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Fungi and fire in Australian ecosystems: a review of current knowledge, management implications and future directions

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Abstract. Fungi are essential components of all ecosystems in roles including symbiotic partners, decomposers and nutrient cyclers and as a source of food for vertebrates and invertebrates. Fire changes the environment in which fungi live by affecting soil structure, nutrient availability, organic and inorganic substrates and other biotic components with which fungi interact, particularly mycophagous animals. We review the literature on fire and fungi in Australia, collating studies that include sites with different time since fire or different fire regimes. The studies used a variety of methods for survey and identification of fungi and focussed on different groups of fungi, with an emphasis on fruit-bodies of epigeal macrofungi and a lack of studies on microfungi in soil or plant tissues. There was a lack of replication of fire treatment effects in some studies. Nevertheless, most studies reported some consequence of fire on the fungal community. Studies on fire and fungi were concentrated in eucalypt forest in south-west and south-eastern Australia, and were lacking for ecosystems such as grasslands and tropical savannahs. The effects of fire on fungi are highly variable and depend on factors such as soil and vegetation type and variation in fire intensity and history, including the length of time between fires. There is a post-fire flush of fruit-bodies of pyrophilous macrofungi, but there are also fungi that prefer long unburnt vegetation. The few studies that tested the effect of fire regimes in relation to the intervals between burns did not yield consistent results. The functional roles of fungi in ecosystems and the interactions of fire with these functions are explained and discussed. Responses of fungi to fire are reviewed for each fungal trophic group, and also in relation to interactions between fungi and vertebrates and invertebrates. Recommendations are made to include monitoring of fungi in large-scale fire management research programs and to integrate the use of morphological and molecular methods of identification. Preliminary results suggest that fire mosaics promote heterogeneity in the fungal community. Management of substrates could assist in preserving fungal diversity in the absence of specific information on fungi.

Introduction

Both fire and fungi affect most other biota, particularly in fire-prone Australian ecosystems. Despite their obvious importance, the two have rarely been considered together. Warcup (1981) briefly summarised the interaction between fire and non-vascular plants (including fungi) in Australia. For the Jarrah and Karri forests of south-western Australia, Robinson and Bougher (2003) concluded that fire favours some fungi but not others. Globally, Cairney and Bastias (2007) found that fire generally alters the community structure of fungi in soil, with site- or fire-specific effects, which are more pronounced with repeated burning. In this review we collate and interpret data from published Australian studies dealing with the influence of fire on fungi, in the context of the ecological roles of fungi in ecosystems and their interactions with other organisms.

The fungal kingdom is extremely diverse, with a range of vital ecological roles and a high degree of interdependency with other organisms. Fungi are heterotrophic and employ a variety of nutritional strategies including saprotrophism, parasitism and the formation of mutualistic partnerships such as mycorrhizas and lichens (May and Simpson 1997). Saprotrophic or decomposer fungi grow in soil (Bridge and Spooner 2001) or directly in litter and wood (Rayner and Boddy 1988). Due to their ability to break down complex compounds such as cellulose and lignin they are particularly important in the degradation of organic matter. Most plants form mycorrhizas, and this partnership is particularly

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important in old, highly weathered and nutrient-poor soils (Brundrett 2009), such as those found across the majority of the Australian landscape. Fungi are essential participants in the cycling of carbon, nitrogen, phosphorus and other nutrients in ecosystems (Berg and Laskowski 2006). Consumption of fruit-bodies and mycelium of fungi by mycophagous animals, particularly invertebrates, also contributes to nutrient cycling. Another critical role of fungi in ecosystem function is their influence on soil in relation to ionic exchange, particle aggregation, carbon content, water holding capacity and water infiltration (Bastias *et al*. 2006*a*; Claridge *et al*. 2009*a*).

Fungi are a significant but often overlooked component of the Australian biota. Some 11 846 described species of fungi are known from Australia, of which 3495 form lichens (Chapman 2009). Estimated diversity is at least 10 000 species for macrofungi (about twice as many as are currently known) and as high as 250 000 species for microfungi (Chapman 2009). Not only are there many species awaiting formal description, but the biology and ecology of named species is usually poorly known. Very few fungi are formally listed on state or national conservation schedules (May 1997, 2003). Management of fungi in native ecosystems is compromised by the almost total lack of staff with expertise in or responsibility for fungi in conservation and management agencies.

Fire, both planned and unplanned, is an integral part of Australian ecosystems and impacts on fungi in various ways through physical and chemical changes to habitats and substrates. Heating during fire causes sterilisation of upper soil layers and loss of nutrients and carbon via volatilisation and combustion of litter and soil organic matter (Certini 2005). Most soil nutrients are concentrated in these upper layers (Jobbágy and Jackson 2001) as are most organisms (Lee and Foster 1991; Dahlberg 2001; Huang *et al*. 2005). For most fires, radiation provides enough heat to kill soil organisms including fungi, in the upper soil layer; although heat intensity declines rapidly with depth (Humphreys and Lambert 1965; Raison *et al*. 1985). Heating to 60°C is sufficient to kill living tissue, particularly unprotected fungal mycelia (Schenck *et al*. 1975; Klopatek *et al*. 1988) and upper layers of soil often reach this temperature during fires (Humphreys and Lambert 1965; Bradstock *et al*. 1992; Pattinson *et al*. 1999). Nevertheless, fungi that have evolved in fire-prone Australian environments have adaptations to cope with fire such as heat-resistant spores or other resting structures (Warcup 1981). Fire can also affect fungi by removing and creating substrates for saprotrophs, such as litter and woody debris, or by detrimental effects on mutualistic partners, such as spore dispersers or mycorrhizal hosts (Dahlberg 2002).

Soil nutrients are altered by fire, which in turn impacts the utilisation and genesis of nutrients by fungi and consequently other biota. Despite a direct loss of nitrogen from soil via volatilisation, nitrogen and phosphorus availability in soil following fire can increase or decrease depending on fire intensity (Raison 1979; Raison *et al*. 1985; Gray and Dighton 2006). Changes in nutrient availability subsequently impact on recovery of vegetation and nutrient cycling (Neary *et al*. 1999, 2005; Howell *et al*. 2006). Fire also alters soil fungal communities involved in decomposition (Neary *et al*. 1999; Boddy 2001) therefore altering carbon : nitrogen ratios and mineralisation rates, which ultimately affect plant growth and productivity (Neary *et al*. 1999, 2005; Boddy 2001).

The understanding of fire regimes and the effects of fire on Australian vegetation has developed rapidly from the generally science-based endeavour of ‘Fire and the Australian Biota’ (Gill *et al*. 1981) to a much more management-, consequence- and biodiversity-orientated approach (see Bradstock *et al*. 2002; Abbott and Burrows 2003). Recent extensive fires that have occurred on most continents have prompted recognition that the incidence and characteristics of large fires may alter in the future as a consequence of global climate change (Williams and Bradstock 2008). Fires, whether planned or unplanned, independent of season, are patchy and the effects on soil are equally irregular (Bradstock 2008). It is now widely recognised that no single optimum fire regime will meet all management objectives (Burrows 2008) and diversity of fire regimes among landscapes, including long unburnt patches, is now being accepted by land management agencies in adaptive fire management programs. Fire mosaics resulting from cumulative heterogeneity (patchiness) from successive fires may contribute to increased local biodiversity (Grove *et al*. 2002; Bradstock 2008; Burrows 2008). Although fire management policies aim to maximise biodiversity, the data upon which decisions are based predominantly concern vegetation, fuel quantities and conditions, and the likely locations of recognised threatened species. Thus, most biota, especially fungi, are not explicitly covered by current fire management policies.

Recently, concern has been expressed that management of fire for vegetation may not provide the best outcomes for other biota (Clarke 2008; New *et al*. 2010). In turn, due to the interconnectedness of fungi with the biota in general, other organisms that rely on fungi could also be compromised by knowledge deficiencies about their fungal partners. The purpose of this review is to summarise the current understanding of how fire affects fungi in Australian ecosystems, to identify knowledge gaps and to suggest steps by which fungi and fire may be better managed. After an overview of the current literature on fungi and fire in Australia, and discussion of fungi that do or do not require fire (and the optimum fire frequency for fungi), we deal with fire and fungi in the framework of fungal trophic groups and substrates in order to highlight the functional roles of fungi and to suggest a context that will aid integration of fungi into ecosystem management.

Fire and the fungal community in Australian ecosystems

Studies of the effect of fire on fungal communities in Australian ecosystems are summarised in Table 1. The 30 field studies identified utilised a range of techniques, but all compare the fungi present on sites with different times since fire. Most studies included recently burnt sites, but in some cases (e.g. Ratkowsky and Gates 2008), the comparison was among sites of known fire history that had not been burnt for several years to many decades. In general, long unburnt (commonly referred to as control) sites were incorporated but some studies focussed only on recently burnt sites, where the fire was less than 10 years ago (Theodorou and Bowen 1982; Warcup 1990; Bellgard *et al*. 1994; Launonen *et al*. 1999; Vernes and Haydon 2001; Vernes *et al*. 2001, 2004;

George 2008; Catcheside *et al*. 2009; Claridge *et al*. 2009*a*; O'Bryan *et al*. 2009; Ratkowsky and Gates 2009; Robinson 2009). Nine studies (some involving multiple publications) incorporated a comparison of different fire regimes in relation to different frequencies of burning (Hilton *et al*. 1989; Bastias *et al*. 2006*a*, 2006*b*; Brundrett *et al*. 1996*a*, 1996*b*; Tommerup *et al*. 2000; Glen *et al*. 2001; Vernes and Haydon 2001; Vernes *et al*. 2001, 2004; Anderson *et al*. 2007; Osborn 2007; Campbell *et al*. 2008; Artz *et al*. 2009; O'Bryan *et al*. 2009).

Most of the studies listed in Table 1 focussed on particular groups of fungi. Group distinctions were based on taxonomy, morphology or trophic assemblage, with most studies surveying fruit-bodies of macrofungi (inclusive of both saprotrophs and ectomycorrhizal species). Only one study involved lichens and two studies investigated the effect of fire on cryptogamic soil crusts, of which lichens are an important component. Few studies attempted to identify microfungi and those that did either focussed on a specific group such as the Trichocomaceae (McGee *et al*. 2006) or included soil microfungi as part of sampling of soil fungi across all taxonomic groups (Bastias *et al*. 2006*a*). No studies dealt with microfungi of aboveground plant tissues, such as the highly diverse suite of leaf-inhabiting fungi of indigenous Australian plants (May and Simpson 1997; Cheewangkoon *et al*. 2009).

The way that fungi were sampled varied considerably across the studies included in Table 1. A few studies determined general fungal biomass (e.g. Osborn 2007) or biomass of particular groups such as truffle-like fungi (Vernes and Haydon 2001); estimated the number of ectomycorrhizal root tips (Malajczuk and Hingston 1981); or utilised hyphal-ingrowth bags to specifically target ectomycorrhizal fungi (Bastias *et al*. 2006*b*). Isolation into pure culture was utilised to study Trichocomaceae in bark (McGee *et al*. 2006) and fungi in general as a component of the soil microbial community (Theodorou and Bowen 1982). Isolation into culture is well known to have serious limitations as a means of assessing the fungal community present in soil or other substrates because most fungi will not grow or are outcompeted on standard media (Bridge and Spooner 2001).

Most surveys were based on recording fruit-bodies of epigeous macrofungi (such as mushrooms and coral fungi) or hypogeous macrofungi (sequestrate or truffle-like fungi). Fruit-bodies do indicate active growth of underlying mycelium, but, particularly for fleshy macrofungi, they are often ephemeral and sporadic in occurrence. Thus, intensive sampling at times of peak production (such as autumn) over several years is required to detect a significant proportion of the species present at a site. For ectomycorrhizal fungi it is also clear that there is a mismatch between the species detected on root tips and those present as fruit-bodies (Gardes and Bruns 1996). For example, using restriction fragment length polymorphism (RFLP) analysis, Glen *et al*. (2001) detected many more species in Jarrah forest soil than were recorded by fruit-body surveys.

Molecular methods show great promise for characterisation of the fungal community in soil and other substrates. Direct isolation of DNA from the substrate can be utilised in tandem with community profiling techniques such as denaturing gradient gel electrophoresis (DGGE) or terminal restriction fragment length polymorphism (T-RFLP) (Anderson and Cairney 2004). Molecular sampling is particularly useful for soil, where it can detect macrofungi not producing fruit-bodies at the time of sampling, as well as saprotrophic, mycorrhizal and parasitic microfungi. However, as with culturing, DNA sampling does not distinguish active mycelium from resting stages such as spores or sclerotia (Bridge and Spooner 2001). Sampling of DNA from soil has been used to study the effects of fire on fungal communities in eucalypt forests in New South Wales and Victoria (Chen and Cairney 2002; Osborn 2007) and in a long-term prescribed burning experiment in *Eucalyptus pilularis* forest at Peachester State Forest in southern Queensland (Bastias *et al*. 2006*a*, 2006*b*; Anderson *et al*. 2007; Campbell *et al*. 2008; Artz *et al*. 2009).

Assignment of fungi to trophic groups is important for interpreting ecological roles. While DNA primers specific for fungi can be utilised (e.g. Chen and Cairney 2002), it is not possible to separate fungal DNA neatly into different trophic groups by use of specific primers. Although the trophic status of fungi can vary considerably within higher taxa such as families and orders, it is highly correlated with phylogeny and is generally uniform within genera (Tedersoo *et al*. 2009*b*). Therefore, most individual sequences can be assigned to trophic groups (Bastias *et al*. 2006*b*) as can fungi sampled as fruit-bodies. In addition, the presence of particular trophic groups has been targeted in soil samples by the use of functional molecular markers such as basidiomycete laccase genes putatively involved in decomposition (Artz *et al*. 2009). Other assays targeted at particular fungal activity were phenol oxidase activity (Artz *et al*. 2009) or stable isotope probing to assess cellulolytic activity of soil fungi (Bastias *et al*. 2009).

Identification of fungi to species is one of the most challenging components of fungal ecology and difficulties of identification are compounded by the large number of species yet to be formally described that are routinely encountered in fungal surveys. Traditional morphological identification utilises microscopic characters and the differences between species are often subtle. In studies where fruit-bodies were sampled, identification of fungi was mostly on morphological characteristics. For surveys of epigeal macrofungal fruit-bodies, substantial inventories of species were accumulated in some studies, such as the 307 taxa observed by Gates *et al*. (2005) in southern Tasmania and the 322 taxa observed by Robinson and Tunsell (2007) in south-west Western Australia. All taxa were identified to species level, but in both studies only about half the taxa were formally described; the rest were assigned 'tag' or 'field' names. Other studies utilising morphological identification also included a substantial number of 'tag' names.

Molecular methods not only allow isolation of fungi, they also facilitate identification of fungi. Molecular community profiling techniques such as DGGE produce banding patterns where each band is more or less unique at the species level, alleviating the necessity for identification of the fungi concerned (Anderson and Cairney 2004). To identify species, the closest match for a particular sequenced DNA region [such as the internal transcribed spacer (ITS)] can be compared with samples lodged in GenBank. The sequenced DNA may come from samples isolated as DNA in the first place, such as through DGGE and other profiling techniques, or from conventional samples such as fruit-bodies or ectomycorrhizal roots tips. In comparison to the several hundred species identified from some fruit-body surveys (Gates *et al*. 2005; Robinson and Tunsell 2007), relatively few taxa have so far been identified to species level where molecular community profiling has been used, because only a selection of the numerous bands present were selected for sequencing (Bastias *et al*. 2006*a*).

Where molecular methods were utilised to identify fungi from soil samples, species were rarely able to be determined. Among the ITS sequences generated by Bastias *et al*. (2006*b*) and Chen and Cairney (2002) to identify RFLP types, there were few matches to named species above the 97% level that is indicative of species identity for this region in many groups of fungi (Hughes *et al*. 2009). Bastias *et al*. (2006*a*) were not able to identify any of 39 selected bands from DGGE profiles to species level on the basis of ITS sequences, with some bands matched only at order or phylum level. The inability to identify many sequences from the studies listed in Table 1 to species is either because the sequences with high identity in GenBank were from unidentified fungi in the first place, or because the level of matching with sequences of known identity was low, implying that reliably named sequences of most Australian soil fungi are not yet available in GenBank.

Many studies listed in Table 1 were unreplicated or, when there was some replication of sites within treatments, surveys were limited to repeated collection of data at different times after a fire. Replicated sampling tends to occur more with planned experimental studies (Theodorou and Bowen 1982; Warcup 1983; Bellgard *et al*. 1994; Launonen *et al*. 1999; McGee *et al*. 2006) compared with descriptive or ecological studies. Unreplicated studies can be regarded as indicative of effects, but need to be backed up by well replicated investigations before their conclusions can be accepted. Due to the variable nature of fire, analysis of results is particularly difficult as sufficient statistical power is hard to obtain and fire conditions are hard to replicate. The within-site variability may be so great that any differences among treatments may be hard to discern. Only nine of the Australian studies used plot-based, replicated sampling and attempted to identify the target fungi to species level; and all nine utilised counts of fruit-bodies (Hilton *et al*. 1989; Claridge and Barry 2000; Claridge *et al*. 2000*a*, 2000*b*; McMullan-Fisher *et al*. 2002; Packham *et al*. 2002; Robinson and Bougher 2003; Claridge and Trappe 2004; Kantvilas and Jarman 2006; Robinson *et al*. 2008; Ferguson *et al*. 2009; O'Bryan *et al*. 2009).

Studies combining fungi and fire in Australia have been concentrated in *Eucalyptus* forests of south-eastern and south-western Australia (Table 1). There is a lack of data for other vegetation types, notably grasslands, arid areas and woodlands. Forests dominated by *Eucalyptus marginata* (Jarrah) and *E. diversicolor* (Karri) in south-west Western Australia have been relatively well studied and fungal communities have been investigated in relation to fire using both morphological and molecular techniques (Malajczuk and Hingston 1981; Hilton *et al*. 1989; Tommerup *et al*. 2000; Glen *et al*. 2001; Robinson and Bougher 2003; Robinson *et al*. 2008). Another comparatively well studied ecosystem is wet sclerophyll forest with *E. obliqua* as a dominant or subdominant tree component with investigations of macrofungi (Packham *et al*. 2002; Gates *et al*. 2005, 2009; Ratkowsky 2007; Ratkowsky and Gates 2009), lichens (Kantvilas and Jarman 2006) and the soil microbial community including fungi (Theodorou and Bowen 1982).

In addition to the chronosequence studies that compare fungal communities on sites of different fire history (Table 1), inventories of fungi from individual sites of known time since fire could be relevant when considering the effects of fire on fungi. Examples of such inventories come from repeated sampling for fruit-bodies of various groups of macrofungi on Mt Wellington in Tasmania, which was last burnt in 1967 (Ratkowsky and Gates 2002; Gates and Ratkowsky 2004, 2005; Trappe *et al*. 2008). Such inventories have the potential to contribute to the pool of knowledge about fungi in different vegetation types of particular fire histories, but at present the information available is too limited to make meaningful comparisons.

The studies listed in Table 1 investigated widely different functional and morphological groups of fungi and used a variety of different survey techniques and methods for identification of the samples generated. Fire history also varied among the studies. Such diversity makes comparison of results difficult, and similar difficulties in comparing studies were encountered by Cairney and Bastias (2007) in their global review of the effects of fire on forest soil fungi. Nevertheless, most studies in Australian ecosystems reported some consequence of fire on the fungal community and these effects are elaborated on below. First, we discuss fungi that occur after fire, including consideration of both immediate post-fire (pyrophilous) fungi and also those that require long unburnt vegetation, as well as the effects of repeated fire on fungal communities. Second, we use the framework of trophic roles and substrates to discuss effects of fire on particular trophic groups, such as parasites, saprotrophs and mycorrhizal fungi, and interactions between fire, fungi and other organisms.

Effects of time since fire

Pyrophilous fungi

A suite of pyrophilous fungi produce fruit-bodies on recently burnt sites. Many of them are cosmopolitan and most typically fruit in the first and second years after fire, often in large numbers (Petersen 1970; Warcup 1981, 1990; Robinson 2001; Robinson *et al*. 2008; Claridge *et al*. 2009*a*). Concomitantly, on recently burnt sites, fruit-bodies are not produced by most fungi typical of mature vegetation. Fire can also stimulate the soil microbial community as indicated by colony counts in cultures of soil samples. In soil from dry sclerophyll woodland in South Australia, fungal colony counts decreased immediately after fire, but were significantly higher 2 months after fire in burnt compared with unburnt soil and remained so for at least 7 months (Theodorou and Bowen 1982). In other parts of the world, depending on fire intensity, microbial biomass may either decrease or increase (Cairney and Bastias 2007).

The first and most conspicuous fungi observed after fire in Australia are those that produce fruit-bodies from subterranean storage organs called sclerotia or pseudosclerotia (McMullan-Fisher *et al*. 2002; George 2008; Robinson *et al*. 2008; Robinson 2009). Fruit-bodies of the pyrophilous basidiomycetes *Neolentinus dactyloides*, *Laccocephalum mylittae*, *L. tumulosum* (Fig. 1*d*), *L. sclerotinium* (Fig. 1*f*), and an unnamed *Laccocephalum* species (Fig. 1*e*) are common in

Table 1. Studies of fungal communities in Australian ecosystems using sites of known fire history

Multiple studies on the same sites are grouped together. Fire ages with an asterisk are the frequency for sites that had undergone repeated burns

Vegetation type (dominant vegetation)	State	Sites (age since fire, in years)			Fungi groups studied		Sampling and identification techniques and/or estimation of fungal activity			Reference
		Fire 0–12 months	Fire >1–10 years	Mature	Trophic group	Morpho-logical group	Sample collection technique	Identification technique (method or scope)	Estimate of fungal activity (method)	
Wet sclerophyll forest (*E. obliqua* and/or *E. delegatensis*)	Tas.	–	–	+(25–30; >100)	All	EM	FB	MOR (SP)	–	**Packham *et al.* (2002)**
Wet sclerophyll forest (*E. obliqua*)	Tas.	+	+(3)	+(65–101)	L	L	FB	MOR (SP)	–	**Kantvilas and Jarman (2006)**
Wet sclerophyll forest (*E. obliqua*)	Tas.	+	+	+(73)	All	EM	FB	MOR (SP)	–	Gates *et al.* (2009)
Wet sclerophyll forest (*E. obliqua*)	Tas.	+	+(2–3)		All	EM	FB	MOR (SP)	–	*Ratkowsky and Gates (2009)*
Wet sclerophyll forest (*E. obliqua*)	Tas.	–	+(2–3)	+(70)	All	EM	FB	MOR (SP)	–	Gates *et al.* (2005)
Wet sclerophyll forest (*E. obliqua*)	Tas.	–	–	+(73, 109, 200–300)	All	EM	FB	MOR (SP)	–	Ratkowsky and Gates (2008), Gates *et al.* (2010*a*, 2010*b*)
Wet sclerophyll forest (*E. regnans*)	Tas.	+	+(2, 4, 7)	+(57)	All	EM	FB	MOR (SP)	–	**McMullan-Fisher *et al.* (2002)**
Wet sclerophyll forest (*E. regnans*)	Vic.	+(2 months)	+(14, 25 months)	–	M (ECM)	SF	SO	MOR (MG)	BA, BM (ERG)	*Launonen et al. (1999)*
Sclerophyll forest (*E. diversicolor*, regrowth forest)	WA	+	+	+(17–25)	All	EM	FB	MOR (SP)	–	**Robinson and Bougher (2003)**, **Robinson *et al.* (2008)**
Sclerophyll forest (*E. marginata*)	WA	+	+(6)	+(45)	M	SF	SC	MOR (MG)	RT	Malajczuk and Hingston (1981)
Sclerophyll forest (*E. marginata*)	WA	–	+(2–4)*	+(28–30)	All	EM	FB	MOR (SP), BM (WEI)	–	Tommerup *et al.* (2000)
Sclerophyll forest (*E. marginata*)	WA	–	+*	+	All	EM	FB	MOR (SP)	–	**Hilton *et al.* (1989)**
Sclerophyll forest (*E. marginata*, *Corymbia calophylla*)	WA	–	+(6–7)*	+(66)	M (ECM)	SQ, EM	FB	MOR (SP)	MOL (RFLP)	Glen *et al.* (2001)
Dry sclerophyll forest (*E. maculata*)	SA	+	+(2, 3)	–	All	EM (Disc)	FB	MOR (SP)	–	Warcup (1990)
Sclerophyll woodland (*E. cladocalyx*, *E. baxteri*)	SA	+	–	–	All	SQ, EM	FB	MOR (SP)	–	George (2008), Catcheside (2009), Catcheside *et al.* (2009), Robinson (2009)
Low open dry sclerophyll woodland (*E. baxteri*, *E. obliqua*)	SA	+(1, 2, 7 months)	+(12 and 20 months)	–	S	SF	SO, CU	MOR (MG)	–	*Theodorou and Bowen (1982)*
Dry sclerophyll woodland (*E. rossii*, *E. macrorhyncha*)	ACT	+	+(4)	+(21)	All	SQ, EM	FB	MOR (SP)	–	**Trappe *et al.* (2006)**
Woodland (*E. albens*, *Callitris glaucophylla*); riparian strips (*E. viminalis*), grassy or shrubby woodland (*E. melliodora*), woodland (*E. nortonii*) grading to open forest (*E. dalrympleana*)	NSW	+	+	–	All	EM	FB	MOR (SP)	–	Claridge *et al.* (2009*a*)

Sclerophyll shrubland (*Angophora hispida*)	NSW	+	+(8)	+	M (AM)	SF	SS	MOR (MG)	–	*Bellgard et al. (1994)*
Dry open sclerophyll forests (*E. gummifera*, *Syncarpia glomulifera*, *E. squamosa*, *E. resinifera*, *E. haemastoma*, *E. bauerana*, *Allocasuarina littoralis*, *Angophora hispida*)	NSW	+(2 weeks)	+(8, 10)	+(25)	All	SF	SO	MOL (RFLP, DNA)	–	Chen and Cairney (2002)
Sclerophyll forest (*E. pilularis*) and mixed eucalypt forest (*E. obliqua*, *E. rubida*, *E. radiata*)	NSW, Vic.	–	+(3, 10)*	+(>60)	All	SF	FB, SO	MOR (MG), MOL (IS, RFLP, T-RFLP)	BM (ERG)	**Osborn (2007)**
Sclerophyll forest (*E. pilularis*)	Qld	–	+(2*, 4*)	+(31–34)	S, M (ECM)	SF	SO, HI	MOL (DGGE, RFLP, T-RFLP, DNA, SIR)	BM (PLFA), GL, PO, IS	*Bastias et al. (2006a, 2006b), Anderson et al. (2007), Campbell et al. (2008), Artz et al. (2009)*
Sclerophyll forest (*E. pilularis*)	NSW	+(48 h)	–	+	S	MI (Tric)	CU	MOR (SP)	–	*McGee et al. (2006)*
Tropical *Allocasuarina* forest, *Eucalyptus* woodland and tropical rainforest	Qld	+	+(4–5)*	–	M (ECM)	SQ	FB, SP	MOR (SP)	BM (WEI)	*Vernes and Haydon (2001), Vernes et al. (2001, 2004)*
Tropical savannas	NT	+	+*	+	M (ECM and AM)	SF	SO, SS	MOR (MG)	BA	**Brundrett *et al.* (1996*a*, 1996*b*)**
Temperate grassland (*Themeda australis*, *Poa sieberiana*)	NSW	–	+(2, 4, 8)*	+	L	CS	FB	MOR (SP)	–	**O'Bryan *et al.* (2009)**
Tussock grassland and hummock sedgeland	Tas.	+(3 months)		+	L	L	FB	MOR (SP)	–	**Ferguson *et al.* (2009)**
Alpine woodland (*Eucalyptus pauciflora*, *E. dalrympleana*), tall wet sclerophyll forest (*E. regnans*, *E. fastigata*), dry sclerophyll forest (*E. mannifera*, *E. macrorhyncha*)	Vic. and NSW	+	+(>1–10)	+(11–20, 21–30, >30)	M (ECM)	SQ	FB	MOR (SP)	–	**Claridge and Barry (2000), Claridge *et al.* (2000*a*, 2000*b*), Claridge and Trappe (2004)**
Alpine heath	Tas.	–	–	+(39, 56)	All	EM	FB	MOR (SP)	–	**McMullan-Fisher *et al.* (2003)**
Mallee (*Callitris preissii* subsp. *verrucosa*)	NSW	+	+(3, 4, 7)	+(13, 16, 18, 35, 100)	L	CS	FB	MOR (SP)	–	Eldridge and Bradstock (1994)

References in **bold** are for studies that have replicated sites for all age classes, those in *italics* are for studies with replicated samples within unreplicated fire events. Abbreviations: Trophic group: All = all trophic groups except lichens, L = lichens, M = mycorrhizal fungi (ECM = ectomycorrhizas, AM = arbuscular mycorrhizas) and S = saprotrophs; Morphological group: CS = cryptogamic soil crusts, EM = epigeous macrofungi (Disc = Discomycetes), MI = microfungi (Tric = Trichocomaceae), SF = soil fungi and SQ = sequestrate macrofungi; Sample collection technique: CU = cultured, FB = fruit-body survey, HI = mycelium from hyphal ingrowth bags, SC = ectomycorrhizal root tips from soil sample, SO = bulk soil sample, SP = spores from scats and SS = spores from soil; Fungal identification technique: MOL = identification of taxa by molecular methods (method: DGGE = denaturing gradient gel electrophoresis, DNA = DNA sequencing and matching against sequence databases, RFLP = restriction fragment length polymorphism, SIR = substrate induced respiration; T-RFLP = terminal restriction fragment length polymorphism) and MOR = identification of taxa from morphology (scope: SP = mostly identified to species level taxa, MG = identified to broad morphogroups); Estimate of fungal activity: BA = Bioassay of extent of mycorrhizal colonisation of seedlings, BM = fungal biomass (method: ERG = ergosterol analysis, PLFA = phospholipid-derived fatty acids, WEI = weight of fruit-bodies), GL = genetic diversity of laccase genes, IS = isotopic analysis, PO = phenol oxidase activity, RT = counts of ectomycorrhizal root tips.

Fig. 1. (*a*) *Anthracobia muelleri*, a saprotrophic ascomycete. (*b*) *Geopyxis carbonaria*, a mycorrhizal ascomycete and fire moss *Funaria hygrometrica*. (*c*) *Peziza tenacella* a common mycorrhizal ascomycete after fire. (*d*) *Laccocephalum tumulosum* fruit-bodies appear immediately after fire. (*e*) *Laccocephalum* sp., a saprotrophic basidiomycete, showing pseudosclerotium. (*f*) *L. sclerotinium* showing sclerotia. Photographs (*a*), (*b*), (*e*) D. Catcheside; (*c*), (*d*), (*f*): R. M. Robinson.

both wet and dry eucalypt forests across southern Australia. These species are well adapted to fire and can develop large fruit-bodies as rapidly as 2 days after fire (Robinson 2001). Their mycelia decay logs and buried wood and subterranean sclerotia or pseudosclerotia develop under or adjacent to host logs (Wills 1983). It is not known how long it takes for these fungi to recolonise logs following fire or how long sclerotia take to mature to the stage where fruit-body development can occur.

The majority of pyrophilous macrofungi produce fruit-bodies in the first autumn following a spring or summer fire (Robinson *et al*. 2008). Several basidiomycetes fruit in the first year after fire including agaricoid (mushroom-like) decomposer fungi in the genera *Coprinus* (Fig. 2*a*), *Pholiota* and *Psathyrella* (Gates *et al*. 2005; Robinson and Tunsell 2007; Robinson *et al*. 2008; Catcheside *et al*. 2009; Claridge *et al*. 2009*a*). Most pyrophilous fungi, however, appear to be ascomycetes (Petersen 1970; Warcup 1990) of which some are mycorrhizal (Warcup 1990). Species of *Anthracobia*, including *A. muelleri* (Fig. 1*a*) and *A. melaloma*, and other ascomycetes produce abundant fruit-bodies over extensive areas and their mycelial mats may be important in minimising soil erosion following fires by aggregating soil particles (Claridge *et al*. 2009*a*).

A post-fire flush of ascomycetes is a global phenomenon (El-Abyad and Webster 1968*a*, 1968*b*; Petersen 1970, 1971; Wicklow 1975; Zak 1992; Cairney and Bastias 2007) and several Australian studies have reported an abundance of ascomycete fruit-bodies (Fig. 1*a–c*) associated with recently burnt sites (Warcup 1981, 1990; Gates *et al*. 2005; Robinson *et al*. 2008; Catcheside 2009; Catcheside *et al*. 2009). The causes have been widely investigated and include decreased competition from antagonistic soilborne taxa allowing post-fire germination of spores, heat stimulation of spore germination and tolerance to post-fire soil conditions such as increased pH (El-Abyad and Webster 1968*a*, 1968*b*; Petersen 1970; Wicklow 1975).

A direct and immediate effect of fire is soil heating, which can potentially kill mycelia and spores of fungi (Pattinson *et al*. 1999). However, certain fungi are adapted to being heated. For example, some species of Australian ascomycetes that produce fruit-bodies immediately after fire have been shown to germinate from resting spores in heat-treated soil (Warcup and Baker 1963). Similarly, various Trichocomaceae (including species of *Aspergillus*, *Eupenicillium* and *Penicillium*) were recovered from heat-treated and burnt bark from a variety of native plant species (McGee *et al*. 2006) as well as from heat-treated soil (Warcup and Baker 1963). Many pyrophilous fungi appear to be totally dependent on fire to stimulate spore germination and mycelial growth but some grow and fruit readily on both burnt and unburnt sites (Robinson *et al*. 2008).

Fungi that require long unburnt vegetation

In the northern hemisphere, there are several fungi, many of which are included in Rarity, Endangerment and Distribution lists, whose fruit-bodies are only associated with large well decayed logs in long undisturbed sites (Ing 1993; Berg *et al*. 1994; Odor *et al*. 2006). These fungi are probably not themselves sensitive to fire *per se* but are associated with substrates or microclimate that are most common in areas which have not been disturbed for a long time. In dry eucalypt forests of Australia, large, well decayed logs are more likely to be consumed by fire than undecayed logs (Hollis *et al*. 2008). In Victoria, fruit-bodies of *Hypocreopsis amplectens* (Fig. 2*c*, *d*) have been found predominantly in long unburnt, over-mature stands of Heath tea-tree, *Leptospermum myrsinoides* (Johnston *et al*. 2007). The rare lichen *Roccellinastrum flavescens* is found exclusively on leaves of *Arthrotaxis cupressoides*, a tree found in long unburnt areas in Central Tasmania (Kantvilas 1990, 2000). Some species in the ectomycorrhizal genus *Russula* were found more frequently in long unburnt Jarrah forests than in sites with a prescribed burn frequency of 6–8 years (Hilton *et al*. 1989; Glen *et al*. 1998, 2001).

Cool temperate rainforests in Tasmania and Victoria support large and diverse communities of macrofungi (Fuhrer and Robinson 1992; T. W. May, pers. obs.) and lichens (Kantvilas and Jarman 1993; Kantvilas 2000; Morley and Gibson 2004). Many are restricted to rainforest, either because they are ectomycorrhizal fungi strictly associated with the dominant *Nothofagus cunninghamii* (Fuhrer and Robinson 1992) or because they apparently prefer the cooler and moister microclimate generated by closed canopies. Thus, many fungi appear to rely on the lack of fire that allows rainforest to flourish. In wet eucalypt forest, mature (100–200 years) and over-mature (200–400 years) stands appear to be important for maintaining biodiversity, particularly wood-decay fungi that rely on large well rotted logs (Wardlaw *et al*. 2009). Fruit-body surveys in mature, long unburnt (~80 years) *Eucalyptus obliqua* forest on the Fleurieu Peninsula in South Australia yielded an unusually high diversity of macrofungi (Catcheside and Catcheside 2008). In *E. obliqua* forest in Tasmania macrofungal species assemblages differed between mature and 25–30-year-old regrowth forest regenerated following fire (Packham *et al*. 2002) and between very long unburnt plots and those burnt in 1934 and 1898 (Gates *et al*. 2010*a*, 2010*b*). In the latter study, the distinctiveness of the litter assemblage on sites of different age since fire was not so pronounced as for the soil and wood fungi. Overall, these studies suggest that long unburnt, wet eucalypt forests are important habitat for the fruiting of macrofungi. The degree to which species that preferentially produce fruit-bodies in long unburnt forest are present in recently burnt forest as vegetative mycelium or resting stages is unknown.

Effects of repeated fire

Despite the increasing use of prescribed burning across Australia, there is limited information on how fungi are affected by repeated burning in Australian ecosystems. The effects of repeated fire on fungi are difficult to test experimentally because the post-fire succession may extend over several or more years. Macrofungal communities in some eucalypt forests differ each year after fire for at least 5–7 years (McMullan-Fisher *et al*. 2002; Robinson *et al*. 2008), and little is known about the consequences of interrupting this succession before communities recover to their pre-fire composition. Ideally, sites of different fire history, including long unburnt controls, need to be burnt simultaneously and succession followed on each site to assess whether successional communities differ between treatments (Wittkuhn *et al*. 2010). Sites with different repeated fire regimes will have different species compositions at the end of their respective cycles but the key question is: are the changes permanent?

Results from the few studies on fungi and fire regimes are not consistent. In mixed eucalypt forests in Victoria, repeated low-intensity prescribed fire of 3- and 10-year cycles at different seasons (spring or autumn) had little effect on the richness and

Fig. 2. (*a*) *Coprinus angulatus*, a saprotrophic basidiomycete fruiting in the first year after fire. (*b*) *Pycnoporus coccineus*, a common saprotroph on fallen and standing timber. (*c*, *d*) *Hypocreopsis amplectens* growing on fallen branches of senescing *Leptospermum* in long unburnt woodland. (*e*) *Daldinia* sp. a semi-parasitic ascomycete fruiting on *Hakea* in the second year after fire. (*f*) *Mesophellia trabalis*, a truffle-like ectomycorrhizal fungus, excavated from soil at a recently burnt site; this species also fruits on unburnt sites. Photographs (*a*), (*b*), (*e*): D. Catcheside; (*c*), (*d*): T. W. May; (*f*): R. M. Robinson.

diversity of fungal communities as measured by T-RFLP profiling, nor on diversity of fruit-body morphotypes and trophic groups (Osborn 2007). In *E. pilularis* forests in New South Wales, ergosterol concentrations (a chemical measure of living fungal biomass) in the topsoil (0–5 cm) from frequently burnt (every 3 years) sites were, on average, 35% lower than in soil from long unburnt (45 years) sites; but because of considerable within-treatment variability the differences were not significant (Osborn 2007). In *E. marginata* forest in south-western Australia, in terms of fruit-body yield, a long unburnt site had fewer decomposer and more mycorrhizal fungi than a site which was burnt every 10 years (Tommerup *et al*. 2000) and long unburnt sites also had more ectomycorrhzal root tips (Glen *et al*. 1999). In the same forest type, in the only study where all treatments (including controls) were sampled at the same time (4 and 5 years) since fire, the composition of macrofungal communities on sites with repeated fire at short ($\leq$5 yrs) intervals differed from those on sites that had long ($\geq$10 years) intervals between fire; but neither differed significantly from communities on sites with moderate (6–9-year) fire intervals (Wittkuhn *et al*. 2010).

In *E. pilularis* forest at Peachester State Forest in Queensland, several studies have utilised molecular characterisation of soilborne fungal communities and determination of basidiomycete enzyme activity and cellulose utilisation with respect to 2- and 4-yearly repeated fire regimes and unburnt (since 1972) controls (Bastias *et al*. 2006*a*, 2006*b*, 2009; Anderson *et al*. 2007; Campbell *et al*. 2008; Artz *et al*. 2009). While species richness was similar across the treatments, community composition was altered by repeated burning and the effect was greatest in the biennially burnt treatment (Anderson *et al*. 2007). Similarly, the community of ectomycorrhizal fungi in samples from the upper 10 cm of soil from burnt plots differed from long unburnt plots, but at the 10–20-cm depth there was no difference (Bastias *et al*. 2006*a*). Biomass of both fungi and bacteria were reduced by 50% on plots burnt at 2-year intervals compared with the 4-year interval and long unburnt plots (Campbell *et al*. 2008) and there were fewer active cellulolytic fungi in the biennially burnt plots (Bastias *et al*. 2009). Phenol oxidase activity due to saprotrophic fungi also decreased, but not significantly, with increased fire frequency but the community of basidiomycete laccase genes from frequently burnt plots was more diverse and more even than that from the long unburnt plots (Artz *et al*. 2009). Observations from 'green islands' within sites burnt every two years were included by Bastias *et al*. (2006*a*, 2006*b*) to demonstrate that the most recent fire on the 2-year sites was patchy and of low intensity and thus the short-term effect of fire was similar on both 2- and 4-year sites and was not confounding the long-term effects. However, as with most other studies discussed in this section, the post-fire fungal succession was not followed throughout its course on all treatments (including unburnt controls). Ideally, intensive documentation of fungal communities after fire should be complemented by longer-term studies of succession across all treatments.

For biological soil crusts, which include lichens, responses to fire frequency vary with vegetation type. In mallee woodland, fire frequencies of less than 10 years alter soil crusts to favour algal-dominated crusts and lichen composition was highest when time since fire was between 13 and 35 years (Eldridge and Bradstock 1994). In contrast, in temperate grassland lichen cover was found to be greatest on sites burnt every second year (O'Bryan *et al*. 2009).

Fire frequency affects vegetation composition through effects on propagules. For plants, species that rely on seed production for post-fire recruitment will be eliminated when the time between fires is shorter than the time required for recruitment, maturation and replacement of the seed store before the next fire (Ooi *et al*. 2006; Yates *et al*. 2008; Watson *et al*. 2009). Recovery of fungal biomass after fire requires either regeneration of existing communities from surviving spores or mycelia or recolonisation from surrounding unburnt areas (Bruns 1995). Indirect effects of fire on soil, such as loss of nutrients through erosion and leaching, change in water repellence, greater absorption of heat by blackened soil surfaces and loss of the shading cover of vegetation (Gochenaur 1981), will also affect recolonisation by soil fungi.

Little is known about the dynamics of the 'bank' or store of fungal propagules, which includes spores, hyphal fragments and resting structure such as sclerotia. Fungal propagules such as spores may survive independently of hosts. Data on the longevity of ascomycete spores in soil are available (Warcup and Baker 1963; El-Abyad and Webster 1968*a*; Warcup 1981) and research on spore banks in North American conifer-grassland communities suggests that spores of the truffle-like *Rhizopogon* can persist for up to 20–30 years (Kjoller and Bruns 2003; Izzo *et al*. 2006). Some fungi may also survive within or in association with host tissue, such as in mycorrhizas. Hyphae that remain associated with roots may survive better than those that are not (Pattinson *et al*. 1999). Propagules at greater depths will be less affected by heating from fire but the relative colonising potential of propagules at different depths is unknown. Some macrofungi develop underground storage organs that allow fruiting after fire, but we know little about the time they take to develop and mature, or how long they persist before production of fruit-bodies is triggered by fire (Robinson *et al*. 2008).

Other factors that could influence recolonisation by fungi after fire include the size of disturbance – a large burnt patch may make recolonisation from spores more difficult compared with a small patch. The age of the vegetation (and the corresponding stage of succession in the fungal community) around a burnt site may also be critical, as could be the intensity with which a patch burns. In addition, recolonisation by fungi that require vectors such as mammals may be affected by changes in the abundance and movements of the vectors. All these factors remain to be tested experimentally.

The effect of fire on different trophic and substrate groups of fungi

The variation in physiology and ecological roles among fungi and the range of substrates and mutualistic partners mean that different trophic and substrate or host groups merit separate consideration when considering the effects of fire on fungi. This is because fire may have quite different effects on the genesis and consumption of substrates for fungi on the one hand and on the growth and survival of mutualistic partners on the other hand. Consideration of the functional significance to other biota of fire-mediated changes to fungal communities will also be facilitated by discriminating the different trophic functions of fungi (Cairney and Bastias 2007).

Saprotrophic fungi

Saprotrophic fungi decompose dead organic matter including dead wood on live trees, coarse woody debris (CWD) and litter on the forest floor, as well as some materials of animal origin. The process of decay and decomposition of wood and other substrates is facilitated by the succession of specialist fungi. Some saprotrophic fungi are host specific while others can utilise a wide range of hosts. In addition, many are substrate specific and prefer wood of a particular size or stage of decay (Boddy 1984; Spooner 1987).

On living standing trees, high intensity fires cause scars that act as entry points for decay-causing and pathogenic fungi (Parmenter 1977; Abbott and Loneragan 1983; McCaw 1983). Some decay fungi are important in the development of habitat for other organisms, including invertebrates and small reptiles and for generating nesting hollows for birds and animals (Kile and Johnson 2000; Hopkins *et al*. 2005). Alternatively, trees may become stressed or weakened, making them more susceptible to attack from root and canker pathogens (Parmenter 1977) or they may be killed, creating new habitat for wood decay fungi (Penttilä and Kotiranta 1996) either as standing dead trees or fallen log and branch material. In Finland, 65% of polypore and corticioid fungi recorded on dead standing spruce trees before a high intensity fire were not found after the fire, with species colonising dead trees in an advanced stage of decay being the most affected. However, 46% of species recorded post-fire were not recorded before the fire because the disturbance reduced competition or provided new substrates in the form of freshly fallen trees and branches for the establishment of early colonisers (Penttilä and Kotiranta 1996).

Consideration of CWD in forest management has recently been recognised as important because of its role in long-term nutrient cycling, maintenance of biodiversity, carbon storage, moisture retention, tree health, forest structure and habitat for fauna and fungi (Grove *et al*. 2002). Saprotrophic fungi are important in CWD decomposition (Grove and Meggs 2003; Mackensen *et al*. 2003) which involves a succession of fungal species (Dix and Webster 1995; Boddy 2001). Many saprotrophic fungi that colonise CWD have specific associations with size, wood type, decomposition stage or moisture level (Johnston 2001; McMullan-Fisher *et al*. 2002; Grove and Meggs 2003; Berg and Laskowski 2006; Wardlaw *et al*. 2009; Gates *et al*. 2010*b*).

Timber harvesting, silviculture practices and firewood collection impact on the amount and quality of CWD which in turn affects species and communities dependent on large diameter logs including saproxylic (wood-inhabiting) invertebrates and fungi (Huston 1996; Jonsson *et al*. 2005; Wardlaw *et al*. 2009). Fire can reduce the total amount of CWD and alter its characteristics (Robinson and Bougher 2003; Hollis *et al*. 2008). Alternatively, fire can increase heterogeneity of CWD by altering decay processes, changing microclimates and by generally increasing the diversity of species which contribute to the woody debris pool (Grove *et al*. 2002). Fire is a key cyclic disturbance that kills trees, thus contributing to the production of CWD in forests.

Intense fires may reduce the amount of CWD on the forest floor and impact significantly on species of fungi that colonise and decay dead wood (Penttilä and Kotiranta 1996; Robinson *et al*. 2008). In regrowth Karri forest in Western Australia, the number of species fruiting on wood was shown to be significantly lower for 3 years following an intense wildfire, but after 5 years species richness had increased and was higher than on comparable unburnt sites (Robinson *et al*. 2008). Other studies have shown similarly decreased species richness of fruit-bodies of wood-inhabiting macrofungi on more recently (2–5 years) burnt sites (McMullan-Fisher *et al*. 2002; Gates *et al*. 2005).

Litter is composed of dead leaves and fine woody material from plants. The time since last fire is particularly relevant when studying fungal communities as litter is generally consumed by fire. Short-term loss of litter-decomposing macrofungi after fire has been reported for several Australian ecosystems (McMullan-Fisher *et al*. 2002; Robinson *et al*. 2008) and elsewhere (Berg and Laskowski 2006). In *E. marginata* and *E. diversicolor* forests in Western Australia, fruit-bodies of litter-dwelling fungi such as *Mycena* and *Marasmius* appear as soon as 2 years after fire, while other genera, such as *Entoloma*, did not fruit until an organic layer had formed below the litter layer (Robinson *et al*. 2008). Litter-dependent fungi in *E. regnans* forest in Victoria did not fruit until after the canopy had closed; 7 years after fire (McMullan-Fisher *et al*. 2002). Such differences will be related to the rate of accumulation of litter after fire which depends on fire intensity and varies significantly across forest types and ages (Ashton 1975; McCaw *et al*. 1996, 2002; Department of Sustainability and Environment 2003). Production of fruit-bodies is also influenced by microclimate, season, canopy development, tree health and other factors. Fires reset or interrupt the succession of litter–decomposing fungi and studies from a range of eucalypt forests (McMullan-Fisher *et al*. 2002; Gates *et al*. 2005; Robinson *et al*. 2008) suggest that it may take 5–10 years for litter-dwelling macrofungal communities to recover and produce fruit-bodies present in the pre-fire community.

Litter saprotrophs may be influenced indirectly by fire due to restricted associations with plant hosts whose presence is reduced or enhanced by fire. For example, on Mt Wellington in Tasmania, fruit-bodies of an unidentified discomycete were restricted to litter produced by *Orites acicularis*, a plant whose cover was significantly more abundant on sites burnt 56 years previously compared with sites burnt 39 years previously (McMullan-Fisher *et al*. 2003). Conversely, there may well be fungi restricted to plants that are favoured by fire.

All above-mentioned studies in this section utilised sampling of fruit-bodies from wood or litter. An alternate approach is to measure decomposition activity through substrate or gene assays. Bastias *et al*. (2009) amended soil with ^{13}C labelled cellulose, and compared soil fungal communities that did and did not utilise cellulose, by stable isotope probing in combination with DGGE. In a comparison of long unburnt and regularly burnt (every 2 years) sites in *E. pilularis* forest, they conclude that the diversity of cellulolytic fungi was reduced by repeated burning. On the same sites, Artz *et al*. (2009) found that repeated burning caused a significant shift in the basidiomycete laccase-encoding gene pool. Laccases are involved in the breakdown of wood, although they may also be produced by some ectomycorrhizal fungi.

Parasitic and endophytic fungi

Parasitic fungi, most of which are microfungi, are highly diverse because they are often host-specific at the species, genus or family level. Despite this high diversity, little is known of the ecology of native parastiic fungi, especially in relation to fire. There is a post-fire (3–5 years) increase in fruiting of semi-parasitic ascomycetes such as *Daldinia* spp. (Fig. 2*e*) and *Hypoxylon* spp. (Gates *et al*. 2005; Robinson *et al*. 2008). These fungi live within the wood of healthy understorey trees and shrubs and rapidly form macroscopically visible fruit-bodies after the host plant has been weakened or killed by fire (Robinson *et al*. 2008). For the numerous parasitic microfungi that cause cankers and leaf-spots on native plants in Australia there is no information available about the effect of fire. Many healthy plants contain endophytic fungi, some of which may become parasites or saprotrophs when the plants become weakened by stress or die. Again, information on the response of such species to fire is lacking.

Information on interactions between parasitic fungi and fire in Australian ecosystems is mostly limited to studies about control of two high profile root pathogens. In an attempt to control dieback disease caused by Cinnamon fungus, *Phytophthora cinnamomii* (a fungoid member of the Chromista), high intensity fire was successfully trialled in Jarrah forest in Western Australia (Shea *et al*. 1979). The spread of the pathogen was reduced through promotion of a resistant leguminous understorey. High intensity fire may also be detrimental to the root pathogen *Armillaria luteobubalina* as fire has the potential to destroy the outer sapwood of stumps and to burn tree buttress and lateral roots on which the fungus would normally survive (Kile 1980, 1981). Ironically, the increased accumulation of fuel caused by such parasitic fungi may promote fire (Robinson and Bougher 2003).

Mycorrhizal fungi

Mycorrhizal fungi associate with the fine roots and occasionally with other underground structures of plants and facilitate exchange of nutrients between plant and fungus (van der Heijden and Sanders 2002; Brundrett 2004; Cairney 2005). They can also help to protect plants against some pathogens (Zak 1964; Marx 1972) and increase tolerance to environmental stress such as drought (Tommerup and Bougher 2000). Several different types of mycorrhizas are known including ectomycorrhizas (ECM), arbuscular mycorrhizas (AM, formerly known as vesicular arbuscular mycorrhizas, VAM), ericoid mycorrhizas and orchid mycorrhizas, each association formed by particular groups of fungi and plants and each with a characteristic structure. Apart from a few families, notably the Proteaceae, most vascular plants and some liverworts form mycorrhizas of one sort or another. Surveys of a variety of Australian ecosystems with *Eucalyptus* or *Angophora* overstoreys detected mycorrhizas in 66–96% of the plant species present, with AM being the most common type (Brundrett *et al*. 1996*a*; May and Simpson 1997).

Arbuscular mycorrhizal fungi are probably the most widespread and common mutualistic fungi. Their responses to fire have been shown to be quite variable but fire usually impacts negatively (Hart *et al*. 2005; Cairney and Bastias 2007). In an open sclerophyll shrubland in New South Wales, spores of AM declined in abundance immediately after fire, although no long-term effect on infectivity and spore abundance was recorded (Bellgard *et al*. 1994). In tropical savannah woodlands in the Northern Territory, inocula of fungi that form AM did not seem to be affected by fire intensity (Brundrett *et al*. 1996*a*, 1996*b*). Pattinson *et al*. (1999) suggest that it is the loss of the mycelial network after fire rather than modifications to inoculum potential which drives post-fire reductions in AM. Given that early seedling development may well depend on arbuscular mycorrhizal fungi (Adjoud-Sadadou and Halli-Hargas 2000), such disruption to the mycelia network may be important in the development of the post-fire plant community (Bellgard *et al*. 1994; Pattinson *et al*. 1999).

Ectomycorrhizas are common in eucalypt forests and woodlands (Dell 2002). Ectomycorrhizal roots predominate in the top 10–20 cm of soil and in leaf litter (Bastias *et al*. 2006*a*) and can be impacted significantly, at least in the short term, by prescribed burning (Chen and Cairney 2002). Several studies have noted a predominance of fruit-bodies formed by ectomycorrhizal fungi in mature forest compared with recently burnt (2–3 years) sites (Glen 2002; Gates *et al*. 2005). Once forests have matured, the species richness of macrofungi that form ECM is similar in forests of different ages, although individual fungal species may favour forest stands of a particular age (Packham *et al*. 2002). Furthermore, preferences for host plants by ectomycorrhizal fungi may affect plant communities (Allen *et al*. 1995). For example, host generalist ectomycorrhizal fungi facilitate seedling establishment in late succession forests but fire-dependent tree species such as *Pomaderris apetala* and *E. regnans* may competitively exclude each other through the low compatibility of their respective ectomycorrhizal fungi (Tedersoo *et al*. 2008).

In Jarrah forest, the number of mycorrhizal roots on trees was dramatically reduced following removal of litter and soil organic layers by fire (Reddell and Malajczuk 1984) and subsequent recovery was related to time since fire and litter accumulation (Malajczuk and Hingston 1981). In *E. pilularis* forest, the community of ECM in the upper soil from burnt plots differed from long unburnt plots (Bastias *et al*. 2006*a*). Seedlings of *E. maculata* grown in heat-treated or untreated soils all had abundant mycorrhizal associations, but those grown in heat-treated soils had lower diversity and different types of mycorrhizas (Warcup 1983). Similarly, the frequency of ECM and the growth of *E. regnans* seedlings were greater in burnt black soil when compared with unburnt soil, which was attributed to changes in soil nutrition and the presence of different ectomycorrhizal fungi (Launonen *et al*. 1999). In tropical savannah woodlands in the Northern Territory, for sites that had hot annual fires, ectomycorrhizal fungi were restricted to infrequent patches in the surface horizon and in unburnt sites the inocula of ectomycorrhizal fungi were more frequent (Brundrett *et al*. 1996*a*, 1996*b*).

Mycelia of most ectomycorrhizal fungi grow in the upper organic layer of the soil. However, CWD may house a range of ectomycorrhizal fungal mycelia, particularly when associated with seedlings of trees such as *Nothofagus cunninghamii* (Tedersoo *et al*. 2009*a*). In addition, some ectomycorrhizal fungi in the Thelephoraceae produce their fruit-bodies on CWD (Tedersoo *et al*. 2003). This suite of ectomycorrhizal fungi will be particularly sensitive to changes and/or loss of CWD after fire.

Orchids are particularly dependent on their fungal symbionts for survival (Rasmussen 1995; Smith and Read 2002; Dearnaley and Le Brocque 2006). Fire stimulates the flowering of some terrestrial orchids such that declining populations may need regular disturbance by fire to maintain their on-going viability. For other terrestrial orchids, fires that occur too frequently have a negative impact on populations, presumably due to the effect of fire on fungal symbionts as well as on the host plants (Brundrett 2007). High fire frequency has been shown to reduce the number of epiphytic orchids in tropical savannah both directly and indirectly due to decreased numbers of host trees on burnt sites (Cook 1991). Many orchid species are listed as being 'threatened' and altered fire regimes are considered to be one of the causes for this status. An understanding of the ecology of the fungal symbionts of orchids has an important role in promoting orchid conservation (Brundrett 2006). Ericaceae, which are partners in ericoid mycorrhizas (Cairney and Burke 1998; Chambers *et al*. 2008), are common plants in Australian woodlands and heathlands, but there is no information on the response of their mycorrhizal fungi to fire.

Lichenised fungi

Lichenised fungi often have strong associations with particular substrates and habitats (Brodo 1973; Brodo *et al*. 2001). When fires modify microclimatic and substrate conditions, lichen communities are often greatly altered, particularly as few lichens survive fire and are slow to recover (Stevens 1997). Lichens are so sensitive to changes in vegetation occurring over time since fire that they have been used as bio-indicators for determining the age of *cerrado* vegetation in central Brazil (Mistry 1998). However, where knowledge about distribution and ecology is limited, care needs to be taken when assigning indicator species. For example, two lichens which were thought to be indicators of old growth wet sclerophyll forest in Tasmania (Kantvilas and Jarman 2004), were later found to be common on recently burnt sites (Kantvilas and Jarman 2006). In the latter study, which surveyed wood- and tree-dwelling lichens, the post-fire lichen community was dominated by common cosmopolitan species and drier climate specialists and species changes were attributed to the different microclimate and habitat characteristics after fire (Kantvilas and Jarman 2006). Several rare lichens are limited to rainforests where fire has not been present for 100–500 years (Kantvilas and Jarman 1993; Rogers 1995; Kantvilas 2000; Morley and Gibson 2004).

Soil lichens are a component of biological soil crusts that are particularly important in arid and semiarid ecosystems because of their role in preventing soil erosion (Eldridge 2003). Soil crusts tend to be damaged by extreme disturbances such as high intensity fires (Eldridge and Bradstock 1994; Eldridge 1996; Eldridge and Tozer 1997), but local species richness may be maintained with lower impact disturbances (Eldridge *et al.* 2000, 2006; O'Bryan *et al.* 2009). In Tasmanian tussock grassland, cover and abundance of soil cryptogams in general were found to remain high after a fuel reduction fire (Ferguson *et al.* 2009). In contrast, soil crusts in the mallee region were dominated by algae on sites burnt less than 10 years previously while lichen cover and composition was highest 13–35 years after fire (Eldridge and Bradstock 1994). Lichen species and communities are rarely included in studies on fire ecology in Australia and further research on their fire responses is required across a range of ecosystems.

Fire and fungal-faunal interactions

Fungi-invertebrate interactions

Despite the prevalence of larvae and adults of many invertebrates utilising macrofungal fruit-bodies for habitat and food, there is only limited information about the interactions of invertebrates with fungi and the effect that fire may have on these relationships (Wardle *et al*. 2004). Frequent fire has recently been shown to disrupt the nature of fungal-invertebrate interactions in leaf litter leading to substantial changes in rates of decomposition (Brennan *et al*. 2009). Belowground, larger organisms such as earthworms, mites and collembola (springtails) are likely to be involved in transport of spores (Brown 1995; Dighton *et al*. 1997; Dighton 2003; Dromph 2003). Fire can reduce the abundance of these and other soil- and litter-dwelling invertebrates (Neumann 1991; Neumann and Tolhurst 1991; Collett *et al*. 1993; York 1999). Grazing of soil-borne mycelia by invertebrates including collembola, mites and nematodes can influence fungal biomass and community composition (Dighton 2003). This could have flow-on effects on leaf litter decomposition and the efficiency of mycorrhizas to facilitate nutrient uptake of host plants (Hanski 1989; Shaw 1992; Brennan *et al*. 2009). Preferential grazing by collembola can affect interactions between fungi that form AM and saprotrophic fungi (Tiunov and Scheu 2005). A single low intensity fire was shown to alter the abundance and composition of collembolan communities (Greenslade 1997) and long-term frequent burning can reduce collembolan numbers by more than half (York 1999). These changes may alter nutrient availability and in turn alter plant growth and vigour and community structure.

Fungi–vertebrate interactions

The interactions of fire, fungi and mycophagous animals are complex. Many native Australian animals consume fruit-bodies of hypogeal truffle-like and some epigeal fungi. Spores are subsequently dispersed in scats, sometimes a considerable distance away, where they germinate and form mycorrhizas with trees or shrubs (Claridge and May 1994; Blaney 1996; Johnson 1996; Vernes 2009; Vernes and Dunn 2009). As a result of digging for hypogeal fruit-bodies, soil aeration and water incursion are enhanced (Garkaklis *et al*. 2000, 2003), and consequent changes to soil surface topography assist seed settlement and establishment. It has been suggested that the loss or reduction of mycophagous animal populations may have a deleterious impact upon the long-term health, viability and diversity of truffle-like fungi, and consequently on soil structure and nutrient cycling and eventually mycorrhizal plant communities (Claridge 2002), although exotic rodents such as *Rattus rattus* may also disperse fungal spores (Vernes and McGrath 2009).

The focus of considerable research has been on mitigating the effects of fire on mycophagous animals and their habitat (Catling 1991). However, there are still large gaps in the understanding of interactions among mammals, fungi, fire events and vegetation development. In the only comprehensive longitudinal study of the ecology of truffle-like fungi (Claridge *et al*. 2000*a*, 2000*b*), fruiting of some individual species was shown to be influenced by many factors, including the time since fire, climatic variables such as temperature and moisture levels, topographic position, geology, soil fertility, depth of litter, diversity of mycorrhizal hosts and abundance of mycophagous animals. Two taxa, *Cortinarius globuliformis* and *Mesophellia trabalis* (Fig. 2*f*), decreased in occurrence with increasing time since fire (Claridge *et al*. 2000*a*). However, subsequent studies showed that *C. globuliformis* was dominant on unburnt sites whereas *M. trabalis* appeared on both burnt and unburnt sites and fruit-body production of both species was influenced by many other environmental factors (Claridge and Trappe 2004; Claridge *et al*. 2009*b*).

In regard to the community of truffle-like fungi, studies in the Australian Capital Territory and New South Wales demonstrated that prescribed burning decreased the overall diversity and abundance of fruit-bodies of truffle-like fungi (Claridge *et al*. 2000*a*; Trappe *et al*. 2006). Conversely, several Tasmanian and Queensland studies suggest that prescribed burning may stimulate the fruiting of some species of truffle-like fungi (Taylor 1992; Johnson 1994, 1997; Vernes *et al*. 2004). Comparison and interpretation of studies relating fire and truffle-like fungi should be undertaken carefully as survey methods can differ greatly and fungal communities should not be assumed to be similar in different ecosystems (Claridge and Trappe 2004; Trappe *et al*. 2005, 2006).

Mycophagous macropods and rodents are likely to be critical for dispersal of fungal spores into disturbed habitats as well as across the mosaics of vegetation types and ages that exist in many Australian landscapes (Vernes and Trappe 2007; Vernes and Dunn 2009; Vernes and McGrath 2009). Investigation of the foraging habits of mycophagous animals before and after fire showed that they foraged preferentially on burnt ground and frequently moved between burnt and adjacent unburnt habitat (Johnson 1994, 1996; Vernes and Haydon 2001; Vernes and Trappe 2007). Exclusion of small animals from plots in Queensland rainforest resulted in lower seedling colonisation and an altered community composition of AM (Gehring *et al*. 2002). Comparable studies would be instructive to determine the response of truffle-like fungi in fire-prone forests when mycophagous mammals are excluded.

Future directions for research and management in relation to fire and fungi

Fungi are clearly relevant to research programs on fire in ecosystems, because of their direct roles and interactions with other biota. Providing clear management recommendations is currently hampered by the lack of comparability among existing studies and the many gaps according to geography, habitat type and ecosystem (especially for grasslands, arid and alpine environments, and northern Australian savannahs). There is also a lack of information for the full range of fungal taxonomic and trophic groups. It is not practicable to sample all fungi in every ecological study. However, it would assist to have comprehensive data on the taxonomy, biology and ecology of selected groups of fungi representative of phylogeny and trophic mode as candidates for surveys. As well as a sound taxonomic underpinning, autecological data for such selected groups, such as in relation to life history characteristics (e.g. size of individuals, longevity of spores and mycelia, recolonisation strategies) and host, habitat and substrate specificity, would assist greatly in interpreting observations of fungi and fire. Further practical challenges for studies of fire and fungi are the inclusion of fungi in monitoring programs and the integration of molecular and morphological data.

Fungi in monitoring programs

Greater understanding of the effect of fire on fungi relies on generation of substantial datasets. Ideally, fungi should be integrated into established monitoring and survey projects to achieve this. At present, the Department of Environment and Conservation (DEC) in Western Australia is the only land management agency in Australia that includes fungi in permanent monitoring programs. DEC has a permanent fungal ecologist on staff with support staff to undertake monitoring and research in programs and projects including FORESTCHECK (Abbott and Burrows 2004) and the Walpole Fire Mosaic (WFM) project (Burrows 2006). The focus is on macrofungi, and more than 750 species are currently recognised, many of which are newly recorded or yet to be formally described.

FORESTCHECK (see: http://www.dec.wa.gov.au, accessed 10 December 2010) was initiated in 2001 as an integrated, long-term, landscape-scale program devised to record and monitor the status and response of key forest organisms and communities to both forest management activities and natural variation (Abbott and Burrows 2004). The WFM project was initiated in 2005 to test the notion that fine-grained mosaics, representing various patches of vegetation at different post-fire seral stages, burnt at varying intensities and different seasons, across a landscape can reduce the severity of wildfires as well as be beneficial to the maintenance of biodiversity (Burrows 2006). Macrofungi have been included in both these projects, through fruit-body surveys, leading to a significant increase in knowledge of how macrofungal communities and key species respond to fire in southern eucalypt forests (Robinson 2001, 2006; Robinson and Bougher 2003; Robinson and Tunsell 2007; Robinson *et al*. 2008). Ongoing review of survey methods has also provided techniques that allow monitoring of this traditionally difficult group of organisms to be undertaken in a consistent and cost-effective manner.

There is clearly an urgent need to include fungi in current and planned long-term monitoring programs in relation to the effect of fire across Australia. The taxonomic scope of surveys needs to be widened to cover not only macrofungi, but also the highly diverse and ecologically important leaf-inhabiting parasitic microfungi, endophytes and saprotrophic soil microfungi. Where it is not practical to comprehensively survey for all fungi, consideration should be given to surveying for subsets of readily identifiable taxa representative of trophic, phylogenetic and morphological groups, particularly in adaptive management systems.

Integration of information relating to the fungal community

Collection of information about fungi is particularly difficult as fungi usually reside within their host or substrate, and survey and identification methods vary depending upon whether reproductive structures or symptoms are present or not. Recent studies adopt two quite different approaches. On the one hand, fruit-body surveys allow compilation of inventories across a range of sites, but do not fully recover the species present because of species not fruiting at the time of survey or ever. On the other hand, molecular methods allow a snapshot of all species present, but usually do not identify the particular species involved.

Currently, there is poor integration between the molecular characterisation of known taxa and sequences that are being isolated from environmental samples such as ectomycorrhizal root tips or bulk soil samples. The main problem is a lack of sequence data from authoritatively named material from Australia, which in the first instance usually requires sampling of fruit-bodies or cultures. In the long term, it is essential to have local, accurate and comprehensive barcode databases backed up by voucher material. In the meantime, at the least, it would be useful to have target groups across phylogenetic and functional groups for which the taxonomy (species limits) is reasonably worked out. A barcode library for such targets can then be the basis for molecular identification of at least a substantial subset of environmental samples.

For fruit-body surveys, different studies are poorly integrated with respect to a standard taxonomic framework. While some common and readily recognisable species appear in species lists from across Australia, many collections included in inventories are assigned tag or field names or are not identified to species at all. While tag names can be used consistently within surveys, it is not possible to match them up across different studies without time-consuming examination of voucher material (where this is available). Improved documentation of the distinctive characters of taxa to which tag names have been assigned would assist but, in the end, comprehensive taxonomic revisions are the best way to provide reliable names to species encountered in ecological surveys. Molecular identification of fruit-bodies will also be possible once comprehensive barcode libraries are available.

At present, no one method precisely characterises the fungal community in soil or other substrates. Even when different methods are used in combination there are many fungi that remain unculturable, unrecognisable, unidentifiable or difficult to quantify. The choice of sampling and identification methods often comes down to the resources and funding available within an organisation. Additional information on the cost-effectiveness and accuracy of different methods of isolation and identification would assist in the choice of appropriate survey techniques and identification protocols.

Significant data on fungi and their responses to fire currently reside in unlinked datasets, such as databases and other material held by state management agencies and research institutions, and in unpublished reports and studies by fungal interest groups. A meta-analysis of such data would significantly increase understanding of the distribution, host and habitat associations and responses to fire of individual species of fungi.

Management of fire for fungi

Mosaic burning is becoming an established means of managing fire and biodiversity at the landscape scale (Grove *et al*. 2002; Bradstock 2008; Burrows 2008). Several studies are now under way in the south-west of Western Australia to investigate the effect of fire regimes on the diversity of Jarrah forest biota, including fungi (Burrows 2006; Wittkuhn *et al.* in press). Fire is thought to increase small-scale heterogeneity of fungal communities (Friese *et al*. 1997) and results to date in Western Australia indicate that fire mosaics contribute to maintaining diversity of macrofungi (Robinson 2006; Robinson *et al*. 2008).

In management strategies for the use of prescribed fire in relation to conservation of biodiversity that are currently being developed in Victoria and Western Australia, fire intervals are based on 'vital attributes' (i.e. life history characteristics) of plant species and habitat preferences for endangered animals (Fire Ecology Working Group 1999; Burrows 2008). Some knowledge exists of the seral stages favoured by different fungal species (McMullan-Fisher *et al*. 2002; Ratkowsky 2007; Robinson *et al*. 2008), but there is limited understanding of the biology governing these preferences and distributions. In addition, fire may affect fungi in different ways at different stages in their life cycles. For example, in sclerotia-producing macrofungi, such as *Laccocephalum*, reproduction through fruit-body production is stimulated by fire, but frequent burning may have a negative impact because of the requirement during the vegetative phase for larger logs characteristic of long unburnt sites (Grove and Meggs 2003). Fungi should be incorporated into management schemes that use vital attributes, and collection of the necessary data made a priority.

As an interim measure, the close correlation of substrate condition (including quality and quantity) with time since fire suggests that management of substrate diversity in different vegetation types may be an appropriate approach while specific requirements of fungi are being investigated. In Australian forests, differences in species richness and fungal assemblages at different times since fire have been linked to the availability of suitable substrates (Tommerup *et al*. 2000; McMullan-Fisher *et al*. 2002; Packham *et al*. 2002; Gates *et al*. 2005; Robinson *et al*. 2008; Gates *et al*. 2010*a*, 2010*b*). In the northern hemisphere, a link has been demonstrated between species rarity and loss of suitable substrates (Berg *et al*. 1994; Jonsson *et al*. 2005; Raphael and Molina 2007). The retention and maintenance of a diverse range of substrates within the landscape has been highlighted as important for the conservation of fungi and other organisms in Australian forests (Grove and Meggs 2003).

Conclusions

Fire impacts directly on all elements of the biota, including fungi, as well as indirectly by inducing changes in soil structure, and water and nutrient availability and cycling. Fire ecology is acknowledged as complex and highly variable, with responses of particular species usually dependent on site and species characteristics. Not surprisingly, the effects of fire on fungal species and communities are also complex, but are less well understood than for vascular plants. This review highlights that the effects of fire are often multifaceted with abiotic and biotic interactions often mediated by particular trophic groups of fungi. These interactions are epitomised by the complex relationships among fire, vascular plants, mycorrhizal fungi and mycophagous mammals.

Fungal habitats and substrates are lost, modified or created by fires, and the degree of change depends on fire intensity, fire regime and the age and type of vegetation on site. Short-term effects include sterilisation of upper soil layers, increased pH and reduction or loss of host plants, litter and small woody debris. In the longer term, other elements such as standing dead wood and CWD may be consumed or initiated by fire.

Based on their importance in ecosystems as symbiotic partners, decomposers, nutrient cyclers and as a food resource for vertebrates and invertebrates, fungi should be included in land management decisions. However, an improved understanding of the functional roles of fungi, the effects of fire on fungi and the post-fire interactions between fungi and biotic and abiotic components of ecosystems is needed to help managers make informed decisions on best management practices.

Integration of taxonomic and ecological research is needed to facilitate better management of fungi. Closer coordination of research priorities between management agencies and research organisations would assist in this integration. Ideally, future fungal research would also integrate both traditional and molecular techniques to develop a clearer understanding of the complex nature of communities and ecosystems, particularly in soil and other important fungal substrates such as litter and CWD.

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