998; Trigg and Flasse 2000) or take decades (Haslem *et al.* 2011; Dafni *et al.* 2012; Bright *et al.* 2019), depending on the ecosystem. Burning causes distinct shifts in community composition for both microbes and invertebrates (Vilariño and Arines 1991; Baar *et al.* 1999; York 2000; Simard *et al.* 2001; New *et al.* 2010). A recent meta-analysis of 131 studies across a range of biomes found that, while fire decreases diversity of key taxa, impacts on abundance may differ among organisms: fire reduced microorganism abundance by up to 96% (bacteria were more resistant than fungi) and nematode abundance by 88%, but had no effect on soil mesofauna abundance (Pressler *et al.* 2019). Interestingly, prescribed fires had a more significant impact in the subsoil than wildfires, but the opposite was true for the surface soil fauna. Further, prescribed fire impacts depended on ecosystem types: for example, fire reduced arthropod richness more in grasslands than in forests, probably because vertical movement in the soil is more limited in grasslands (Pressler *et al.* 2019). Surprisingly, Pressler *et al.* (2019) were unable to detect a signal of time since fire, in contrast to studies that focussed on invertebrates (e.g. Barratt *et al.* 2006; Huebner *et al.* 2012; Oliver *et al.* 2012).

The community of decomposers present in the immediate post-fire environment includes species that survived the fire *in situ* and those that dispersed from outside or from refuges inside the fire perimeter following the fire (Robinson *et al.* 2013), including some fire-favoured or even pyrophilic species (Schütz *et al.* 1999; Gibb *et al.* 2006; Johansson *et al.* 2011; Egidi *et al.* 2016; Eliott *et al.* 2019). In climate-limited

ecosystems (those where fires are severe and infrequent), these organisms face a very different environment from that experienced prior to the fire. Following fire, the soil biogeochemistry and organic habitat may be severely altered (Baird et al. 1999; González-Pérez et al. 2004; Dove et al. 2020; Pellegrini et al. 2020). Leaf fall may initially increase as scorched foliage falls, rapidly renewing habitat structure (although resource quality may differ) (Springett 1979); alternatively, all foliage may be consumed by canopy fires (Cruz et al. 2012). In high-severity fires in forests, the destruction of the canopy results in microclimate changes such as increased soil temperatures and decreased soil moisture and humidity (Neary et al. 1999). In such ecosystems, species persisting after the fire are expected to be more generalised and tolerant of a broader range of temperatures and soil moistures than those that existed prior to the fire (Kassen 2002). However, there is little evidence that a single fire event causes strong selection for greater physiological tolerance of variable temperatures or low humidity within species in fire-prone forests (Grubb 2019), and fire regime may be more critical than time since fire in selection for fire-tolerant phenotypes.

In addition to changes in microclimate, severe fire also causes far-reaching changes in the nutrient balance, marked changes in hydrothermal conditions and a loss of micro-habitat heterogeneity (Butler et al. 2019). These factors act as filters that determine the development of post-fire soil communities of microorganisms and invertebrates, which, in climate-limited ecosystems, can be drastically different from the pre-fire community (Certini 2005). Reestablishment of the microbial community after fire may be hampered in such ecosystems by the reduction of labile forms of organic matter, and changes to soil carbon and soil chemical properties. For example, the combustion of wood and litter has been shown to form recalcitrant carbon molecules enriched in aromatic structures that inhibit microbial saprotrophic growth (Kim et al. 2003). Soil N can also be sequestered into recalcitrant carbon compounds, following burning, depleting the soil of readily accessible N and C reserves, which may contribute to reduced decomposition rates (Mastrolonardo et al. 2014). Understanding soil community recovery post burning may assist in understanding decomposition rates in other habit strata during later stages of succession. For example, while woody debris has a community distinct from that of soils, the soil community is highly predictive of the community in a given piece of woody detritus, suggesting decomposer communities are recruited from the surrounding soil (Sun et al. 2014).

Fire-driven shifts in species functional traits also have the potential to alter decomposition rates. For example, fire severity changes in the post-fire size distribution of invertebrate detritivores (Buckingham et al. 2015; Podgaiski et al. 2018) might affect microbial decomposition by altering the size of litter fragments; and, in grassy ecosystems, fire decreases the prevalence of microbial functional traits related to carbon degradation, which may lead to increased stabilisation of recalcitrant C during the post-fire recovery of the community (Yang et al. 2020).

Second-order fire effects – mid-long-term habitat regeneration

The post-fire habitat proceeds through a succession, as the biota recolonise and re-establish and species are filtered by the changing environment (Sasal et al. 2010; Huebner et al. 2012; Gongalsky and Persson 2013; Haslem et al. 2016; Auclerc et al. 2019). In many fire-prone ecosystems, this return to a pre-fire-like state may be rapid, but in others, habitats may continue to regenerate for decades or even centuries (Haslem et al. 2011; Dafni et al. 2012; Bright et al. 2019). Further, depending on the potential for multiple stable states and the fire interval, the ecosystem may not converge on the pre-fire state (Beckage and Ellingwood 2008; Wood and Bowman 2012; Auclerc et al. 2019).

Different inter-fire intervals (or fire frequencies) are associated with differences in the way in which species are filtered through their physiological tolerance, behaviour and dispersal ability: ecosystems with rapid fire cycles support species that survive the fire or are able to rapidly disperse and re-establish, while those with slower fire cycles support an ongoing succession that may eventually include poor dispersers and fire-intolerant decomposer species (Force 1981; Holliday 1991; Siemann et al. 1997; Malmström 2012). For species unable to survive the fire in situ, dispersal ability is critical to persistence at a landscape scale (Andersen and Müller 2000; Thomas 2000; Whelan et al. 2002; Schmuki et al. 2006). The presence of a mosaic of patches of differing time since fire (pyrodiversity, Parr and Andersen 2006) may provide a colonisation source for species unable to persist during the fire. The interaction between dispersal ability, distance from source populations and the inter-fire interval is thus critical in determining persistence in the landscape (Arnold et al. 2017): low dispersal ability can increase the time for a species to recolonise when inter-fire intervals are long or prevent recolonisation altogether when inter-fire intervals are short (Pippin and Nichols 1996; Panzer 2002; Whelan et al. 2002; Schmuki et al. 2006). While decreased inter-fire intervals might be expected to select for a spectrum of traits that protect species from fire (avoidance behaviours, tolerance and dispersal), fires of increased severity and extent are likely to favour an assemblage dominated by high-dispersal generalist species, which could lead to functional homogenisation of the decomposer community at larger scales (e.g. Clavel et al. 2011; Malmström 2012). Species with traits similar to those of the pre-fire ecosystem are expected to thrive as time since fire increases, but the actual species composition may differ from the pre-fire composition, depending on species' ability to recolonise or survive the fire. For example, Korobushkin et al. (2017) and

Moretti *et al.* (2006) showed that less-mobile invertebrates suffered the greatest declines and recovered poorly 5 years after fire.

Fire-induced changes in soils may be long-lived in some ecosystems. For example, in coniferous forest, reductions in microbial N/organic N ratios remained 12 years after controlled burns, particularly in the surface layer (0–5 cm) (Fritze *et al.* 1993; Prieto-Fernández *et al.* 1998). However, organic carbon has been shown to increase or remain unchanged in most pine-dominated communities, where fire intervals are short (McKee 1982; Godwin *et al.* 2017; Pellegrini *et al.* 2018). Shorter inter-fire intervals may also increase the temperature and reduce the moisture of soils, which can reduce decomposition rates (Silveira *et al.* 2009). The result is that decreased inter-fire intervals are associated with distinct decomposer communities (e.g. fungi, Oliver *et al.* 2015) and declines in decomposition rates across a range of ecosystems (e.g. temperate forests, Brennan *et al.* 2009; subtropical sclerophyll forests, Butler *et al.* 2019; pine savannas, Semenova-Nelsen *et al.* 2019; Hopkins *et al.* 2020). However, the impacts on one taxon may be compensated for by another (e.g. invertebrates may compensate for reduced microbial litter decomposition, Butler *et al.* 2019).

Most studies of fire effects on invertebrate and microbe assemblages in ecosystems with long fire cycles focus on the period prior to vegetation recovery, but it is critical that we understand the full cycle of decomposer communities between fires. Where inter-fire intervals are shortened by management or anthropogenic global change, impacts on decomposer communities and decomposition are expected to be greatest in ecosystems where fire cycles were historically longest.

How do fire and decomposition interact?

Whether dead plant material follows the pathway of biological decomposition or consumption by fire depends on the traits of leaves, the spatial distribution of vegetation, and climate, all of which vary among biomes (Cornelissen *et al.* 2017; Pausas and Bond 2020). Leaf biochemical traits determine the decomposability of leaves: leaves that are high in nitrogen but low in lignin and with a low leaf mass per unit area are more decomposable (Cadisch and Giller 1997, p. 409; Cornwell *et al.* 2008) (Fig. 2). Further, plant traits (such as leaf and stem size) and eventually their litter particle size and shape (particularly curliness) are critical in the ignitability and flammability of litter because larger leaves produce a less compact and more ventilated litter bed that dries more rapidly and is more flammable (Scarff and Westoby 2006; Cornwell *et al.* 2015; Zylstra *et al.* 2016) (Fig. 2). At a larger scale, the continuity of vegetation is important in the spread of fire: discontinuous surface fuels often cannot support surface fires (Cornelissen *et al.* 2017). Finally, climate affects flammability and decomposition through drying – biological decomposition is much slower
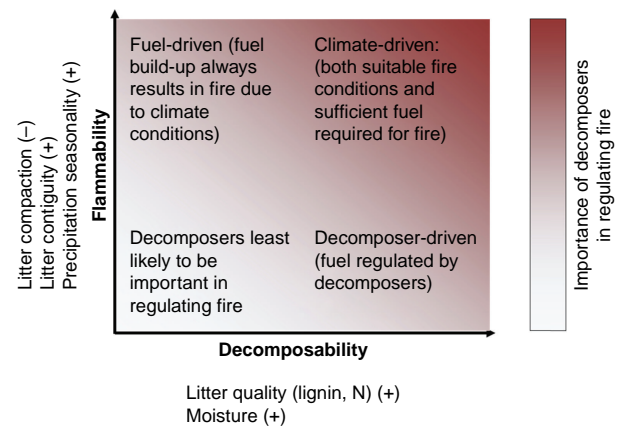

Fig. 2. Conceptual diagram of the spectrum of flammability and decomposability, modified from Cornelissen *et al.* (2017) to emphasise the conditions under which decomposers are most important. Flammability is high in both fuel-limited and climate-limited ecosystems, but low moisture in fuel-limited systems limits decomposition, while fire and decomposers are most likely to compete for fuels where fire regimes are climate-limited, i.e. high fuel loads must coincide with suitable fire weather.

in drier climates, while flammability is higher. The chance of ignition is also climate-dependent, although human population pressure plays a major role (Ganteaume *et al.* 2013). Decomposition has the greatest potential to limit fire where both flammability and decomposability are high and that includes biomes such as savannahs and broad-leaved forests (Cornelissen *et al.* 2017) (Fig. 2).

In the absence of fire, more than half of net primary production returns to the soil through decomposition (Wardle *et al.* 2004). The importance of decomposition in regulating fire is likely to be most important in ecosystems with highly flammable surface fuels, where those fuels are also highly decomposable (Cornelissen *et al.* 2017) (Fig. 2). Globally, approximately 60–70% of litter decomposition rates are explained by climate and litter quality (Parton *et al.* 2007). However, soil fauna enhance litter decomposition by 35% (globally, García-Palacios *et al.* 2013), but their importance varies with biome. Understanding variation in decomposer community contributions and its regulation by climate may therefore be critical in reducing unexplained variation in large-scale decomposition models (García-Palacios *et al.* 2013). We suggest that understanding how fire alters decomposition across different ecosystems may similarly provide an important contribution to our ability to predict fuel accumulation and manage fire.

The decomposition of dead plant matter is not well studied in the context of fire. Most litterbag studies suggest that prescribed fire reduces decomposition rates relative to unburned controls, although the timeframe differs among climates and vegetation types (Springett 1976; Raison *et al.* 1983, 1986; Monleon and Cromack 1996; Brennan *et al.* 2009; Toberman *et al.* 2014; Köster *et al.* 2016). However,

studies have also found no impacts of time since fire or fire severity on decomposition (Grigal and McColl 1977; Raison *et al.* 1986; Buckingham *et al.* 2015; De Long *et al.* 2016) and even increased decomposition following fire (Throop *et al.* 2017; Bryanin *et al.* 2018), highlighting the context dependency of fire impacts on decomposition. Repeated fires create different biodiversity dynamics from single-fire events, and changes in fire frequency (or inter-fire interval) may change the microhabitat and resources for decomposer organisms. More frequent fires decrease decomposition rates and create hotter and drier microclimates, lower litter quality and C:N ratios, and reduce soil C and N, pointing to mechanisms through which litter consumption by decomposer organisms is affected (Hernández and Hobbie 2008; Brennan *et al.* 2009; Toberman *et al.* 2014; Cornelissen *et al.* 2017; Pellegrini *et al.* 2018). However, detritivore assemblages may change following fire without altering decomposition rates (Vasconcelos and Laurance 2005; Buckingham *et al.* 2015). Although this suggests that functional redundancy could be high in some ecosystems, most studies indicate a strong link between decomposer assemblages and decomposition (reviewed in García-Palacios *et al.* 2013).

Functional diversity among detritivores, rather than species richness, drives decomposition rates in laboratory experiments (Heemsbergen *et al.* 2004). Dynamics of decomposer recolonisation thus do not necessarily indicate rates of functional recovery, particularly if a function is largely driven by a small number of functionally important species. The relationship between decomposition by invertebrates and the traits involved in recolonising an area following fire remains an important knowledge gap. Function is commonly strongly dictated by phylogeny (e.g. Martiny *et al.* 2013), as are traits associated with recolonisation (e.g. thermal tolerance, Sunday *et al.* 2012), so it is likely that different functional groups return to the system at different rates. This might reflect availability of their resources, for example, scavengers often increase in abundance with time since fire (e.g. Driscoll *et al.* 2020). Where inter-fire intervals vary substantially in a landscape or change over time, the period for recolonisation of populations may exceed the inter-fire interval. The result could be that functional groups within the decomposer community are lost, altering rates of decomposition and potentially leading to increased fuel accumulation.

Surface fuel loads are expected to reach an asymptote (equilibrium) over time since fire, with a steady state achieved where litter fall is offset by decomposition (Olson 1963; Fensham 1992). However, litter and woody surface fuel loads show a range of responses to time since fire, remaining constant, peaking, or continuing to increase over time depending on the ecosystem (Schimmel and Granström 1997; Moritz *et al.* 2004; Gosper *et al.* 2013; Eskelson and Monleon 2018). Surface fuel loads are often predicted using coarse-scale vegetation maps and time-since-fire relationships (Tolhurst *et al.* 2008; Price and Gordon 2016). Most models of surface fuel accumulation assume constant decomposition rates throughout post-fire succession (Olson 1963; Raison *et al.* 1983; McCarthy *et al.* 2001), although the influence of climatic factors on decomposition is sometimes considered (e.g. Miller and Urban 1999). Inclusion of decomposition as a constant rate in models has long been considered a gross simplification, with early studies acknowledging the importance of season and recent fire history in determining decomposition rate (e.g. Fox *et al.* 1979; Birk and Simpson 1980), but none to date tackling the complex issue of decomposer assemblages.

The assumption of functional redundancy among decomposer organisms is not supported by laboratory studies (e.g. Heemsbergen *et al.* 2004; Zimmer *et al.* 2005) and has not been addressed in the field. This limits our ability to understand spatial and temporal variation in fuel–fire relationships. Oversimplification of the biology and function of decomposer communities reduces the likelihood that we are accurately modelling decomposition (Prescott 2005). It is particularly important to get this right if there is a risk that some approaches to fire management may threaten the very organisms that control fuel loads.

Feedbacks

Surface fuel loads depend on decomposition rates, coming to an equilibrium when decomposition equals input (Minderman 1968). Biological decomposition is slower following fire, explaining why litter build-up following fires is accentuated, particularly where fires are frequent (Raison *et al.* 1983; Fernandes and Botelho 2003; Litton *et al.* 2003; Yang *et al.* 2020). This is likely a direct result of the documented negative impacts of fire on the decomposer community (Pressler *et al.* 2019) (Fig. 1). Most fire dampening provided by hazard-reduction burns lasts no more than 10 years (*Eucalyptus* forest and heathland, south-eastern Australia, Sackett 1975; *Pinus ponderosa*, USA, Wagle and Eakle 1979; *Eucalyptus* forest, south-eastern Australia, Rawson *et al.* 1985; shrublands in Western Australia, McCaw *et al.* 1992; heath and open woodland (mallee) in southern Australia, Grant and Wouters 1993; *Pinus pinaster*, Spain, Moreira da Silva 1997; shrublands in France, Lambert *et al.* 1999; *Pinus ponderosa*, Pollet and Omi 2002), and effectiveness is highly weather-dependent (Fernandes and Botelho 2003). This rapid return to initial fuel loads in some ecosystems with historically long inter-fire intervals encourages forest managers to reduce the inter-fire interval for prescribed burning. However, increased fire frequency (or fire interval squeeze) decreases decomposition rates (Brennan *et al.* 2009; Butler *et al.* 2019; Hopkins *et al.* 2020), thus leading to a greater perceived need for prescribed burning.

The impact of prescribed burning on soil communities may be very different from the impact of the cyclical natural fire regimes to which the biota are adapted (Knapp *et al.* 2009). In addition to the impacts of increased frequency

described above, this may be due to differences in intensity or the timing of fires relative to species' phenology. For example, in south-eastern Australia, prescribed burns typically occur in spring or autumn, when soils are moister, which is generally when soil communities are more active and, therefore more prone to perturbation (Menz *et al.* 2016). Further, although moist soils have a reduced heating capacity, the lethal temperature needed to kill soil microbes is dramatically reduced as soil moisture facilitates more effective heat penetration and faster heat distribution: lethal temperatures for bacteria are in excess of 200°C for dry soils, but considerably lower (50–60°C) in moist soils (DeBano 1991). However, moist soils can also protect soil biota: in grasslands, where fires are short-lived, the high specific heat of water can serve to buffer the effects of heating and reduce the likelihood of ignition of organic matter in the soil (Wells 1979).

If inter-fire intervals are 'squeezed' (Enright *et al.* 2015) such that decomposer assemblages are unable to recover within the inter-fire interval, then litter decomposition rates will decrease (Springett 1976; Raison *et al.* 1986; Monleon and Cromack 1996; Brennan *et al.* 2009), which may increase the risk of future fires. The recovery of decomposer assemblages is likely to be dictated not only by fire frequency, but also by seasonality, severity and extent, as

these factors interact with recolonisation and persistence traits of species, determining whether an assemblage is dominated by superior dispersers or *in situ* survivors. More frequent, severe, or larger-extent fires may compound the local loss of decomposer diversity. At a landscape scale, source populations may be eliminated. Even if functional effects are not immediately obvious, species richness is associated with functional diversity in heterogeneous environments (Tylianakis *et al.* 2008) and over time (Reich *et al.* 2012). It is thus likely that the maintenance of decomposer assemblages is critical in maintaining function and allowing ecosystems to self-regulate litter loads.

Global change, fire and biological decomposition

Biological decomposition is performed by biota, so prediction of the consequences of global change for decomposition requires a better knowledge of how those organisms respond to threats such as landscape modification, climate change and species invasions. These threats will impact fire regimes, altering fire severity, seasonality, extent and frequency (Fig. 3) (third-order fire effects). At the same time, they will alter species assemblages. Further, changes in fire regimes and assemblages of detritivores may act synergistically to complicate outcomes for decomposition.
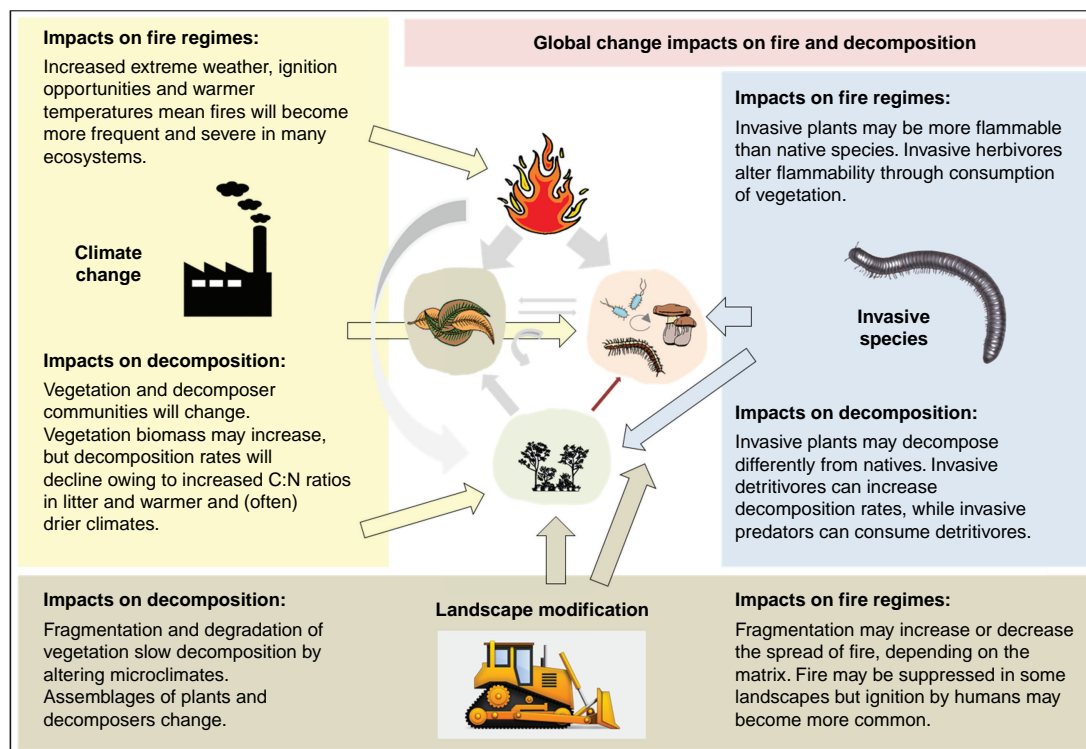

Fig. 3. Key predicted impacts of the global change drivers of climate change, landscape modification and invasive species on fire regimes and decomposition. Coloured arrows illustrate where global change drivers influence fire and/or decomposition and if this occurs through their impacts on decomposer organisms or vegetation.

Landscape modification

Landscape modification remains the most significant threat to biodiversity (Segan *et al.* 2016). A range of studies have explored the impact of anthropogenic modifications, such as habitat fragmentation, on biodiversity. Fragmentation of forests results in exposure to warmer and more desiccating microclimates, and stronger winds (Malcolm 1998; Briant *et al.* 2010). This leads to changes in plant species composition (sometimes leading to N-poor litter in small fragments) (Riutta *et al.* 2012) and vegetation structure (Didham and Lawton 1999). It also decreases rates of litter decomposition in small, isolated fragments and at patch edges (Didham 1998; Martinson and Fagan 2014). Declines in decomposition rates in habitat fragments have been attributed to microclimate (drier climates at forest edges decrease decomposition rates) and changes the composition of detritivore assemblages (de Souza and Brown 1994; Grove 2002; Vasconcelos and Laurance 2005).

At a landscape-scale, the likelihood of fragments burning may differ substantially from the original continuous habitat. Increased anthropogenic use of fire in the modified matrix acts synergistically with the drier edges and decreased decomposition rates of fragmented tropical forests to increase the frequency of fire (Laurence and Vasconcelos 2004). However, fragmentation of flammable habitats can inhibit fire spread at a landscape scale (Duncan and Schmalzer 2004). Protection of small urban fragments from fire can result in less flammable plant communities and fundamental changes in the species composition of litter invertebrates (Gibb and Hochuli 2002). Where fragments do experience fire, they are less likely to be recolonised by dispersal-poor detritivores (Driscoll and Weir 2005; Schmuki *et al.* 2006). The impacts of habitat fragmentation on fuel loads may thus be difficult to predict, depending on the balance between reduced fire spread and altered fuel loads, and any fragmentation impacts on the decomposers.

Climate change

Global models show that climate is an important driver of litter decomposition (Liski *et al.* 2003; García-Palacios *et al.* 2013), and it is therefore likely that changing climate will change decomposition rates. Climate change encompasses a variety of changes, including increasing carbon dioxide (CO_2) and temperature, changes in precipitation, and increases in the frequency of extreme weather events (IPCC 2012; National Academies of Sciences, Engineering, and Medicine 2016), including the extremely hot and dry conditions that commonly precede major fires (Hennessy *et al.* 2005; Nolan *et al.* 2020). Climate change is thus likely to alter many elements of fire regimes, including fire extent, severity, frequency and seasonality (Fig. 3). As a result, the interaction between future climate projections, fuel loads and decomposition is likely to be complex.

An accurate prediction of how the decomposition of fuel will respond to changes in climate is dependent not just on changes in physical factors, but also shifts in species distributions and changing plant and decomposer communities (Castro *et al.* 2010; Harris *et al.* 2016; Koltz *et al.* 2018). Whereas warming and increased CO_2 may increase decomposition rates, studies also predict that under warming conditions, plant communities will change (e.g. Davidson and Janssens 2006; Scherrer *et al.* 2017), altering the type of litter available to decomposers. Where plant community composition remains unchanged, the nutrient content of fresh litter may decline (Manea *et al.* 2015; Kasurinen *et al.* 2017), thus altering the quality of litter (De Long *et al.* 2016). Further, interactions between invertebrates and microbes change with temperature and soil moisture (Coulis *et al.* 2013; A'Bear *et al.* 2014) and the synergistic impact of these changes on decomposition is likely to differ among ecosystems.

In a rapidly changing climate, establishment conditions are also likely to change with time, such that recovering ecosystems may not converge on a pre-fire state. For example, seasonal increases in soil moisture following fire are hypothesised to be critical in facilitating the recovery of soil microbial community structure and function to a pre-burnt state (D'Ascoli *et al.* 2005; Prendergast-Miller *et al.* 2017). This suggests that any changes in fire seasonality may alter the direction of community recovery. The same is likely to be true of climate-limited changes in fire frequency, severity and extent.

Species invasions

Invasive species may enhance or inhibit fire, depending on the species and ecosystem. Exotic plants can alter ecosystem flammability (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998; Brooks *et al.* 2004; Rothstein *et al.* 2004; Arthur *et al.* 2012), for example, buffelgrass (*Cenchrus ciliaris*) invasions increase fuel loads and burn severity (Miller *et al.* 2010). Litter of invasive species may also decompose more rapidly than native litter (Jo *et al.* 2016): many successful invaders possess traits, such as limited investment in permanent structures, that are also associated with rapid decomposition (Van Kleunen *et al.* 2010). Although decomposers are rarely species-specific, they are often adapted to particular plant traits (Kembel and Mueller 2014), such that plant invasions result in changed decomposer assemblages (Cameron and Spencer 1989). Invasive plant species may also alter decomposition through their impact on microclimates, since decomposition rates depend on temperature and moisture (Vallés *et al.* 2011; Watling *et al.* 2011). Alternatively, they may affect decomposition indirectly, by altering habitat suitability for decomposer species (Gratton and Denno 2005; Foster *et al.* 2021).

Invasive predators may dramatically alter ecosystems through their impacts on detritivores. For example, exotic crazy ants (*Anoplolepis gracilipes*) on Christmas Island

caused dramatic increases in forest floor litter loads through predation on native red crabs, a key litter consumer (O'Dowd *et al.* 2003). Invasive decomposers also affect fuel loads: invasive earthworms are important litter decomposers in the USA and are therefore likely to inhibit fire. However, they live in the litter layer, so are more negatively affected by fire than are native earthworms, which tend to be soil-living (Callaham *et al.* 2003; Ikeda *et al.* 2015). In contrast, high abundances of invasive detritivores, such as bark beetles, can increase tree death following fire (Houston 1981; Goldammer and Penafiel 1990), thus increasing fuel for future fires. The feedbacks among species invasion, decomposition and fire are poorly understood, but are clearly important in understanding fire risk in a changing world.

Management implications

Within those fire-prone forests, fire management occurs largely through hazard reduction burns aimed at reducing fine surface fuels, which are the critical habitat of detritivores that naturally undertake biological fuel reduction. The appropriateness of this approach may depend on where on the spectrum of climate-limited to fuel-limited an ecosystem belongs and a one-size fits all approach may lead to negative outcomes in some ecosystems. Inappropriate fire management, i.e. management that leads to population extinctions (Kelly *et al.* 2015), may lead to a negative feedback loop (Fig. 1). In that case, fire would cause declines in detritivore assemblages, leading to a reduction in litter decomposition, which would be expected to accelerate the accumulation of flammable fuel. This could lead to a requirement for more frequent managed burns, but increased fire frequency is associated with greater loss of biodiversity and function (Hernández and Hobbie 2008; Brennan *et al.* 2009; Toberman *et al.* 2014). It is therefore critical that fire managers recognise that surface fuel loads are controlled by organisms and that these organisms and their interactions must be better understood if we are to rebuild diverse and functionally intact decomposer communities and retain the function of decomposition following fire. Active monitoring of not just surface fuels, but also decomposition rates and litter fall would provide the detailed information required to better model this ecosystem service.

Conservation of functionally intact decomposer communities will be achieved through attention to *in situ* conditions during and after prescribed burns, burn season and the scale and heterogeneity of those burns, and proximity to refuges or other potential colonisation sources in the landscape. Like most species, detritivores have evolved with a natural fire regime. Conflicts between frequent hazard reduction and conservation will be low if there is a history of frequent low-intensity surface fires, but high if the natural fire regime consists of infrequent high-intensity fires (Fernandes and Botelho 2003). Managers may be able to alter the intensity, frequency, seasonality and extent of prescribed fires to mimic natural fires, but mimicking high-intensity, large-extent fires may not be desirable if the aim of prescribed burning is to minimise damage to human populations and infrastructure.

In addition to difficulties in mimicking 'natural' fire regimes, today's unmanaged fires may differ considerably from those of the recent past. A range of anthropogenic factors functioning at larger scales than most fire management operations conspire to alter fire regimes. These include climate change, anthropogenic alteration of landscape structure and composition and changes in the role of people in starting and managing fires, for example, the loss of indigenous fire management, long-term fire suppression or increases in accidental or intentional arson (Bradstock 2010; Ganteaume *et al.* 2013). Some of the same factors may also limit the ability of species to respond, e.g. temperature affects invertebrate development rates and willingness to fly (Bale *et al.* 2002; Abram *et al.* 2017), while habitat degradation and fragmentation drive species loss and limit sources for recolonisation (Didham *et al.* 1996). Of these factors, landscape structure offers the greatest opportunity for manipulation at a local scale, for example by regulating burn heterogeneity (Kral *et al.* 2017). However, management must be based on sound knowledge of the dispersal or *in situ* survival capacities of decomposers across functional groups. It should also be tailored to the ecosystem, considering landscape structure, the position on the climate- and fuel-limited spectrum and traits of the biota.

Additionally, active management of the decomposer communities could provide an avenue for overcoming some of the negative feedbacks associated with increasing fire size, severity and frequency and its interactions with global change. This could involve preserving small-scale litter refuges during management burns (e.g. Holland *et al.* 2017), enabling recolonisation to occur over much smaller spatial scales, or addition of cellulose into severely burnt soils to favour the development of fungal mycelium and increase microbial C (Fritze *et al.* 1993). Alternatively, following extreme fires, active litter transplants or targeted transplants of key decomposers to rapidly restore both the invertebrate and microbial components of decomposer communities and their critical ecosystem processes could be used the way that faecal transplants are used for human health or soil transplants for agricultural health (Contos *et al.* 2021). Similar treatments following hazard reduction burns might assist in lengthening their effectiveness, but these potential solutions remain untested.

Synthesis

Decomposer organisms are important in regulating surface fuels in many ecosystems and fuel loads drive fire. Feedbacks among fire, fuel and decomposer organisms are likely to be important in determining fire regimes (Fig. 1) and how they will respond to global change and should be

Table 1. There are many gaps in knowledge that limit our ability to manage litter decomposers in fire-prone ecosystems. Here, we outline a set of key research questions that, if answered, could improve conservation of decomposers and decomposition in the context of fire.

Broad topic	Key questions
Adaptation	Which decomposer species struggle to adapt to altered fire regimes? Which traits determine persistence and are they related to decomposition function?
Landscape structure and refuges	To what extent does fire fragment populations? Do conceptual frameworks for fragmentation apply equally well to fire? In what sorts of ecosystems or fire regimes are small-scale fire refuges important in allowing detritivore persistence at a landscape scale?
Dispersal and recolonisation	What are the relative roles of habitat suitability and dispersal limitation in determining recolonisation success of decomposers? Do litter transplants or targeted reintroductions lead to desirable outcomes for biodiversity and decomposition following severe fires? Which species traits best predict recolonisation ability?
In situ survival	What are the behavioural and physiological traits that allow *in situ* survival of decomposers? How does the relative importance of *in situ* survival and dispersal vary among ecosystems or fire regimes?
Interactions	Are macroinvertebrates vectors of important microbe decomposers following fire?
Decomposition function	How does decomposition rate recover following fires in different ecosystems with different fire regimes? How does decomposer diversity relate to decomposition over space and time? How much functional redundancy is there among decomposer organisms and does this differ among ecosystems? Is the composition of key decomposers stable over space and time?
Global change	What impact do climate-, fragmentation- or invasion-driven changes in vegetation have on fire regimes and the capacity of decomposers to persist? Do invasive decomposers or predators of decomposers alter decomposition rates?
Fire prediction	What is the impact of decomposer-driven differences in fuel loads on fire regimes? Does inclusion of varying decomposition rates in fire models improve their predictive power?
Fire management	In which ecosystems do repeated hazard reduction burns have long-term effects on decomposition function? Does the impact of hazard reduction burns on decomposers depend on the proportion of *in situ* survivors?

incorporated into management. However, key questions regarding the relationship between fire, fuel and decomposers remain unanswered (Table 1). For example, data on the importance of decomposer organisms and changes in decomposition rates following fire are currently insufficient to incorporate into models predicting fire risk or spread. In addition to their important functional roles in nutrient cycling and in terrestrial food webs, decomposer organisms present a significant portion of the biodiversity supporting and supported by the surface fuel layer. Efforts can and should be made to conserve and manage these functionally critical taxa in fire-prone ecosystems, particularly those with historically long inter-fire intervals.

Supplementary material

Supplementary material is available online.

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