



Review on fire effects on ectomycorrhizal symbiosis, an unachieved work for a scalding topic



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ARTICLE INFO

Article history:

Received 31 October 2016

Accepted 20 February 2017

Keywords:

Ectomycorrhizal symbiosis

Wildfire

Fungal ecology

Disturbance

Prescribed burning

Forest management

ABSTRACT

Millions of hectares of ectomycorrhizal (ECM) forests provide most of the wood resource in the northern hemisphere. Among these forests, those that are fire-prone concentrate an astonishing diversity of mutualistic soil fungi that are pivotal for seedling establishment, tree growth and forest functioning and dynamics. Here, we review the effects of fire on ECM symbiosis in these forests using a systematic screening of the literature. We reveal that a low number of field studies (73) directly address fire effect on ECM symbiosis, in a restricted geographic area that partially represents the geography of ECM biodiversity stakes and fire risk. The analyzed literature consensually reports long-term shifts in the composition of ECM fungal communities after fire. Contrastingly, the effects of fire on fungal diversity and richness at the local scale continue to be debated among researchers, and need to be documented further using adequate experimental device to limit the effects of some identified methodological biases. Furthermore, our analysis emphasizes the urgent need to carefully consider the belowground effects of prescribed burning. This is an important conclusion because this widely implemented and efficient management tool to prevent wildfires may impact ECM soil communities in the same way as uncontrolled events. Our analysis finally highlights the need of refining the concept of post-fire ECM fungi, by taking advantage of promising tools, such as next-generation sequencing and quantitative PCR applied to mycelia and spores, to integrate the vegetative traits of fungi in integrative definitions.

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1. Introduction

Ectomycorrhizal (ECM) symbiosis occurs in only 3% of the plant species on the Earth; thousands of fungal species provide access to belowground resources for ECM autotroph organisms (Smith and Read, 2008). Otherwise, fire is the main terrestrial disturbance (Bond and Keeley, 2005) and has likely since hundreds of million years (Scott and Glasspool, 2006; Bowman et al., 2009). Despite the low number of plant species involved, fungal ECM associations transcend plant strategies with respect to their response to fire.

Fire is a global phenomenon that affects population dynamics, community structure and biodiversity, and has consequences for biogeochemical cycles, landscape properties and climate dynamics (Johnson, 1992; Whelan, 1995; Bond and Wilgen, 1996). Current ongoing global change linked to climate or land use should alter fire risk at the local-to-global scale, with a general increases of this risk (Moritz et al., 2012; Bedia et al., 2015), although some regions may experience a decrease due to complex passive or active land-use effects (Pausas and Fernández-Muñoz, 2012; Fréjaville and Curt, 2015) and to the spatial heterogeneity of climate dynamics (Girardin et al., 2009). Globally, this is likely to result in altered biogeochemical cycles (e.g. Abbott et al., 2016) and threats to biodiversity (e.g. MacKey et al., 2012; Moritz et al., 2014). Thus, more comprehensive and functional studies are needed to improve understanding of the biota–fire relationships and trajectories likely to be associated with current global scale changes. Among these studies, better knowledge of ECM symbiosis in relation to fire is crucial. Fire-induced ecological strategies of ECM plants range from the post-fire favored species (pyrophilous; e.g. Cistaceae, Myr-

taceae *pro parte*, Pinaceae *pro parte*) to the sensitive pyrofugals (e.g. *Fagus sylvatica* in Europe; *Pinus cembra* in Siberia and European mountains; *Thuja* spp. in North America, etc.). As a consequence, ECM symbioses represent an illuminating model for understanding the ability of fire to shape the distribution of soil biota, and for highlighting the biology and the ecology of fungi and symbiotic relationships regarding fire disturbance.

The ectomycorrhizal obligatory symbiosis is found in the belowground part of most terrestrial biomes, and currently dominates the boreal, temperate, and Mediterranean forests, in both sclerophyllous and deciduous vegetation (Smith and Read, 2008). The around 6000 species of known ECM fungi are mostly uncultivable organisms, dependent on their host for carbon and vitamins, while they provide water, nutrients and root protection for autotrophs (Smith and Read, 2008). Studies have shown that numerous fungal ECM species are sensitive – in terms of occurrence, distribution, abundance, colonization rate – to abiotic shifts, including nitrogen variation in soil through natural (Kranabetter et al., 2009) or anthropic processes (Lilleskov et al., 2004), and climatic conditions that affect both their vegetative and reproductive structures (Shahin et al., 2013; Boddy et al., 2014). These organisms also respond to biotic signals from their host under stressed conditions (Karst et al., 2014) or after disturbance (e.g. clear cutting; Jones et al., 2003), and from interactions between ECM fungal species (Courty et al., 2016).

We have arranged our review in four distinct sections that are introduced in the following paragraphs. During the last decades, four reviews (Fig. 1) successively addressed: (i) the consequences of fire on ECM fungal diversity in boreal forests, with a special

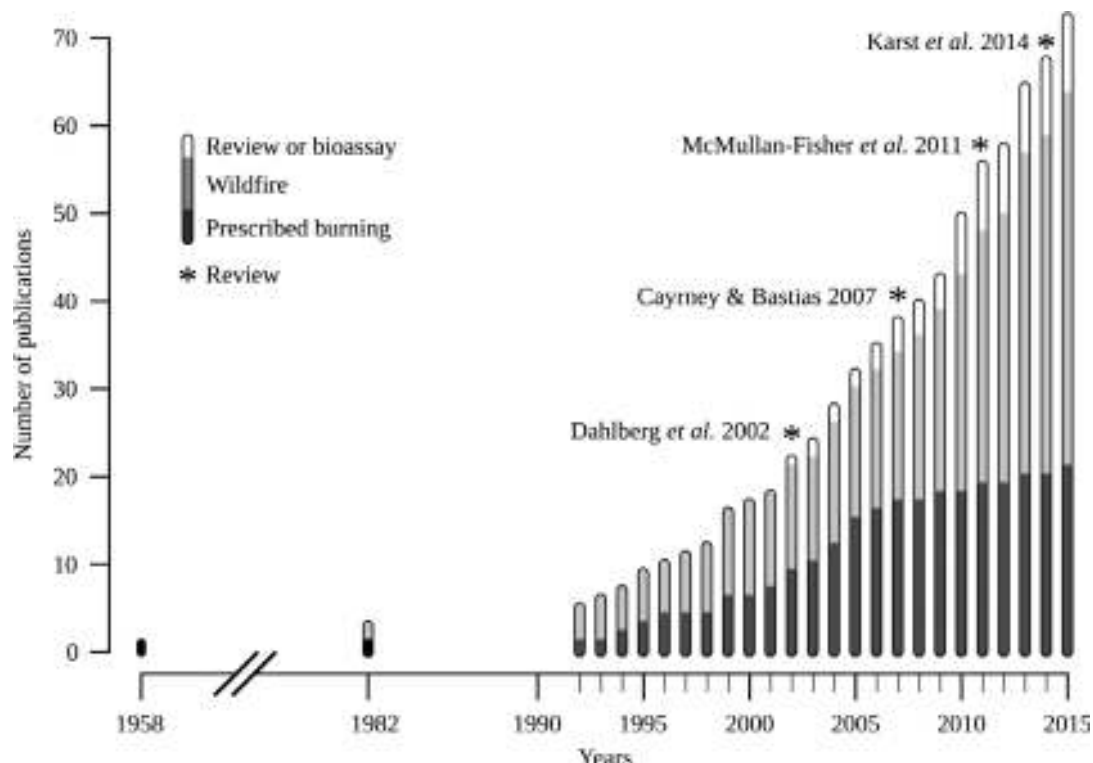


Fig. 1. Timeline of publications included in the review (total = 73) dealing with prescribed burning (dark grey), wildfire (grey) or bioassay/review (white). Stars indicate the four reviews dealing, at least in part, with the effect of fire on ectomycorrhizal interactions.

focus on Fennoscandian ecosystems (Dahlberg, 2002); (ii) the post-fire response of global soil fungal diversity (Cairney and Bastias, 2007) with a focus on Australian ecosystems (McMullan-Fisher et al., 2011); and (iii) the specific response of ECM fungal communities in *Pinus* dominated forests (Karst et al., 2014). Here we aim

at extending these analyses by delivering the first exhaustive global review addressing the response of ECM fungi to fire, i.e. without restrictions regarding the taxonomy or biogeography of hosts.

Whereas fire is of growing concern for stakeholders and an inexhaustible subject for researchers (Figs. S1 and S2), with its

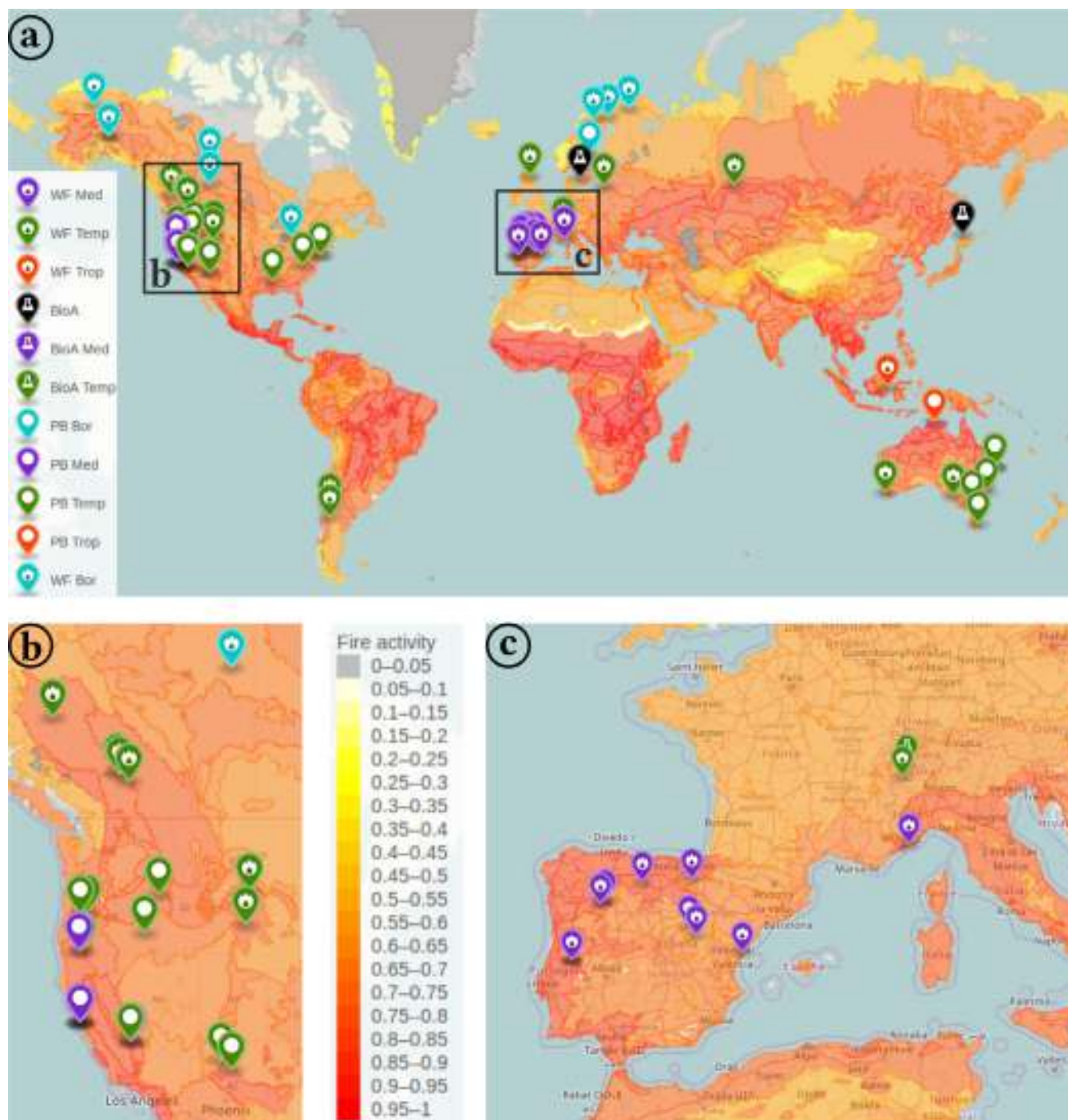


Fig. 2. Geographical distribution of the areas studied in the published data on the effect of fire on ectomycorrhizal interactions. The two lower panels depict a zoom of the western coast of North-America (b) and Western Europe (c). Marker colors correspond to biomes (blue: boreal; purple: Mediterranean; green: temperate; orange: tropical; black for bioassay-based studies). Marker icons correspond to the type of fire (fire icon for wildfire, Erlenmeyer flasks icon for bioassay and circles for prescribed burning). Terrestrial ecoregions follow the World Wildlife Fund classification (WWF; Olson et al., 2001; Fig. S4). Global fire activity information data by ecoregion are from Pausas and Ribeiro (2013) using FIRMS (Fire Information for Resource Management System, NASA from January 2001 to December 2009; see Fig. S3 for publication locations and ecoregions only) where the fire activity index was defined as the logarithm of the average number of fire incidences per region, divided by the region area. The interactive version of this map is available online (<https://github.com/adrietaudiere/ReviewFireEcmMap>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

continuing social relevance, we show in the following Section 2 of the present review that studies ecologically linking ECM and fire are geographically restricted (Figs. 2 and S3).

If fire directly affects ECM tree and shrub communities, there are consequent changes to the temporal dynamics of plant communities (e.g. Blarquez and Carcaillet, 2010), biogeochemical cycles and ecosystem processes (e.g. Wardle et al., 2003; Certini, 2005), and favorable conditions for secondary succession are created (Whelan, 1995). In soil, host signals (stress or death) and fire induced-abiotic shifts drive post-fire dynamics of the ECM fungal community. These widely described patterns, essentially *in situ* studied, are the theme of Section 3 of this review.

Recurrent fires impose selection pressures on organisms, creating plants with physiological adaptations (e.g. Sala et al., 2001) and a wide variety of life history traits, such as cone serotiny (e.g. Habrouk et al., 1999) and thick bark (e.g. Jackson et al., 1999; Keeley et al., 2011; Frejaville et al., 2013) or adapted regeneration strategies (e.g. Armstrong, 2011). By analogy, ECM fungi exhibit a wide spectrum of functional diversity, with underlying vegetative (Agerer, 2001 for a review), enzymatic (Courty et al., 2010) and reproductive attributes (e.g. production of resistant propagules such as sclerotia; Smith et al., 2015) that have been related to their ability to respond to fire at the species level. The synthesis of this body of knowledge is the central goal of Section 4 of our review.

Ongoing climate change will increase fire areas during the 21st century in most regions of the Earth (Pechony and Shindell, 2010; Flannigan et al., 2013; Moritz et al., 2014), despite regional-scale heterogeneity of fire responses to global warming (Girardin et al., 2009). As a consequence, managing fire risk, including using prescribed burning as a tool, has become timely in many contexts

and opens up new fields of study. It is, therefore, time to highlight potential future issues concerning ECM-fire ecology; these are covered in the last section of this review, namely “5 Future directions”.

2. Recent and spatially clustered research

We found a total of 182 publications that potentially examine the effect of fire on ECM symbioses. The bulk of publications (171) was found by searching the Web of Science™ (“All Databases”) using the term “fire AND ectomycorrh*” in the topic the 11 April 2016 (Complete list available in Table S1a). Additional publications were located using Google Scholar (two additional publications) and references found in the publications initially identified (9 publications). Of these 182 publications, only 73 bring some insights on the effect of fire on ECM symbiosis (publication list in Table S2; flowchart of the publication selection in Fig. 3). For each publication, we characterized the biome, the geographical coordinates, the origin of fires (wildfire vs prescribed burning), the fire modalities tested (e.g. fire frequency), the type of analysis (e.g. diversity or community analyses), the ECM host(s), the chemical and morphological analyses performed, and the identification methods used for taxonomic assignment; we then summarized the most relevant results in Tables 1 and 2 (see Table S3 for complete data and supplementary methods S1 for details).

Most of the research on the fire effect on ECM symbioses has been carried out since 2000, and half of these studies were published after 2005 (Fig. 1), indicating an apparent increase in this issue. However, the ratio between the number of publications dealing with fire impact on ECM symbiosis and the total number of publications about fire ($0.35 \pm 0.19\%$) or about ECM interactions

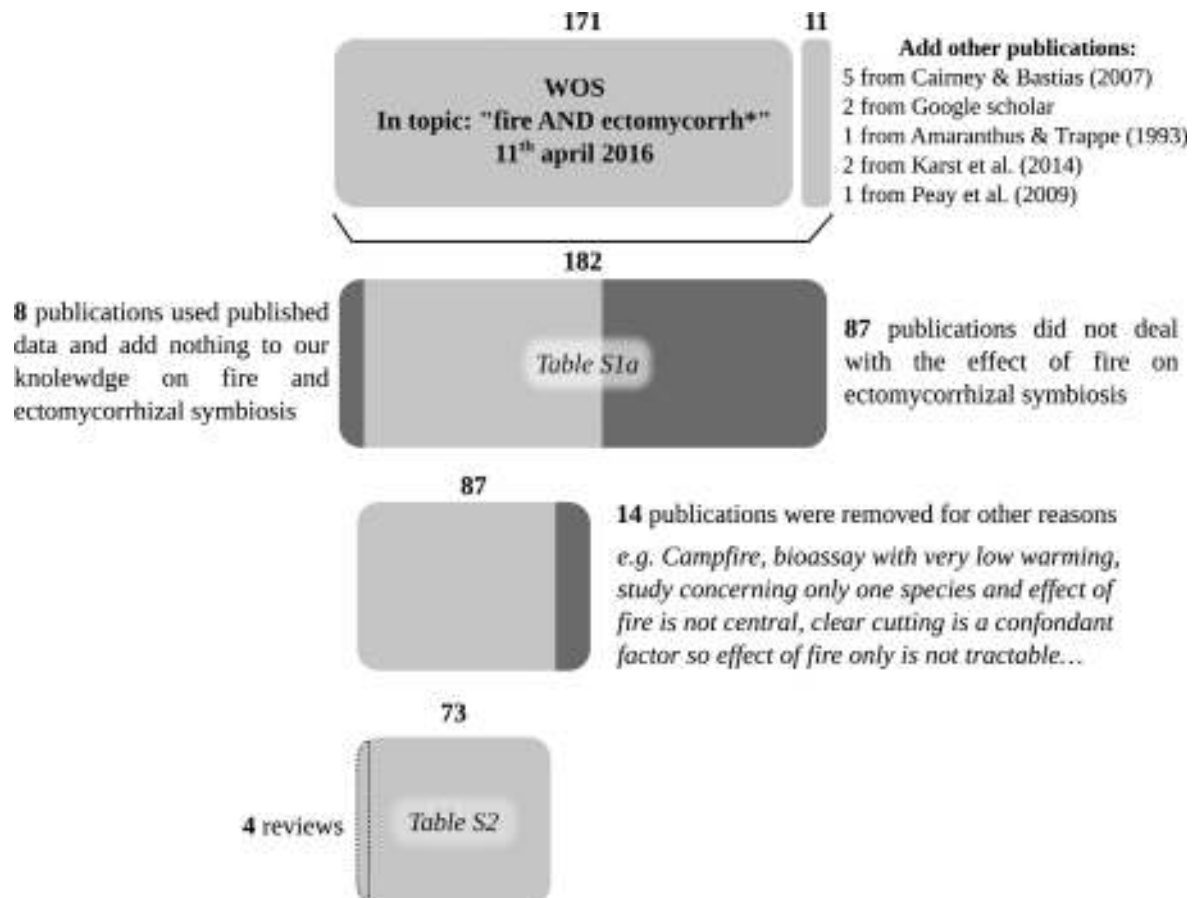


Fig. 3. Flowchart of selection of the 73 publications included in the review.

Table 1

Qualitative effect of fire on different components of biodiversity. Numbers correspond to the publication reporting the effect of interest (publication list in Table S2). Publications highlighted in bold used molecular techniques and an asterisk (*) indicates publications using Next-Generation Sequencing (NGS). +, −, = and ~ denote respectively significant positive effect, significant negative effect, no significant effect and significant change due to fire (i.e. change without clear and univocal direction). **Ab**: Abundances (e.g. Tip numbers or hyphal Length); **BioM**: Fungal Biomass; **Col**: Colonization of roots (e.g. root tip numbers, percentage of root with ECM); **Com**: Community composition and/or structure (e.g. DCA, CCA, PERMANOVA, NMS, anosim) using DNA analysis of root tips (**Com**) or sporocarp survey (**Sporoc. Com**); **Div**: Taxonomic Diversity (e.g. Simpson index); **FD**: Functional diversity (Enzymatic activities); **PD**: fungal Phylogenetic diversity; **Prod**: Production of sporocarps (e.g. dry weight); **S**: Species richness.

	Fungal component	+	−	=	~
Wildfire	Ab		70	33	12, 19* , 22, 46, 51, 65, 72
	BioM		1		
	Col	50, 51	22, 42, 57, 59, 70	67	
	Com			22, 33	6, 12, 14*, 19*, 24, 32, 51, 67, 71
	Div		6, 33, 46, 67	13, 22, 42	
	FD			32	19*
	Sporoc. Com				1, 58, 71, 72
	Prod		23, 46, 48	33, 58	18, 31
	S		1, 39, 46, 48, 65, 72	6, 13, 22, 33, 42, 58	14*
Prescribed burning	Ab		17, 21, 49		10
	BioM		25, 27, 61, 63	4	
	Col		9, 73	38	
	Com			62	3, 7
	Div		21, 27		
	PD	4			
	Prod		49	52	
	S		17, 21, 27, 49, 60, 61	3	

Table 2

Qualitative effect of severity, frequency and times since fire on different components of biodiversity (same legend as for Table 1).

	Fungal component	+	−	=	~
Severity	Ab		21	70	
	BioM		1		
	Col		40, 73	70	
	Com			28, 35	40
	Div		6, 21	28, 35, 56	
	S		1, 21	28, 35, 56	
Frequency	Ab		68		
	Com				3, 7, 8*, 13, 15
	Div		15, 68		
	S		8*, 15, 68		
Chronosequence	Ab	29*, 64*			69
	BioM			27	
	Col	22		55, 71	66
	Com				26, 29*, 37, 41, 57, 69, 71
	Div	41	27		26, 69
	S	37, 41, 71		27, 29*	26, 69

(1.09 ± 0.53%) was constant from 1991 to 2015 (Fig. S2). Thus, even if the publication numbers on the fire effect on ECM symbiosis increase apparently, the relative importance of the subject regarding ECM and fire literature is stable.

Studies were mostly located in temperate (35 pub.) and Mediterranean (20) ecosystems, with some in boreal (10) and few (2) in tropical (Figs. 2 and S3). More than one third (26) of the publications report on studies located in the USA, and only 14 are located in the southern hemisphere, including 10 in Australia. Three intensively studied areas, namely the west coast of the USA (11), southwestern Europe (12) and, to a lesser extent, southeastern Australia (5), accounted all together for 40% of all the publications excluding the four reviews (Fig. 2). This geographic distribution of field studies reflects more the location of ECM research groups around the world than the geography of ECM forests. Thus, there are extensive publication-free areas (e.g. southern and eastern parts of the Mediterranean basin, tropical Americas, most of Asia), and there is a discrepancy between the geography of fires and that of the research on the effect of fire on ECM forests (Fig. 2). Only two publications (Brundrett et al., 1996; Akema et al., 2009) reported studies located in tropical forests, and only one (Akema et al., 2009) focused on the Diptero-

carpaceae, despite the great ecological (Peay et al., 2015) and economic importance (Kettle et al., 2012) of this ECM plant family.

In addition to geographical clustering, the majority of research dealing with the fire impact on ECM symbiosis focused on *Pinus*-dominated ecosystems (Fig. 4, 44 pub. including 5 bioassay pub.; 60% of total pub. number) in the contexts of both prescribed burning (27 pub.) and wildfires (12 pub.), and to a lesser extent on *Eucalyptus* spp. (10 pub. of which 7 covered prescribed burning and the remaining three, wildfire; 15% of total pub. number). Regarding ECM shrubs, five studies explored the response of ECM communities associated with species in the Cistaceae (e.g. Martin-Pinto et al., 2006; Hernandez-Rodriguez et al., 2013) in the Mediterranean.

When cross-referencing fire risk and research locations, our analysis reveals concentrations of documented case studies in three main regions of the world, with most attention paid to two tree genera. Our study underlines the absence of research in the eastern Mediterranean basin, in Africa (e.g. about the *Cedrus atlantica* ECM symbiosis in northeastern Africa), and in Central America (e.g. forests of endemic oaks and firs). To a lesser extent, this overview reveals a lack of knowledge in tropical biodiversity hotspots where ECM tree species are also present (e.g. white-sand forest in South America [Roy et al., 2016]; Dipterocarpaceae forests in

Indonesia [Akema et al., 2009]; members of Caesalpinoideae such as *Gilbertiodendron* spp. in Africa [Bâ et al., 2012]). The *Gilbertiodendron* spp. may even be favored by human-induced fire in Africa (Tovar et al., 2014), the history of which remains largely unknown on this continent, but which would have started during the African Iron Age, sometime between 4000 and 2000 yrs ago according to model-based simulations (Archibald et al., 2012) and charcoal-based fire reconstruction (Marlon et al., 2013). It would certainly have had strong ecological effects on ecosystems (Bayon et al., 2012). Tovar et al. (2014) do shed light on the ecology of ECM tropical trees in these poorly described ecosystems (Bâ et al., 2012), which are severely impacted by human activities and fire regime (e.g. *Coccoloba uvifera* in Antilles; Sène et al., 2015).

3. Fire alters hyper-diverse ECM fungal assemblages

3.1. Weak statistical support for the effect of fire on ECM fungal communities

The way researchers analyze the response of ECM fungal communities to fire varies widely between studies (Fig. 4, Tables 1

and 2). In total, five types of descriptors were used to study the response of ECM fungi to fire, namely: (1) the abundance, measured as the number of mycorrhizal tips or the hyphal length; (2) the biomass, estimated as either the amount of mycelium or the dry weight of fruiting bodies; (3) the root colonization, based on the number of root tips or percentages of root with ECM tips; (4) the taxonomic (e.g. Simpson's index), phylogenetic or functional diversity (catabolic enzyme profiling); and (5) the community composition or structure. The gathered body of work includes a minority of studies (26 out of 69, i.e. 38%) based on the direct sequencing of biological material (Fig. 4d), while three quarters primarily take a morphological approach to diversity, examining either ECM fruiting bodies or root tips (morphotyping).

Interestingly, 25% of the [community parameter \times publications] combinations (numbers in Tables 1 and 2) failed to find statistical support for the fire effect on ECM fungal community descriptors. There are many potential causes for this lack of significance, including case studies with no clear evidence of fire on the measured parameter (real biological patterns in a robust dataset; e.g. Robinson et al., 2008); but also studies with methodological limitations (e.g. only morphotype identification; de Roman and de

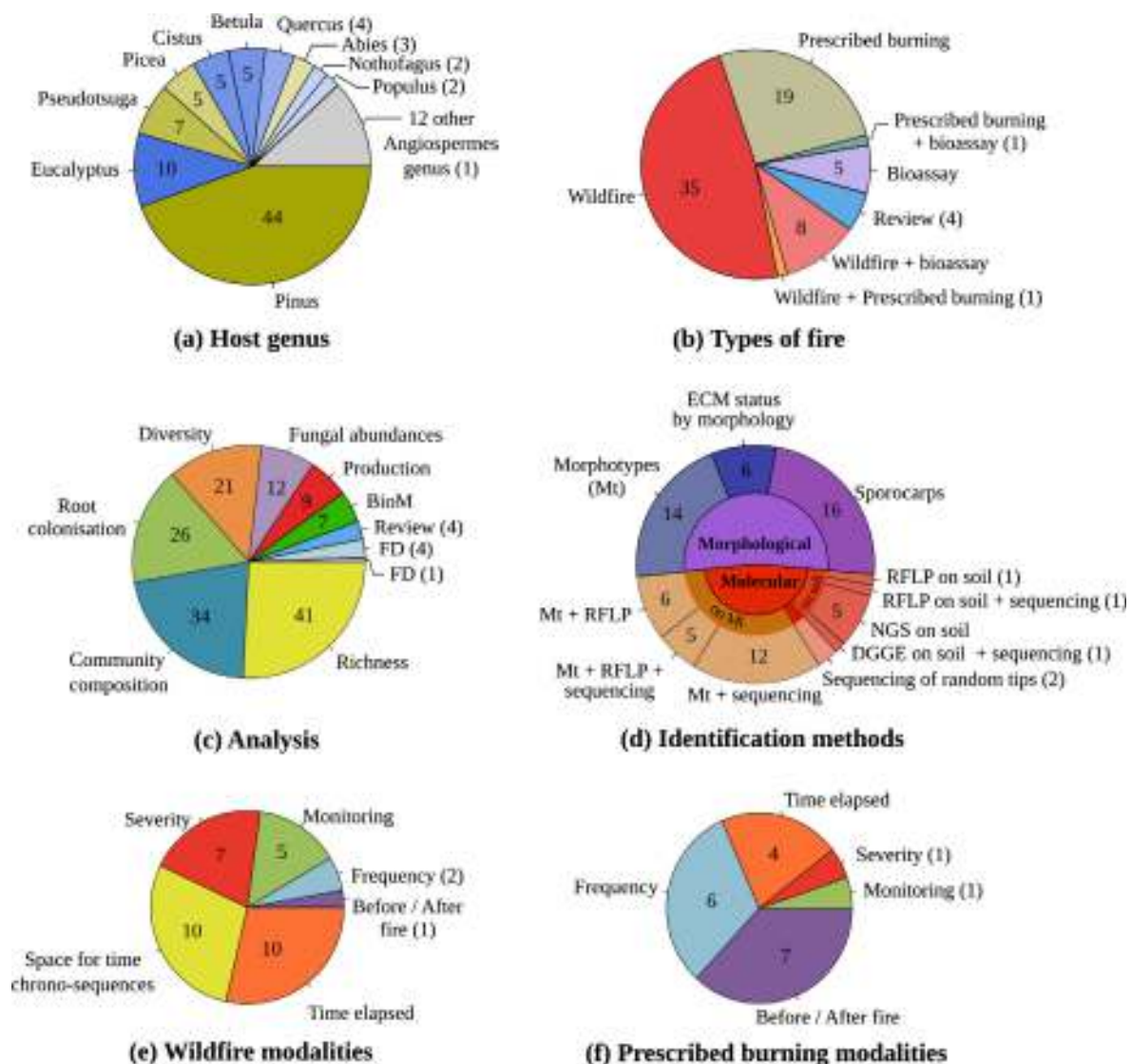


Fig. 4. Distribution of plant host genus (a), types of fire (b), types of analysis (c), identification methods for fungal taxonomy assignment (d) and fire modalities (e–f) in the literature. See [supplementary methods](#) for details. **FD:** Functional Diversity; **PD:** Phylogenetic Diversity; **BioM:** Biomass; **Production:** Sporocarp production; **Mt:** Morphotype; **RFLP:** Restriction Fragment Length Polymorphism; **NGS:** Next-Generation Sequencing; **DGGE:** denaturing gradient gel electrophoresis.

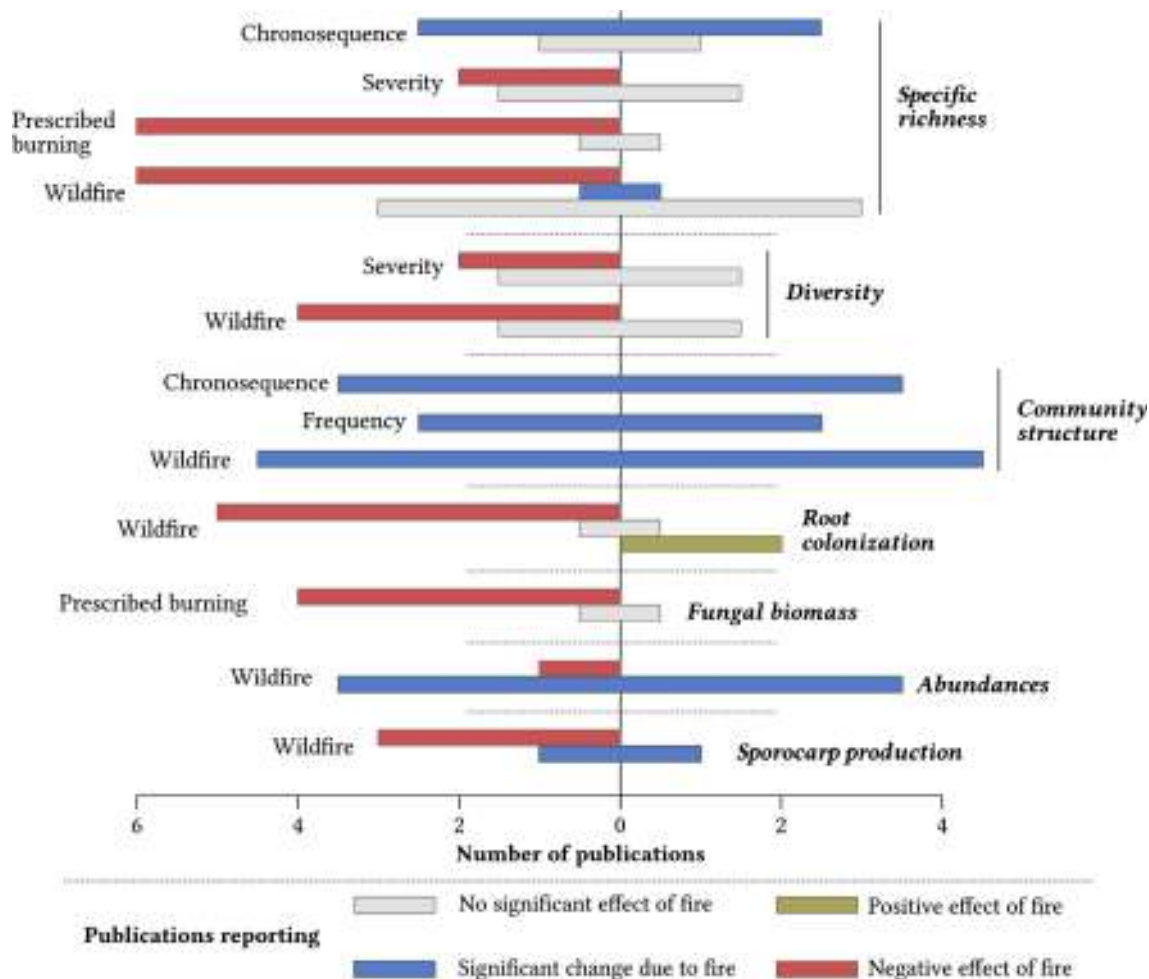


Fig. 5. Number of published results (based on Tables 1 and 2) treating the effect of fire on ECM fungi. Only cases documented in more than 4 publications are shown.

Miguel, 2005) or low statistical power due to the limited number of samples (e.g. $n = 9$ for three modalities in Kennedy et al., 2015) or species (Longo et al., 2011). In the last study, the low richness (i.e. species number; in total there were 23 morphotypes, 11 morphotypes per sample on average) limited the chances of detecting a significant effect of fire on richness, but the high number of ECM root tips analyzed (22 449) strongly increased the chance of spotting a significant effect on species abundances. Accordingly, they found a fire effect on diversity, i.e. taking into account species abundances, but no effect on richness. Finally, richness is an intrinsically 'degraded' information of community composition: it is possible to calculate richness from community composition, but the same richness can hide very different community compositions (Wilsey et al., 2005). Therefore, detecting a shift in richness requires large numbers of samples and/or fungal assemblages that are highly sensitive to fire. One possible way to solve this issue is to use abundance-based diversity metrics such as Chao (Chao et al., 2004) or the Hill index (Hill, 1973), which have not yet been used to assess the fire effect on ECM fungal communities. Beyond statistical significance (p -value), future studies need to assess the effect size of a fire on ECM interactions (e.g. percentage of variation in root colonization or fungal biomass, proportion of variance explained in community variation using PERMANOVA; Anderson, 2001) to understand the magnitude of the fire effect in relation to other driving factors (e.g. dispersion, limiting similarity, habitat filtering) that shape ECM symbioses dynamics.

3.2. A lack of consensus about the effect on fungal richness and diversity

In all, 20 publications out of 69 (29%) examined the effect of fire on fungal richness, including studies of 13 wildfires and seven prescribed burnings (Table 1, Fig. 5). For this widely documented parameter of ECM fungal communities, no consensus emerged about the effect of wildfire, with an equal number (6 pub. each) recording negative and neutral effects but, interestingly, no positive response (Table 1, Fig. 5; one publication report variation with no clear direction). Moreover, the aboveground parts (sporocarps) of ECM fungal communities exhibit negative responses to fire in terms of richness (6 out of 8 studies), while belowground mycelia mostly (5 out of 7) showed no fire effect. In conclusion, wildfires may primarily cause a decline in reproductive emergence of some ECM fungal species, with a weaker vegetative dimension of this impact. From nine publications documenting change in ECM fungal diversity due to fire, seven were carried out in wildfire contexts. In terms of richness, wildfires negatively affect ECM fungal diversity in half of the studies (4 pub.), while there was no detectable effect in others (3, Fig. 5).

In contrast, studies pertaining to prescribed burnings tend to reveal a more consistent (6 out of 7 pub.) negative impact on ECM fungal community richness. The reported impacts appear consistently belowground (using either soil sequencing [2 pub.] or root tip morphotyping [4 pub.]). This is an unexpected conclusion concerning a widely used management tool, particularly in the

Mediterranean. This result suggests that the distinction between the effects of prescribed burning and wildfire should be examined with more scrutiny, for instance with a clear understanding of implementation regarding the prescribed environmental conditions window. Furthermore, belowground views may be complemented by (i) studies extending over a longer period and (ii) aboveground investigations questioning the effect of the extensively used practice of burning on ECM fungal diversity, including the reproduction of edible post-fire mushrooms. Providing such a comprehensive overview may allow stakeholders to use this management tool with better knowledge of its impacts on ECM symbiosis, this mostly invisible part of forest biodiversity and functioning (Richard et al., 2005).

3.3. Fires drive marked shifts in ECM fungal community composition

While richness is a poorly informative proxy of fire impact on ECM fungal communities, this review underlines the fact that fire does drive marked changes in local (i.e. stand-level) fungal assemblages. Indeed, the most striking feature of this review is the strong fire effect on the composition of ECM fungal communities both on the reproductive (fruiting bodies) and vegetative (belowground root tips) *apparatus* of ECM fungi. In all, most publications (21 out of 26) reported a significant compositional response of ECM fungal communities to fire at the local scale (Tables 1 and 2, Fig. 5). As expected based on the physics of wildfires, all publications documenting soil depth, frequency and/or severity show a greater fire impact on soil surface horizons compared to deeper horizons (Table S4), along with cumulative effects with frequency and severity of the event (Table 2).

Our searches identified studies conducted in a wide variety of fire contexts (Fig. 4e and f): wildfire (44 pub.), prescribed burning (21) and bioassay (14 pub. including 5 limited to *ex-situ* bioassays). With respect to wildfire, the most frequently used sampling designs are space for time substitution (10 “chronosequences”), and one-shot post-fire approaches (10 “time-elapsé”). For prescribed burning, the majority of results are based on either repeated sampling (7 “before/after”) or comparisons of sites which undergone different frequency of fire (6 “frequency” pub.).

The few studies using controlled experimental designs (Fig. 4b), with *ex-situ* set ups (5 “bioassay”) or both *in-* and *ex-situ* (1 “prescribed burning + bioassay” and 5 “wildfire + bioassay”) allow the mechanisms of the observed changes in ECM fungal communities to be deciphered with respect to the complexity of fire disturbance (e.g. heat, chemical changes, physical and/or microclimatic shifts, etc.). For instance, the experimental addition of ash was used in bioassays, with contrasted results regarding the measured “community parameter” (4 pub., Table S4). While Mahmood et al. (2003) found a positive effect of ash on fungal biomass, Grogan et al. (2000) found no effect on richness, diversity or on community composition, and Peay et al. (2009) found a significant effect on community composition when “ashes” were added in combination with a heat treatment. These contrasting outcomes also reveal marked differences in experimental designs. For instance from removing “ash” from wildfire stands (Grogan et al., 2000) to introducing “ash” from a prescribed burning area into experimental pots (Peay et al., 2009). Unfortunately, in these ash-based studies, the term “ash” does not distinguish pure ash (mineral particles) from small charcoal fragments (charred organic matter), which have strong ecosystem effects (Zackrisson et al., 1996) because of polyphenol adsorption and affecting the nitrogen cycle through microbial activity (Hättenschwiler and Vitousek, 2000; DeLuca et al., 2006). Furthermore, ash and the charcoal-controlled nitrogen cycle have a confounding effect on the soil by modifying its pH in relation to time since the last fire (Keeley and Fotheringham, 1998), and thus affecting fungal ecology.

3.4. Fire modifies root colonization

Numerous studies illustrated decreasing root colonization by ECM fungi (i.e. the proportion of short roots associated with ECM fungi) after wildfire and prescribed burning (Table 1). Unsurprisingly, increasing fire severity augments this negative effect on the vegetative component of ECM symbiosis (e.g. Launonen et al., 1999). However, Palfner et al. (2008) found that 2 year-old *Nothofagus alpina* seedlings that established after fire tended to harbor more root tips in the deepest soil horizons and higher root biomass than seedlings of the same age established in undisturbed soils. Post-fire *Nothofagus alpina* still formed ectomycorrhizas below 25 cm depth whereas fine roots of control seedlings did not reach that depth. More studies are needed to confirm whether there is increasing ECM colonization at depth, induced as a positive consequence of fire affecting water distribution down the soil profile (Palfner et al., 2008), possibly caused by combustion of hydrophobic soil organic matter or volatile organic compounds.

3.5. Fire shapes ECM fungal biota over a long period

Sixteen studies examined the temporal trends exhibited by ECM fungal communities after fire, 10 using wildfire chronosequences and six using monitoring mostly following wildfire (Fig. S5). Looking aboveground fructifications, Mediavilla et al. (2014) reveal that ECM sporocarps production may recover pre-fire value five years after the fire in *Pinus nigra* forest. Furthermore, Kipfer et al. (2011) found that belowground ECM fungal richness decreases shortly after fire and stabilizes 15–18 years after this event. This is probably due to the fact that complete soil recolonization by fungi takes several years, i.e. the “resilience time”. Treseder et al. (2004) found that the root ECM colonization takes up to 15 years to return to pre-fire levels. Moreover, Holden et al. (2013) provided evidence that fungal hyphae need at least 24 years to recover their pre-fire length. Diversity indices show the same trends more than 10 years after fire both in boreal (15–20 years; LeDuc et al., 2013) and in temperate ecosystems (>26 years; Twieg et al., 2007). An interesting perspective for further research is exploring the mechanisms that delay the recovery of ECM fungal communities after fire across a wide range of fire regime and environmental conditions.

Because the resilience time can be very long, empirical or experimental studies that measure the community composition within a time period <20 years might conclude that there is a lack of resilience in ECM fungal communities exposed to a fire event (Robinson et al., 2008; Twieg et al., 2007; Visser, 1995; Kipfer et al., 2011). For instance, community composition was still different from that of unburned sites five years after burning of *Eucalyptus diversicolor* forests (Robinson et al., 2008) and 18 years after burning in *Pinus sylvestris* stands (Kipfer et al., 2011). Finally, two studies found restoration of community composition 41 years (Visser, 1995) and 65 years (Twieg et al., 2007) after wildfire. This potential lack of resilience might also question the resistance of ECM communities to fire. However, resistance is never uncoupled from resilience in the corresponding field studies (9 references; Table 2) which explored the effect of fire severity on ECM communities.

This rather long resilience delay of ECM fungal communities may be the result of (i) the low dispersion ability of some ECM fungal species (Peay and Bruns, 2014), (ii) the prolonged effect of fire on soil physical and chemical characteristics (Certini, 2005) or (iii) the prolonged effect of fire on other partners of ECM fungal organisms including microbiota dynamics (e.g. the mycorrhiza helper bacteria; Frey-Klett et al., 2007) and host physiology (Franklin et al., 2014). These three hypotheses could be tested by measuring the temporal patterns of microbiota, plant physiology, and soil

characteristics across a distance gradient from unburned areas in a single ecological system.

4. ECM fungal species respond differently to fire according to their ecological strategies

Post-disturbance changes in fungal community composition and structure are driven by the ecological strategies of species (for example “ruderal” species including pyrophilous; Danielson, 1984; Warcup, 1990; Martin-Pinto et al., 2006; Buscardo et al., 2011). By analogy with plants, some fungal species are considered to be fire-dependent, i.e. dependent upon fire and/or the immediate post-fire conditions to complete their life cycle, and secure their long-term survival through sexual reproduction. For instance, in Swedish boreal forests, 40 macrofungal species, mostly saprotrophs, are considered fire-dependent (Dahlberg, 2002). Inspired by previous works on fungal succession (Dighton et al., 1986; Last et al., 1987), Visser (1995) proposed classifying ECM fungal fruiting behavior after fire into three groups: early-stage (e.g. *Coltricia perennis* and *Thelephora* spp.), multi-stage (e.g. *Suillus brevipes* and *Cenococcum geophilum*) and late-stage fungi (e.g. *Cortinarius* spp., *Russula* spp. and *Suillus tomentosus*). The following section summarizes the response diversities of ECM fungal communities to fire, in terms of spore bank assemblages.

4.1. Contrasting strategies based on spore bank composition

After disturbance, ECM fungi colonize the roots of surviving trees or establishing seedlings from sexual spores, sclerotia (asexual resistant propagules), or remnant mycelia still established on surviving trees (e.g. after clear cutting; Jones et al., 2003). The influence of fire on spore germination still remains poorly studied (but see Glassman et al., 2016). With respect to sclerotia, only one study (Torres and Honrubia, 1997) has documented a positive wildfire effect on the formation of these vegetative propagules. On the other hand, the importance of the establishment of new individual fungi from spore germination after fire has been well illustrated in the specific case of *Suillus pungens* population genetics (Bruns et al., 2002a). This case, and the case of the hypogeous Basidiomycete *Rhizopogon*, both illustrate (i) the spore longevity of these early-stage fungi, as dormant propagules in soils, (ii) the capacity of spores to stay receptive to tree roots and form ECM on newly established seedlings and (iii) that the role of the spore bank may be central during the temporal sequence of post-fire ECM colonization (Glassman et al., 2016).

4.2. Contrasting vegetative responses among species

In the context of fire, contrasting responses among co-occurring species forming ECM fungal communities have been widely documented. Among the positive responses, it has been observed that the Basidiomycetes *Thelephora terrestris* and *Suillus brevipes* increased in abundance during a post-fire succession in the *Pinus banksiana* Canadian boreal forest (LeDuc et al., 2013), as did *Descolea antarctica* on seedling roots of *Nothofagus alpina* in Patagonia (Palfner et al., 2008). From a functional perspective, Clemmensen et al. (2015) recently illustrated the dominance of cord-forming ECM fungi (aggregations of hyphae, e.g. in *Cortinarius* spp. and *Suillus* spp.; Boddy, 1993) in early-successional stages after fire, and the role of these fungi in the mobilization of nitrogen and carbon from sequestered forms in boreal soils. Finally, bioassays using seedlings grown in heated soil indicate that spores of some species are heat resistant (Peay et al., 2009) and belong to species favored by fire in terms of relative abundances (e.g. *Rhizopogon* spp.; Baar et al., 1999; Izzo et al., 2006). At the other extreme of ecological

strategies, late-stage ECM fungal species show negative responses to fire and are therefore called fire-sensitive species. For instance, LeDuc et al. (2013) identified fire-sensitive species in the *Cortinarius* and *Russula* genera, recovering 19 years after the fire. These few fire-sensitive species, all macrofungi belonging to dominant genera aboveground in the studied systems, require further research involving more robust sampling designs (larger sample sizes, molecular techniques, etc.) to examine the ECM fungal diversity that is less responsive to fire.

4.3. The functional enigma of massive post-fire fruiting

Post-fire fungi are classically defined as species that massively fruit within the first years after fire. Documented cases mostly concern saprobic macromycetes such as morels (*Morchella* spp.), and species within the genera *Anthracoobia*, *Gyromitra*, *Pyronema*, *Sphaerosporella*, and *Tricharina* (Miller et al., 1998; Richard et al., 2015; Larson et al., 2016) whose ephemeral fruitbodies may cover forest soil immediately after fires. The trophic status of these taxa remain unclear despite experimental evidence of a potential symbiotic life-style for some of them, in particular for few *Morchella* species (e.g. Fujimura et al., 2005). Contrastingly, only very few post-fire ECM fungi fulfill this requirements, e.g. the basidiomycete *Hebeloma antracophilum*, and we still know little about the effect of fire on their biological cycle in soil. Other lineages of post-fire Ascomycetes are likely to be putatively mycorrhizal, such as the Pezizale fungus *Geopyxis carbonaria*. This species massively fruits, only once, a few months after fire (Vrålstad et al., 1998), and remains vegetatively cryptic in the periods between fires. The ECM symbiosis offers an ideal model for conceptualizing the notion of post-fire fungi using both reproductive (fruitbody abundance) and vegetative (soil mycelia and ECM root tip dynamics) responses of ECM fungal species.

5. Future directions

5.1. Mixed methods and knowledge

The development of next generation sequencing (NGS) techniques opens up the possibility of new research perspectives on fungal biology and ecology (e.g. Buée et al., 2009; Öpik et al., 2009). This technology, as yet, is not an efficient way to assess precisely the abundance of molecular taxa within ECM fungal communities (Nguyen et al., 2015). However, its ability to access to the vegetative components of assemblages, combined with its efficiency in detecting rare species, is a strength when examining the effect of fire on the composition of hyper-diverse ECM fungal communities (Glassman et al., 2016), but also a promising tool to integrate the vegetative response of species to fire in an integrative and functional definition of post fire ECM fungi.

Applying NGS methods to vegetative or sexual propagules of ECM fungi is a promising way to understand the mechanisms underlying recolonization by ECM fungi after fire, and to test the importance of spore inflow (vs recolonization via remnant soil mycelia) in determining the composition of early stage fungal communities. In particular, this tool may provide valuable information about the ecology of ECM fungal communities, by estimating the importance of wind- vs animal-dispersal processes (Claridge, 1992) by using molecular analysis to compare spore traps (e.g. Peay and Bruns, 2014), feces (endozoochory; Valentini et al., 2009) and the external surfaces of potential dispersers (ectozoochory, Lilleskov and Bruns, 2005). In addition, the unprecedented sensitivity of NGS methods is a technological opportunity to track post-fire ECM fungal species in unburned ecosystems, and should

solve the mystery of their cryptic biology over the years, often decades, between fires.

5.2. Changes in ECM fungal strategies in response to fire

One fundamental issue that remains for community ecologists is to understand the mechanisms involved in and primarily driving the composition shift of ECM fungal communities affected by fire. Two non-exclusive forces may govern the temporal dynamics of ECM fungal diversity in soil after disturbance.

First, fire induces marked habitat shifts by directly modifying chemical and physical characteristics of the soil organic layer (Certini, 2005) that primarily select for fungal species with post-fire adapted niche requirements. A functional trait-based approach (for instance examining the nutritional status of post-fire species; Courty et al., 2005; Artz et al., 2009) applied to a compatible database (e.g. DEEMY [Agerer and Rambold, 2004] and UNITE [Kõljalg et al., 2013]) could help to evaluate the influence of environmental filtering on the functional diversity of ECM fungal assemblages after fire. Phylogenetic conservatism of traits (Mouquet et al., 2012) could also be tested to provide insights into the changes of functions associated with post-fire ECM fungi.

Second, fire induces plant community shifts and then indirectly affects the taxonomic composition of post-fire ECM fungal assemblages via obligate interactions with a restricted range of hosts (specificities; Bruns et al., 2002b). However, early- and late-successional plant species differ in their ability to accumulate ECM fungal diversity (e.g. Taudière et al., 2015). Thus, one may hypothesize that narrow host-range fungal species are primarily specific to ecological contexts that favor their host with respect to the abiotic niche. Diachronic analyses deciphering the temporal patterns of ECM fungal communities in relation to their specificity to post-fire hosts are needed to provide insights into the role of specificity in the response of ecosystems to fire.

5.3. Forest management and conservation

One of the most striking results of the present review is the consensus that there is a negative effect of prescribed burning on aboveground ECM fungal richness (i.e. reproductive structures), with no consequences on the belowground (mostly vegetative) communities. However, the range of studies is limited, and further work is needed. The literature reports negative fire impact on ECM fungal fruiting, thus contrasting with the massive and positive sexual response of many post-fire saprotrophs (e.g. *Morchella* spp.; Dahlberg, 2002; Richard et al., 2015). Hence, if only the aboveground component of ECM fungal communities was taken into account, fire would be considered a negative process for ECM fungal communities potentially altering the resistance of the system. Nonetheless, a more central role of fire emerges when combining both quantitative and qualitative dimensions of these communities. The documented shift in ECM fungal composition, both below- and aboveground, highlights the need to upscale studies of the impact of fire on ECM fungal community diversity to the landscape scale.

From a functional perspective, the path is now clear: there is a need to investigate the indirect effects of fire (from soft to severe prescribed burnings to wildfires) from sustainable forest management perspectives respectful of ecosystem services provided by ECMs. In particular, further research could address whether fire related-composition shifts in ECM fungal communities alter forest productivity, for instance seedling nutrient uptake and growth, or timber yield. Overall, there is a need to build bridges between ecophysiologicals, plant ecologists and fungal ecologists to develop integrated research on ECM for the benefit of stakeholders and forest managers.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.02.043>.

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